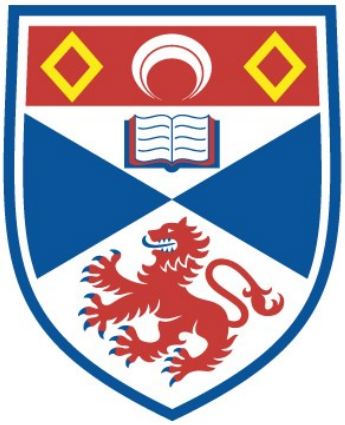
THE DORSAL ORGAN AND OTHER CUTICULAR STRUCTURES IN LARVAL AND ADULT CRUSTACEA : AN ULTRASTRUCTURAL STUDY

Yolanda Barrientos Chacon

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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The Dorsal Organ and Other Cuticular Structures in Larval and Adult Crustacea: An Ultrastructural Study

by

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being a thesis submitted to the University of St. Andrews in canditature for the degree of Doctor of Philosophy

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Declaration.

I declare that the work reported in this thesis is my own and has not been submitted for any other degree. Due acknowledgement has been given for any assistance received.

Supervisors Certificate

I certify that Yolanda Barrientos Chacon has fulfilled the conditions laid down under Ordinance General Number 12 and Resolution of the University Court 1967, Number 1, of the University of St Andrews and is accordingly qualified to submit this thesis for the degree of Doctor of Philosophy.

Curriculum vitae

I graduated from Instituto Universitario Pedagogico de Caracas (Venezuela) in 1974 with a degree in Biology and General Science. I obtained an M.Sc. in Biology in 1980 from the University of Ottawa, Ottawa, Ontario, Canada. The work presented in this thesis was carried out between January, 1982 and December, 1984.

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Subclass	Malacostraca	
Superorder	Eucarida	
Order	Decapoda	
Suborder	Reptantia	
Section	Astacura	
Superfamily	Nephropoidea	
Family	Nephropoidae	
	Homarus gammarus	
	Nephrops norvegicus	
Section	Anomura	
Superfamily	Galatheoidea	
Family	Galatheidae	Porcellanidae
	Galathea strigosa	*Porcellana longicornis*
		Porcellana platicheles
Section	Brachyura	
Subsection	Oxystomata	
Family	Dorippidae	Leucosiidae
	Dorippe lanata	*Ebalia tuberosa*
Subsection	Brachygmata	
Infrasubsection	Oxyrhyncha	
Family	Maiidae	
	Pisinae	
	Hyas cornutatus	
Family	Portunidae	
	Carcinus maenas	
	Portunus puber	
Subsection	Atelecyclidae	
Family	Cancrinae	
	Cancer pagurus	

Subclass	Malacostraca	
Superorder	Peracarida	
Order	Cumacea	
Family	Diastylidae	
	Diastylis cornuta	
Order	Isopoda	
Family	Cirolanidae	Idotheidae
	Eurydice pulchra	*Idothea pelagica*
Order	Amphipoda	
Family	Ampeliscidae	
	Ampelisca typica	
Family	Pontoporeiidae	
	Haustorius spp	
Family	Hyperiidae	
	Hyperia galba	

Subclass	Malacostraca
Order	Isopoda
Infraorder	Bopyrina
Family	Bopyridae
	Pseudione hyndmani

ABSTRACT

SEM observations on the integument of larvae and adult Crustacea Malacostraca indicated differences in setal armature, and in types and frequency of occurrences, which seem to be related with development and sensilla body position.

The Amphipoda and Isopoda species studied share a common type of articulated conical spine on the pereiopod segments. In each species, the conical spine has a modified apex which contains sub-apical setules whose tips are provided with ventrally positioned pores or bifid ends. The epimeral and lateral body plates are covered by short articulated pegs with modified hair bases: asymmetrical lip-like extensions, knobs or vesicle-like projections around the hair rim. An unusual type of aesthetasc sensillum is present on the male Cumacea antennal flagellum. A sub-terminal and ventrally positioned pore is present in these aesthetascs whose tips are divided. Companion and guard hair sensilla are absent. A number of cuticular out/ingrown structures are described in both Decapoda and non-Decapoda Crustacea which cannot be related with any previous classification schemes.

Crustacea Decapoda larvae (Macrura, Anomura, and Brachyura) have a common trichoid sensillum, whose numbers and distributional patterns are specific for each group. There is a tendency for the trichoid sensilla to be arranged in clusters rather than describing ramdon patterns. Setal organization changes according to developmental instars: larva and post-larval forms have small numbers and types of sensilla, or in some cases they possess the incipient forms of receptors such as the funnel-canal organs known to be present in the pereiopods of adult animals. Juvenile stages exhibit a more complex and sophisticated setal arrangement.

Brachyura stage IX-X embryos and hatchling larvae are equipped with well anatomically organized (TEM) sensory hairs. According to their ultrastructural features potential mechano-, and chemoreceptive hairs can be differentiated in the antennules and maxillipeds.

In the dorsal median anterior region of the head, Decapoda larvae possess a discrete organ: glandular-sensory complex. Its external topography reveals the presence of one or two central pores (Brachyura, Anomura) or a poreless central area (Macrura) surrounded by four equidistant plate-pits which contain a central pimple or cone. The Macrura plate-pits lack the central cone but develop a row of diminutive pegs. The

dorsal organ ultrastructure reveals several components: a gland cell, a ductule cell, two supporting cells and eight sensory cells. The gland cell components allow it to be categorized it as an excretory class 3 gland cell; and the the presence of two biciliary sensory cells per plate pit, without scolopale matrix and thick dendritic sheath may identify them as potential chemoreceptors or as bimodal sensitive units. SEM observations indicated that the organ is not present in the integument when juvenile stages are reached. The organ might degenerate or internalize. No definitive function can yet be ascribed to the organ.

SECTION I

INTRODUCTION

It is known that the integument of crustaceans bears numerous superficial sensory and non-sensory structures; outgrowths such as spines, scales and horns may ornament the integument or assist the animal, for instance, during flotation. Pores may be indicative of single or compound integumental glands; and some integumental domes may contain more than one cuticular element which could define more complex organs beneath the cuticle, such as dorsal compound organs in the anterior head region and eye papillae in eyestalks.

These integumental components are not randomly distributed on the animal's body and appendages, and in the majority of cases they define specific patterns which have been of great taxonomic importance for establishing evolutionary traits among groups (Fleminger, 1973; Mauchline and Ballantyne, 1975; Mauchline, 1977). Associations of superficial sensory and non-sensory structures may be important features to take into consideration when ascribing functionality (Ghiradella et al., 1968 c; Thomas, 1970, 1971).

Most of the available information on sensory organs, sensory hairs, and other structures in or on the integument of Crustacea, has been obtained from adult animals. In general, the sensilla are small and difficult to manipulate. Thus, insufficient information about the number, distribution and type of structures in the integument of these growing Crustacea is available to assess their importance in the larvae.

There have been some attempts to classify superficial sensory structures in larval and adult forms of Crustacea (Thomas, 1970, 1971; Fish, 1972; Fleminger, 1973; Factor, 1978); these used external morphological features such as setal dimensions (length, basal diameters), tip angles and setal shaft accessories (setules). These groupings are of limited value when the species diversity of the sample increases and they have been restricted by traditional observational techniques. In the last decade, however, with the use of advanced electron microscopic techniques, the SEM and TEM, it has been possible to demonstrate receptors and other projections which could not be resolved under the light microscope, especially when small forms were considered.

In general, there has been a tendency for sensilla classifications to be concerned with external morphology (Fish, 1972; Factor, 1978) or with sensory modality (Ache and Macmillan, 1980). New schemes will have to combine these two components if a better understanding of sensilla is to be reached. Attempting to combine both characteristics, Bush and Laverack (1982) categorized mechanoreceptors in Decapoda as internal mechanoreceptor, cuticular receptors and supracuticular receptors. The last group are receptors whose dendrites pass through the cutile and make contact with a variety of supracuticular end-organs.

I. Campaniform or funnel canal organs. These receptors are positioned essentially in the dactyl tips of Decapoda Crustacea (Shelton and Laverack, 1968; Barth, 1980); in the antennules they are present at the base of the aesthetasc hairs (Laverack, 1976; Derby, 1982) as a series of pits or canals containing a central cone or pimple. According to the above mentioned authors, these organs were dually innervated by bipolar sensory cells which respond to strain applied to the cuticle with frequencies up to 70/sec. Recently Gnatzy et al. (1984) showed that the ultrastructure of these organs revealed the presence of both chemo and mechanosensitive dendrites

which defined them as bimodal receptors (contact chemoreceptors).

II. Cuticular articulated pegs (CAP ogans). These represent groups of sensory hairs present at specific positions close to the pereiopod joints of Astacura, Palinura, and Anomura and are not found in Brachyura (Laverack, 1978 a; Derby, 1982.

III. Setae (hairs). Most of the sensory projections of the Crustacean Decapoda could be listed in this category. Bush and Laverack (1982) define them as ranging from long and slender to short and stout, all being articulated at their bases to allow bending. These authors considered three main groups: simple unbranched hairs, branched hairs, and hair fans. The last group corresponds with organs which resemble a flower bud placed in a cuticular pit with cuticular projections or accessories at the organ tip. Laverack (1962, 1963) found them in the chela of Homarus gammarus where they contain two directionally sensitive units, each responding to a different direction of movement. Ache and Macmillan (1982) suggested that "hair peg" organs are similar to "hair fans". Single hair pegs are also widely distributed in the integument of decapods, with lengths ranging from 10-50 µm and having asymmetrical hair

depressions with several types of cuticular extensions. Such devices at hair bases may represent preferential directional sensitivity to deflection (Vedel and Clarac, 1976; Derby, 1982). Until now knobs and lip-like extensions have been the only types reported and they were unknown in other groups of Crustacea. Ache and Macmillan (1980) considered that both "hair fans" and "hair pegs" respond to direct contact and/or low frequency water movements and grouped them as tactile receptors because of their sensory modality.

Chemoreceptors, however, generally have a more limited distribution, occurring mostly as clusters of setae on the antennules of decapods, and have been characterized to be involved in distance chemoreception (low threshold) and, when present in the other pereiopods, to be involved in (high threshold) contact chemoreception (Ache and Macmillan, 1980). In antennules, the chemosensory function has been related with the presence of the aesthetasc hairs while the mechanosensitivity has been attributed to guard and companion hairs (Laverack, 1964, 1976). Aesthetascs are long, cylindrical, and with a permeable or "spongy" cuticle (Ache, 1982). In decapods they may or may not have terminal pores (Ghiradella et al., 1968). Flegenhauer and Abele (1983) observed ventrally

positioned pores in the aesthetasc hairs of the freshwater shrimp Atya innocous. This is an important finding because Heimann (1984) concluded that "an apical pore in the sense of an opening to the external medium is never observed in crustaceans".

Classifications based only on the external morphology or sensory modality may result in confusion when trying to typify such sensors as either mechanoreceptors or chemoreceptors. The ultrastructure of a sense organ can provide information about the cellular entities involved in the acceptance of the stimulus energy; its qualitative and quantitative value (Laverack, 1981). Therefore both mechanoreceptors and chemoreceptors must contain cellular components which may facilitate its differentiation.

For instance, mechanosensitive receptors are innervated by one or three sensory neurons and generally several accessory cells. These accessory cells may be outgrowth structures such as pits or plate organs (Laverack, 1968). Sensory neurons are of ciliary and non-ciliary types (Ong, 1969). There are two types of ciliary structures in receptor cells: I- cilia which occur at the stimulus site in some types of mechanoreceptors and which are structurally very similar

to the motile cilia. Mechanoreceptors of this type appear in vibration receptors of ctenophores (Horridge, 1965 a) and equilibrium receptors of cephalopods (Barber, 1968). This type of receptor was called the epithelial cell type by Thurm (1968). II- Modified ciliary structures which lie distant from the stimulus site, occurring mechano-, chemo- and photoreceptors, are called the bipolar-cell type. Mechanoreceptors of this type appear in the hair plate receptors of the honey bee (Thurm, 1964, 1965) scolopidial sensilla (Gray, 1960) and arthropod chemoreceptors (Hayes, 1976; Laverack and Ardill, 1965; Slifer and Sekhon, 1963, 1964).

Mechanoreceptive structures have a nerve scolopale matrix located at the base of the hair which articulates with the socket membrane of the seta (Borg and Norris, 1971; Corbière-Tichané, 1971) and the ciliary portion of its dendrite. Recently a scolopale has been described in all crustacean cuticular sensilla that are supposed to be mechanosensitive (Schone and Steinbrecht, 1968; Ong, 1969; Strickler and Bal, 1973; Anderson, 1975; Mead et al., 1976; Ball and Cowan, 1977; Risler, 1977, 1978; Gun, 1978; Crouau, 1978, 1980, 1981; Kouyama and Shimozawa, 1982; Altner et al., 1983; Schmidt and Gnatzy, 1984). A tubular body is found in the distal region of the dendrites of arthropod cuticular mechanoreceptors (Thurm,

1964;Barth, 1971; McIver, 1975; Harris and Mill, 1973; Gnatzy and Tautz, 1980), and including crustaceans (Strickler and Bal, 1973; Barrientos, 1980). It is believed that the tubular body at the tip of the dendrite is involved in the transduction process and that compression of this body is the effective stimulus (Thurm, 1965; Chapman and Duckrow, 1975).

Schmidt and Gnatzy (1984) described type-I dendrites as being part of the mechanosensitive apparatus of the leg funnel canal organs of C. maenas. This type of dendrite is characterized by a long ciliary segment (6-7 µm); ciliary rootlets are well developed, branching proximally, and interconnected with the scolopale by desmosomes of the macula adhaerens type.

The ultrastructure of chemosensory sensilla has been studied mostly from hair-like setae (Ache, 1982), even though other morphological types have been suggested (Altner and Prillinger, 1980). Essentially they are innervated by multiple (3-50) bipolar sensory neurons. Some problems in hair sensilla characterization may arise when the number of innervating sensory cells is small (three or less); chemosensitive sensory cells could not be differentiated from the mechanosensitive ones because their numbers may be analogous. The sensory cells give

rise to monociliary dendrites (Ball and Cowan, 1977) or biciliary dendrites, as found in the aesthetasc neurons (Ghiradella et al., 1968 c; Snow, 1973; Guse, 1979). The dendrites of the chemosensitive bipolar cells do not end at or near the hair base, which seems to be a common feature in mechanosensitive sensory cells, but rather they branch extensively distally, losing their integrity (Ache, 1982). Dendritic branching may be linked only with antennular aesthetasc hairs; dendrites innervating non-aesthetasc setae do not branch (Guse, 1978; Dahl, 1973).

In antennules and the dactyl the chemosensitive setae must communicate with the external environment via apical pore(s) (Felgenhauer and Abele, 1983), or setal wall pores (Ghiradella et al., 1968 a, c; Snow, 1973; Anderson, 1975; Juberthie-Jupeau and Crouau, 1977). Schmidt and Gnatzy (1984) characterized a second group of potential chemosensitive dendrites, type-II dendrites. They have short ciliary segments (1 µm long) and exhibit a ciliary necklace-like structure along their axonemes. They contain a large vesicle filled with an osmophilic material inside the ciliary and paraciliary segments. The ciliary rootlets are less developed than those of type-I dendrites and lack desmosomal connections and scolopale matrix, however, they may be present in some

chemosensory setae and might suggest a bimodal function (Mead et al., 1976; Seelinger, 1977; Guse, 1978). Until now two types of chemosensory setae have been typified in insects and decapods (Slifer, 1970; Ache, 1982): one type is thin walled, permeable along its length, and innervated by a large (>20) number of sensory cells with branching dendrites; the second type is thick walled, permeable at its tip with a low number (<20) of unbranched dendrites.

The body and pereiopods of Crustacea are sculptured by minute pores which, in most cases, represent openings of gland cells within the epidermis. This is the case in tegumental or dermal glands, whether unicellular or compound, and the pores are located just beneath the endocuticle (Herrick, 1896; Yonge, 1932, 1936; Drach, 1939; Doughtie and Rao, 1979; Johnson, 1980; Felgenhauer and Abele, 1983). In all these cases the single secretory cell contains the typical cell components with prominent organelles such as Golgi profiles with the known secretory function associated with them. In most cases secretions reach the surface via sclerotized ducts. Felgenhauer and Abele (1983) suggested that the presence of a flocculent material within the ducts of integumental shrimp glands may be responsible for the secretion of the epicuticle. The same authors reported

the presence of several multicellular glands, and another type bearing numerous multilamellar whorls. Epidermal glands have been considered to be luminescent glands in the copepod Metridia spp. (Giesbrecht, 1889, 1895; David and Conover, 1961; Clarke et al., 1962; Mauchline, 1977).

On the other hand, glands have been considered basic elements of the excretory system of Crustacea: antennal gland (basal article of the second antennae) and the maxillary gland (basal aricle of the second maxillae) (Kaestner, 1970). The nephridia in crustaceans and the coxal glands of chelicerates have a sacculus, a coelomic remnant which opens through a funnel into an excretory canal which constitutes the opening at the base of the respective appendage. The antennal and maxillary glands do not occur simultaneously during the animal's life.

For instance, antennal and maxillary glands are present in adult Myodocopida, Euphausiacea, Decapoda, Mysidacea, and Amphipoda, while maxillary glands are present in adult forms of Hoplocarida, Cumacea, Tanaidacea, and Isopoda. Early work on segmental excretory organs by Burian and Muth (1921) indicated that the excretory glands of Crustacea could be divided into two groups according to the nature of their efferent

ducts. In one group the duct is intracellular and three cells form the gland, while the other group possesses an intercellular duct and is composed of a large number of cells. Canon (1924) reported that in the nauplius stage of Estheria spp. the antennal glands are not fully formed. After hatching the gland consists of a small end sac joined to the ectoderm by a duct (coelomic system) of three cells. The duct system is long and thin, with a duct cell which opens to the exterior on the posterior side of the antennal basal segment. Proximally the duct ends with two "proximal duct cells" which connect the duct with the end sac. The same author pointed out that the antennal and labral glands (three conspicuous glands, each with two secretory cells with a reservoir of secretion and a tubular duct cell: one of the glands opens medially and the other two laterally) have the same duct system but differ in their coelomic sacs. Therefore, they are not of truly homologous significance.

Canon (1924) also suggested that excretory glands in Crustacea "are evolved from a form in which there was in each segment a pair of coelomic sacs with their coelomic ducts and a pair of true ectodermal nephridia opening into them and acting as the excretory organs, or else that they were not true nephridia and the coelomic ducts

functioned as the excretory ducts". Brinns and Peterson (1969) supported the argument that the antennal gland of Crustacea and the mammalian kidney were two organs which might be regarded as being physiologically analogous in some respects. Riegel (1966) reported the presence of secretory/digestive systems in the antennal gland of the freshwater crayfish, and suspected their presence in the antennal glands of other crustaceans. Walley (1969), working on the larval structure and metamorphosis of the cirriped, Balanus balanoides, showed that antennal glands are present in the nauplius stages but are lost at the nauplius-cypris moult. Each gland has an end sac and an excretory duct which opens to the exterior on the posterior side of the limb. The maxillary glands appear at cypris instars and persist into the adult stage. They have two end sacs and the ducts open on the posterior side of the second maxillae. Cement glands, for instance, start developing during nauplius IV, becoming functional only during the cypris stages, and are related to settlement. The cement glands in the adult appear as a cluster around the collecting duct of the cypris cement glands. Walley also reported the presence of other groups of glands: epidermal and frontal glands which are lost when the cypris larva becomes attached.

In the case of the epidermal glands, each contains two glandular cells approximately 60 µm long opening through a single pore and with a nuclei 12 to 15 µm in diameter. The frontal glands are larger and open through pores situated at the tip of each frontal horn. Nauplius stage VI have a pair of spindle-shaped cells about 130 µm long with nuclei about 15 µm in diameter, at the base of each frontal horn. Both types of glands have similar reactions to staining with iron haematoxylin and light green to the luminescent glands of the copepod Metridia lucens (Boeck et al ., 1962). A more unusual type of unicellular gland was found by Willey (1969) in the anterior dorsal region of the body: the gland opens through a pore in the mid-dorsal line (Kauri, 1962) and its secretion stains pale green with light green and has an unknown function. Some scattered unicellular gland cells may be found in the adult barnacle (Thomas, 1944). The presence of a similar type of unicellular gland cell is completely unknown in the Decapoda during larval or adult stages.

Domes in the carapace of crustaceans have been related to the presence of complex dorsal organs (Calman, 1904; Hansen, 1921; Gurney, 1939; Mauchline, 1977). A particular dome in the carapace may contain some

associated structures such as pits, pores, and cones, plates which could indicate the presence of not just a cluster of cuticular elements but a more sophisticated organization, either sensory or glandular. This is the case in the sensory pore of the eyestalk in Malacostraca, which seems to function as an external chemoreceptor (Altner and Prillinger, 1980).

An unusual organ was reported by Calman (1904) to be present in the dorsal head region of adult Anaspidacea. He described it thus: "on the dorsal surface (of the head) in front of the cervical groove, is a pigmented area with a circular central spot surrounded by four minute pits". The author did not mention its occurrence in other adult groups but stated it was present in the embryos of Tanaidacea, Isopoda, Amphipoda, Mysiadae, but unknown in the Stomatopoda. Hansen (1921) reported the occurrence of the same dorsal organ in several postembryonic forms of Crustacea Malacostraca. It was present in the larvae and adult forms of Nebaliacea, Anaspidacea, and Mysidacea.

Hansen found the organ consistently in the larvae and adults of Penaeidae, Sergestidae and Caridae. In the last group the dorsal organ is placed in a more posterior position, behind the dorsal spine. It is absent in the

adults of Astacidae, Palinuridae, Galatheidae etc. and in the Brachyura; it is also not found in the Amphipoda and Euphausiacea (Hansen, 1921). A vestigial organ on the dorsal side of the keel region was reported in two Euphausiacea spp. by Calman (1904) and Sars (1910).

Studies on integumental sensilla and glands of some pelagic Crustacea showed the presence of a prominent compound organ on the dorsal anterior surface of the head in the larvae and adults of Euphausiacea spp. (Mauchline, 1977). The organ reported by Mauchline is placed in a groove on the top of the dorsal anterior keel. From chemically digested integuments, the organ was observed to contain a number of anterior pores, the number of which was species specific. The pores were anterior to a central area which was not hollow and surrounded by four round or elongated pores. He reported another median compound organ, probably analogous with that of euphausids on the head region of Pasiphaea tarda, P. multidendata, Parapasiphaea sulcatifrons, Ephyrina bifida, Acanthephyra spp. and some other Pacific decapods. Lastly the same author observed the presence of another compound organ consisting of two pairs of pores, each 6 µm in diameter, present in the mid-dorsal region of the carapace and found in a phyllosoma larva of a panulirid lobster. The function this author ascribes

to this type of dorsal organ is a light sensitive one, perphaps involved in detecting downwelling light.

The available information about the general morphology of this dorsal organ as well as the nature of its components have not been studied; also its occurence is unknown in the embryo, larvae, juveniles and adult decapods. Following Calman's description of the dorsal organ, the present study intents to provide some information about the external morphology of the dorsal organ, its ultrastructure, and its occurrence among several species of growing Decapoda. Another important objective of the present work is to suggest a potential function or discard some of the unsubstantiated roles assigned to it in both early embryological and palaeontological reports.

Dorsal organs have been studied widely by embryologists in insects and crustaceans. In collembolan insects, for example, the organ arises from a large group of blastoderm cells placed in an antero-dorsal position, which later enlarge and become incorporated into the yolk. As a result the cell outer regions become reduced in size, reaching a mushroom-like shape with a central narrow opening (Jura, 1972). The dorsal organ is a transitory structure in Collembola and degenerates at the

end of embryonic life. During blastokinesis it reaches its largest size and greatest activity (Jura, 1972). A more elaborated dorsal organ is present in Hypogastrura armata which exhibits tendrils growing from the organ and involving the embryo (Tiegs, 1942). The tendrils were supposed to be devices to attach the embryo to the investing cuticle (Philiptschenko, 1912a). Slifer (1938), however, suggested it was a water absorbing organ. Thermocauterization of the organ brought about yolk rigidity and no chorion disruption, resulting in the cessation of hatching (Jura, 1967 b).

The development of the dorsal organ in Diplura differs from that of Collembola, where the dorsal organ arises before there is any trace of the germinal band. It is formed by a dorsal migration of cells from the serosa (Uzel, 1898 a). It has tendrils as found in Collembola, and after blastokinesis the organ degenerates within the haemocoele (Tiegs, 1942). In Hemimetabolous insects, columnar embryonic ectoderm begins to spread upwards after membrane rupture, to replace the amnion cells (provisional dorsal organ closure) at the surface. This migration of cells effects dorsal closure, ending in the reabsorbtion of the serosal vestige or dorsal organ into the yolk, followed by the shrinking amnion (Anderson, 1972). This process is followed by the

functional differentiation of the epidermis and secretion of the first nymphal cuticle. In holometabolous insects, when the germ band is fully elongated and segmented, the amnion and the serosa fuse beneath the anterior part of the germ band, following which the serosa contracts to form a dorsal organ whilst the amnion forms a provisional dorsal closure over the dorsal surface of the yolk mass.

Early studies on Crustacea Malacrostaca embryos showed the existence of one, two or three dorsal organs. Kinsley (1887), while describing the development of Crangon vulgaris, found on the dorsal surface of the egg opposite to the mouth in the median line, a patch of about twenty to thirty cells much smaller than those of the surrounding blastoderm. According to his observations this dorsal organ is formed by columnar cells with elongated nuclei which form a circular arrangement. It has no resemblance to the dorsal organs found on other species (Herrick, 1891). Brooks and Herrick (1892) reported on Alpheus saulcyi a "dorsal plate" composed of ectodermal cells which sank into the yolk and were all reabsorbed. Terao (1919) found unpaired dorsal organs in Panulirus japonicus, of which the middle one corresponds to the dorsal plate described by Herrick. The organs have a degenerative character at the end of development and were considered as moulting

glands during embryonic life. Studies on the embryonic development of the same species (Shiino, 1950) emphasised the existence of an anterior and mid-dorsal organ which develops in front of the brain as a cup-like group of ectoderm cells, both disappearing after moulting. Piatakov (1925) described two dorsal organs in Asellus aquaticus, each associated with the two embryonic cuticles. He described the organ as being formed by a row of columnar cells with a pit at its posterior end and surrounded by one or two regular rows of flattened cells. He proposed that the degeneration of the first dorsal organ left a seam in the first embryonic cuticle which functions as a mechanical device at the moment of larval hatching. The organ was ascribed by the author as responsible for the secretion of a substance with both a chemical and mechanical function for cuticle shedding and in the elimination of waste products.

Sollaud (1923) observed on Palaemonidae squilla embryos the presence of "la plaque apicale". It was suggested as a releaser site for waste products, and argued that, as it was found in Amphipoda (Nusbaum and Shereiber, 1898), this dorsal organ might represent "une petite glande" where the cellular components could not be distinguished as excretory cells. The author suggested that the organ might filter the soluble waste products

leading to final degeneration. The author, on the other hand, pointed out the possibility that the dorsal organ present in the malacostracan embryo could represent the temporary occurrence of an "ancient organ".

Manton (1928), while studing the embryology of the mysid, Hemimysis lamornae, reported paired dorsal lateral organs and a median dorsal organ. The first group of dorsal organs are formed as result of a thickening of the ectodermal lateral cells to the antennae, followed by cell enlargement, invagination and formation of a narrow channel which opens to the exterior. The cell cytoplasm is homogeneous, with the nucleus placed peripherally, surrounded by secretory granules. The organ is present for most of the embryonic life; only when the first embryonic cuticle is shed does it become vacuolated and degeneration take place. The median dorsal organ appears when the preantennulary mesoderm strands reach the stomodaeum. After the septum formation, a group of ectodermic cells occurs dorsally and it extends from the posterior edge of the septum backwards through the mandibular region as an elongated thickening. According to this author, it must be a site for cellular degeneration. Cell boundaries and nuclei are not well defined; the cytoplasm has a dark appearance as it is seen in areas where yolk cells degenerate. Between the

stomodaeum and the dorsal organ the aorta becomes united through the upper strands. These upper strands originate from a pair of stomach muscles besides the anterior aorta. Then the dorsal organ is gradually absorbed and the muscles are attached directly to the ectoderm, and placed apart when the larval cuticle is shed. Manton also refuted Nusbaum and Schreiber's (1898) suggestion that the dorso- lateral organs in M. chemeleo were involved in the secretion of embryonic membranes, and claimed there was no support for this interpretation. Scheidegger (1976), working on the embryonic stages of the anomuran Eupagurus prideauki, established that the dorsal organ is formed between stage IX and X and degenerated at stage XI. The author concluded that the organ has no relation with the yolk absorption.

As it can be seen, all these embryological studies recognized the presence of paired and unpaired dorsal organs (lateral, median or posterior) with known or, in the majority of cases, unknown functions during embryonic life.

Perphaps one of the most curious findings related to Calman's (1904) description of a dorsal organ in postembryonic forms of Crustacea, relates to a median dorsal tubercle present in the glabella of many

trilobites. Raymond (1920) interpreted this structure as that which evolved later as the posterior zoeal spine of Crustacea. Stormer's (1930) studies on the median tubercle of Tretaspis seticornis (Trinucleidae) revealed the external morphological features of what could be considered the homologous dorsal organ found by Calman (1904) and Hansen (1921) in recent Crustacea Malacostraca. Stormer's description of the organ was "5 distinct pits arranged in a deformed square with a central pit". Pit dimensions were larger in young specimens (0.1 mm) than in adults (0.028 mm). Thus the author concluded that the median tubercle was best developed in the younger specimens, and described the central pit as the opening of the eye- and the four pits indicated the ocelli. Thus it was regarded as a true median eye. Lenses were not found as in the lateral eyes. Hanstrom (1934), on the other hand, indicated that, at least in the Trinucleidae, the median tubercle seemed to have some sort of "sensory complex" similar to that of recent syncarids.

Another two types of median tubercle or nodes on the glabella of Asaphidae, Nileus armadillo and other trilobite species, have been reported by Fortey and Clarkson (1976). The first type corresponds to a glabellar "tubercle" or protuberance situated just

opposite the palpebral lobes and without any indication of symmetrically disposed pits. It was proposed to act in Nileus as a light receptive organ. The second type of organ is placed in a lower position containing four symmetrically disposed pits, as found in Odontopleuridae spp. (Whittington, 1956; Chatterson, 1971; Bruton, 1967) and Scutelluidae (Whittington, 1965). Whittington (1956), working on Diacanthaspis orandensis, found that the tubercle is prolonged into a spine, and comparisons were made with the median "sensorial complex" of Syncarid Crustacea (Hanstrom, 1934). Fortey and Clarkson (1976) suggested that the reduction of a prolongated anterior spine evolved a tubercle during ontogeny. But Raphiophoridae species lack spines and posess prominent glabellar tubercles placed more posteriorly (Fortey, 1975 a). In the raphiophusid both glabellar tubercle and spine did not occur simultaneously so they were considered as homologous.

Most of the information available about sensory structures and non- sensory structures (out/ingrown structures) in Crustacea Malacostraca has been obtained from adult forms. Our knowledge of the precise integumental changes, in terms of types and frequencies of occurrences of sensilla and out/ingrown structures, in the developing and growing Decapoda larvae is far from

being completed. Consequently the present work has three main objectives: 1. To survey the integument, body and appendages of adult and larval forms of some Crustacea Malacostraca species in order to characterize or revise previously reported setae whose descriptions failed to indicate some important morphological features when ascribing functionality to these sensory organs. 2. To interpret the Crustacea Decapoda integument as one more indicator of changes in setal armature coupled with development. 3. To provide a detail study of an unusual "dorsal organ" present in the anterior dorsal side of the head region of Decapoda embryos and larvae (Macrura, Anomura, and Brachyura), its main ultrastructural features, its interpretation as a "sensory-glandular unit complex", and its potential ontogeny in relation to the primitive arthropods, the Trinucleidae:Trilobitae.

SECTION II

MATERIALS AND METHODS

1.1 FIELD COLLECTION

Sampling was carried out from March to November during two consecutive years (1982-1984), animals being collected weekly from St. Andrews Bay, Scotland within an area of 3-10 NM East of St. Andrews. For all the planktonic forms, horizontal tows were done at 0 and 10 m. depth, using fine (150 μm) and coarse (250 μm) plankton nets. The samples were placed in 3 l capacity plastic jars. Offshore and inshore trawls were done for the benthic forms (Isopoda, Cumacea and Amphipoda (*Ampelisca typica*). The sample was sorted in a plastic tray of 1 m. A qualitative record of the seasonality of larval forms was established. Sampling was sometimes limited due to poor weather conditions.

1.2 LABORATORY PROCEDURES

1.2.1 Animal Handling

The sample containing the planktonic organisms was put in a white plastic container of 20cm x 20cm x 15cm. A 60 W light was placed 30cm above the surface of the water and to one side of the container and left for approximately 10 min. Due to phototaxis, the majority of organisms moved towards the source of light, and consequently animals could be picked up using wide glass pipettes. This routine was used to obtain animals whose body length was 0.5 mm or more. These large forms were removed and placed in 50 ml containers of filtered sea water. The remaining sample was filtered, concentrated, and observed under a stereoscope. In this way the small forms, mainly pre-zoeae and eggs of Brachyura, were taken out of the total sample. Each animal was observed under the light microscope in order to establish its developmental stage and taxonomic group according to Lebour (1927, 1928 a, b, 1930, 1931), Gurney (1926, 1939), Sars (1895, 1899), Webb (1921) and Williamson (1957, 1960, 1962, 1967).

1.2.1.1 Rearing the Larvae (Crustacea:Decapoda)

Methods varied according to the groups. The following routine was used for the Brachyura and Anomura larvae. Animals were kept in the laboratory in order to follow development. They were maintained at low densities of 20 organisms per 50 ml glass beaker at 8±2°C with 12D:12L periods (12 h light-12 h dark). Aerated water was renewed, and the animals fed with Artemia salina nauplii, daily. Flasks were examined daily in order to detect any exoskeleton exuviates as a result of moulting. The labelled stock provided a known source of animals in terms of their taxonomic group and stage of development for further research needs.

The rearing of larvae belonging to the Nephropoidae (Homaridae) followed a different routine since these larvae were rare or absent in the plankton samples. An ovigerous berried female lobster Homarus gammarus, was kept in a tank with running sea water and fed with raw fish twice weekly. During the hatching period the larvae were transferred to a large metallic tank (250cm x 100cm x 80cm) with running sea water. They were fed with small fragments of mussel, Mytilus edulis, or raw fish. The larvae were aggressive and territorial so, in order to avoid cannibalism, they were placed individually in modified culture trays. The upper and lower plastic lids

had been replaced by a net cover (250 µm mesh) which allowed water circulation, and the whole set up was maintained at a temperature of 14 ± 2°C. Despite a high mortality it was possible to rear a few up to the post-larval stage II. In the case of Nephrops norvegicus, stage I larvae were obtained in two of the plankton samples. No berried female lobsters of this species were available for rearing the larvae.

Brachyura eggs were obtained in the laboratory from a berried female crab, Carcinus maenas. This source was maintained over a period of time so that any accidental losses could be replaced. The egg strands were placed in a glass tank with filtered sea water, which was aerated, renewed daily and maintained at a temperature of 8 ± 2°C until the hatching period. Some egg strands changed colour from an intense yellow or orange to a pale brown, which revealed the presence of bacteria colonies. Such strands were removed in order to prevent contamination of the rest. It was not found necessary to add antibiotic to the water.

1.2.2 Scanning Electron Microscopy

The procedures of Friedman (1977) and Hayat (1970, 1978) were followed with some modifications. When available, newly moulted animals were used because they had a cleaner integument. Some groups, however, such as the Isopoda, Cumacea, or Amphipoda were limited in numbers and not reared in the laboratory, so special attention was given to the the condition of the animal body. Before the animal was fixed, it was rinsed with 0.1N HCl to remove attached particles and mucous from the integument of the animal. This routine was done once for the newly moulted animals but at least three times for the others.

The animals were heat-narcotized in order to avoid appendage contraction during and after fixation. They were placed in a small petri dish and left on top of a beaker containing 35ml of water at 65°C. They were left for no longer than 15 sec. as they are very sensitive to temperature changes. If overheated, the animal bent the appendages towards the body and thus became useless for any further study. When the swimming movements of the animal diminished and the appendages stretched out from the body, it was ready to be transferred to the fixative. This procedure failed in the case of the Isopoda, Eurydice pulchra. In this case, instead of

heat-narcotization, menthol crystals were added to the water and left overnight. After this treatment animals were less active and were fixed in the following routine:

I. Fixation

2% v/v glutaraldehyde buffered with filtered sea water 1 h at 20°C.

II. Buffer rinse

0.1 M sodium cacodylate, 3 changes, 10 min. each.

III. Post-fixation

1% osmium tetroxide buffered in 0.1 M sodium cacodylate 1 h, 4°C.

IV. Buffer rinse (as II)

V. Dehydration

ethanol series : 35% 75% 95% 100% 10 min. each ethanol-acetone: as above acetone : 100% 2 changes 10 min each

VI. Carbon Dioxide Critical Point Drying.

Dry with CO_2

VII. Mounting (see text)

VIII. Coating: 100 % pure gold

After critical point drying the specimens were mounted directly on SEM aluminium stubs, using a double faced tape, then coated with 100% pure gold using a coating unit (Model 12E6/1688 from Edwards High Vacuum

Ltd, Crawley, Sussex, UK). Specimens were examined in a scanning electron microscope (Cambridge 600) and a JEOL JSM-35CF at 15 kV and photographically recorded on Plus-X Pan Kodak film 32 ASA. Observations of ten larval and postlarval forms were made by means of the scanning electron microscope.

1.2.3 Transmission Electron Microscopy

Several authors have reported the difficulties of fixing crustaceans (adult or larvae) for ultrastructural studies (Ong, 1969; Bielawski, 1971; Lake, 1973).

During this experimental work different methods were used without much success. Special attention was given to pH ranges and osmolalities of fixative and buffer, adjusted by adding sucrose or NaCl in the order of 1.100 mosm, according to Maser et al., (1967). The position of the dorsal organ and its components lying underneath the cuticle and its basal membrane in contact with the haemocoel were two barriers hard to overcome for fixation and sectioning. Despite good fixation, quality, thin sections were always torn up in this area. Decalcification was the only solution for this problem (Kovind and Hill, 1984). Some of the procedures below gave satisfactory results for tissues which were not of

primary interest (eyes, gastric mill, pericardial sacs, etc.

First Protocol:

I. Aldehyde fixation

Glutaraldehyde 2-5% buffered with sea water or in 0.2M sodium cacodylate buffer. 1 h. 4°C.

II. Buffer wash

0.2M sodium cacodylate buffer 3 changes 5-10 min. each

III. Post-fixation

2% osmium tetroxide buffered with 0.2M sodium cacodylate buffer. 1 h 4°C.

IV. Buffer wash (as II)

V. Dehydration

Acetone 1) 10% 30% 50% 70% 90% 10 min. each 2) 100% 2 changes 10 min. each.

VI. Plastic infiltration

Durcupan ACM hard resin mixture (Cobb, pers. comm). 1.Epoxy acetone 1:1 45 min. then 3:1 overnight in rotator 2.Epoxy 1 h. Vacuum for 10 min. to remove air bubbles.

VII. Embedding (in moulds Polysciences, Inc or plastic lids)

Durcupan ACM hard mixture 24-48 hrs. at 60

°C.

Second protocol:

2% osmium tetroxide buffered in 0.2M sodium cacodylate 1 hr. 4°C.

Third protocol:

Glutaraldehyde - Acrolin - Paraformaldehyde - Osmium Tetroxide (Hayat, 1970).

Fourth protocol:

Paraformaldehyde - Glutaraldehyde (Karnovsky, 1965).

I. Fixation

Karnovsky solution buffered with 0.2M sodium cacodylate buffer 1 h. Room temperature.

II-VII. As in first protocol.

Fifth protocol: (best results)

Modified Paraformaldehyde - Glutaraldehyde (Karnvosky, 1965)

I. Fixative preparation: Two grams of paraformaldehyde powder were dissolved in 25 ml of distilled water at 70°C by continous stirring. To clear the solution 1 or 2 drops of 1N NaOH solution were added while stirring. Once the solution was cooled 8 ml of 50% glutaraldehyde, 10

ml of 0.2M sodium cacodylate buffer, 4 ml of 0.2M NaCl solution and 4 ml of 15% sucrose solution were added. The final pH of the mixture was 7.2 . Animals with or without urosome, eggs and embryos were fixed with the above solution for 24 hr. at room temperature using a rotator. For dissecting out, the animals were placed in embryo chambers containing 5 ml of the buffer and the urosomes were cut off using Irex surgical scissors. After this the specimens were put back in the flask with the fixative.

II. Buffer wash

0.2M sodium cacodylate buffer+15% sucrose solution+0.2M NaCl 6:1:1 1 h 2 changes room temperature

III. Post-fixation

2% osmium tetroxide buffered with 0.2M sodium cacodylate+15% sucrose solution.

IV. Buffer wash (as II)

IVa. Decalcification (Raymond, 1979)

1.Rinse in 0.3M NaCl 3 changes 5 min. each 2.2% Ascorbic acid solution+ 0.3M NaCl 1:1 24-48 hr. using magnetic stirrer 3.Rinse in distilled water 3 changes 5 min. each

V-VII. As in first protocol.

Thick and thin sections were cut on an ultramicrotome (LKB 4800 Ultratome, Produkter AB, Stockholm-Bromma 1, Sweden) with glass knives, stained for 7 min. with uranyl acetate (Watson, 1958 a), followed by 5 min. with lead citrate (Reynolds, 1963) and examined with an AEI EM6B and a Phillips 301 trasmission electron microscope at 60 kV. Thick sections for light microscopy were stained with 1% toluidine. Five specimens (Brachyura: embryos, larval and postlarval forms) were sectioned and examined by means of the transmission electron microscope.

1.2.4 Light Microscopy (Brachyura eggs)

The development of the eggs of Carcinus maenas (Crustacea:Brachyura) were followed from the 120-cell stage up to hatching. Egg strands were fixed every four days during development in order to trace the dorsal organ. After stage V (Scheidegger, 1976) eggs were not fixed as a whole. Instead the chorion and blastodermic cuticle were removed before fixation. For this purpose, egg strands were immersed for 1 or 2 min. in Clorazol Black E (Cannon, 1941) staining solution. They were rinsed twice with sea water until most of the stain was

removed. This treatment caused darkening and softening of the membranes, which facilitated dissection. The egg chorion was punctured with the tip of a glass electrode and, after this, the two membranes were removed using two fine tungsten needles. Dissection was carried out in a cavity slide under a stereoscope at 7x.

1.2.5 Physiological Experiments

An intermolt Macropipus depurator (Decapoda:Brachyura), (zoeae IV and megalopa I) was placed on a watch glass (4cm diameter) containing a piece of paper towel which kept the animal moistened and restricted its movements. Under these conditions a 0.5mm long doghair was glued to the animal head (for technique see Alcaraz et al., 1980) on top of the dorsal organ central pore. The animal was returned to a 50 ml glass beaker containing filtered sea water and allowed a period of 24 hr. for adjustment. Control (25) and experimental (25) animals were observed daily over 2 weeks for indications of ecdysis (presence of exoskeletons), apolysis (retraction of the epidermis from the cuticle) and for changes in body colouration. Mortality was in the order of 20% in the experimental group.

SECTION III

RESULTS

3.1 Superficial Sensory and Non-Sensory Structures on the integument of Crustacea: Peracarida, Epicarida, and Eucarida

All the morphological features and measurements were taken from scanning electron micrographs. Hair sensilla patterns and frecuency of occurence were obtained from reconstructional drawings on tracing paper. Several different morphological types of sensilla and cuticular outgrowths were found on the integument (body and appendages) of Crustacea: Peracarida, Epicarida and Eucarida. The distribution, length and species occurence of the sensilla are summarized in Table 1. as peg, conical and "aesthetasc" sensilla. The peg sensilla were observed in six different forms:

The first type was a single, blunt tipped hair of approximately 6 µm length whose socket rim projects a raised lip on one side and there are two neighbouring pores. This peg is widely distributed on dorsal body segments. There are 40 pegs per body plate approx. and describe a specific pattern along the inner and outer edge of each segment (Fig. 1 a, b). Bilateral symmetry

Table 1. Uncharacterized Sensilla of Crustacea: Malacostraca (Peracarida)

Type of Sensilla	Species	Shape	Base	Length (μm)*	Location
Peg I	Hyperia galba	Single-taper	Cuticular lip	6	Dors/Lateral. Body Plates
Peg II	Ampellisca typica	Stout, 10-12 in groove		5	"
Peg III		Squamous-taper		10	"
Peg IV	Haustorius spp.	Single-taper	Knob/Vesicular Plate	8	"
Peg V	Eurydice pulchra	Single-taper + ter. pore		15	"
Peg VI	Idothea pelagica	Squamous-single + term. pore		8	Dors/segment margin P3-P7
Conical I	Eurydice pulchra	Blunted tip, setule with term. pore		100	
Conical II	Haustorius spp.	Blunted tip, squamous setule with bifid ends		200	Inner margin P3-P7
Conical III		Taper tip with squamous setule		48	Outer margin/dorsal side P3-P7
Conical IV		Blunted tip, robust squamous setule and bifid ends		36	Inner margin carpus-propus P3-P7
Conical V	Idothea pelagica	Split tips, setule + term. pore		80	Inner margin propus P3-P7
		Blunted tips, setule + term. pore		60	Dorsal/inner margin P3-P7
Aesthetasc	Diastylis cornuta	Slender hairs, bifid tips + pores		35	Second Antennae

* Approximate length; I- V Arbitrary classification

in the distribution of the pores over the whole animal is pronounced, as found by Mauchline and Ballantyne (1975). This peg was found in the Amphipoda:Hyperiidae Hyperia galba.

The second type are groups of 12-14 single peg-shaped sensilla (each peg approximately 5 µm long) describing a row as an inverted Z. Each peg is placed on a short but well defined circular depression, and the peg tips lack pores or bifid ends. They were found on the outer margins of the lateral epidermal body plates. They resemble greatly the cuticular articulated peg receptors (CAP organs) reported by Laverack (1978 a, b, 1982 unp. data) and Derby (1982) (Fig. 1c). Also in this species occurs another type of peg, short and squamous, of approximately 10 µm long emerging from an oblong pit in the cuticle. The scales forming the hair are broader at the hair base (Fig. 1d). These pegs are present on the Amphipoda: Ampeliscidae Ampelisca typica.

The third type of peg is very similar to the first described peg but with a slightly longer shaft (approximately 8 µm). This peg has a single knob at one edge of the depression (Fig. 1e). There is ring of tiny vesicle-like structures on the cuticle encircling the peg. These outgrowths resemble the peripheral microvilli

tufts reported by Intenic and Bulog (1984) in ampullary organs. The tuft projections extend even further as an heagon with the peg in the center. These peg sensilla are numerous, there being approximately 18 on the epimeral dorsal plates and one on the lateral ones; they may appear singly or in pairs (Fig. 1f). They were found in the Amphipoda: Pontoporeiidae Haustorius. spp.

The last two types of pegs are characterized for being short and for having modified tips instead of modified hair bases. In the case of the Isopoda: Idotheidae Idothea pelagica (Fig. 1g) the sub-apical ventral side of the peg carries a pore with an apparent cone or pimple in the center. On the contrary, in Eurydice pulchra, the pegs show the subterminal pore without modified structures in it (Fig. 1h).

Conical sensilla were observed in five different forms: The first one is stout, approximately 100 µm in length and 25 µm in diameter at the base. This sensillum occurs in groups of approximately 10 at the distal margin of the ischium-merus, merus-carpus, and carpus segments of periopods 3-7 (Fig. 2 a, arrows) and in groups of 4 on their dorsal side. On the propus , they occur ventrally forming three rows each one bearing three hairs; absent on the dactylus (Fig. 2a). Each sensillum

has one setule extending (Fig. 2b) from one face at a site about one third of the distance from tip to base; bearing a terminal pore at the tip (0.69 μm in diameter) indicating an "end organ" of a potential sensory process (Fig. 2c). In pereiopods (3-4), the conical sensilla are placed at the inner ventral side of each limb segment (Fig. 2d). Fish (1972) reported this sensillum on the same species, Isopoda Eurydice pulchra. as a "conical spine with a round apex and projecting flagellum" but failed to observe the sub-terminal pore.

The second type of conical sensillum is approximately 180-200 μm in length. This sensillum is widely distributed on the merus-carpus, and carpus-propodus segments of pereiopods 3 to 7 (Fig. 3 a). Each sensillum has a setule (10-12 μm long) projecting from one third of its length (Fig. 3 b, c, d). Both sensillum and setule tips lack terminal pores but the sensillum tip is modified on one side with a concave surface in which the setule can be accommodated along its whole length. The setule has a squamous appearance with scale-like projections placed ventrally (Fig. 3 b, c, d).

The third type of conical sensillum differs from the aboved mentioned in having a tapered apex (48 µm long) with a projecting setule (20 µm long). The tip of the setule is bifid and carries scale-like extentions. This sensillum is placed on the inner edge of uropods 1 and 2 (Fig. 4a). A similar type of setule is present on short and stout conical spines (IV) limiting the inner margin of the carpus, on pereiopods 5 to 7 (Fig. 4b). The last three types of conical sensilla above described are present on the Amphipoda, Haustorius. spp.

The fifth type of conical sensillum has an approx. length of 80 µm whose split tips bear a setule with a terminal pore placed ventrally (Fig. 5a); there are also cuticular folds on the setule dorsal side. This sensillum occurs on the inner edge of the carpus and merocarpus of the first and second gnathopods (Fig. 5b). In the same species a second type of conical sensillum is present on pereiopods 5 to 7, with a length of 60-65 µm. Half of the sensillum length has longitudinal folds (drying artifacts ?) with a projecting setule at the tip (Fig. 5 c, d). The setule is approx. 1 µm long bearing a terminal pore rather similar externally to the above mentioned. Saudray (1972), working on Gammaridean amphipod spp., reported rather

similar cuticular folds on "sexual spines" and probably involved in mating activities. The last two types of conical sensilla were found on the Isopoda: Idothea pelagica.

The last group of uncharacterized sensilla presented in Table 1 are the aesthetasc hairs found in the male Cumacea D. cornuta Each annulus has a row of 7-10 hairs (35 µm long) (Fig. 6a), and each aesthetasc hair tip has a bifid end and a terminal pore (0.3-0.4 µm) positioned ventrally to the bifid end (Fig. 6 b, c). There are no guard or companion hairs besides the aesthetasc hairs as found in Decapoda antennules by Laverack (1964) and Derby (1982), but the base article (Fig. 6d) is noticeably greater in diameter (as also seen in Decapoda).

The distribution, length and species occurrence of some uncharacterized cuticular out/ingrowths on some species of three Crustacea superorders, are summarized in Table 2. The first group, Pit I, corresponds to asymmetrical blunt sac or conical like-structures with a diameter of 27 µm approximately. The proximal end of the cone is flat and lacks a depression; the distal end is prominent and apparently bulbous (Fig. 7a). This cannot be confirmed due to the slight shrinkage of this part which could not be avoided during drying. At this level

Table 2. Uncharacterized cuticular outgrowths of Crustacea: Malacostraca

Type of Outgrowth	Species	Shape	Diameter (μm)*	Location
Pit I	*Diastylis cornuta*	Dome or sacs with infolding membranes	27	Body dorsal/later.sides
Pit II			15	
Pit III	*Cancer pagurus*	Domes with central ridge	26	Dorsal carapace
Pit IV	*Dorippe lanata*	Flower-shape with cut. projections	12	Dorsal carapace
Pit V	*Monstrilla longiremis*	Dome with infolding membranes	39	Dorsal/lateral/ventral sides metasome segments
Pit VI		Defined outer rim, four cuticular strips folded inside	35	"
Pit VII		Domes with a bell-shape membrane infoldings	7.6	"
Pit VIII			11	"
Scale plates	*Pseudione hydmania*	Rosette with numerous scale e extentions and brush-like tips	46	Ventral side incubatory plates

* Approximate length
I-VIII Arbitrary classification

the cuticle forms a central fold which runs along the whole diameter of the structure. This type of sac-like structure furnishes the moderately vaulted cephalothorax describing regular or irregular rows along the frontal lobe and lateral faces (Fig. 7b). Sars (1900) described them as "curving denticles or pseudorostral projections conically produced, horizontal".

There is a second type of sac-like structure slightly different to the above mentioned having a diameter of 15 µm approximately. The distal end has two prominent ridges with a flat center (no cuticle folding is observed) (Fig. 7c). This structure has a wider distribution on the dorsal surface side of the cephalothorax than the first described. These two outgrowths were found on the Cumacea, D. cornuta.

Within the Decapoda (Brachyura:Cancridae), Cancer pagurus juvenile instars develop a cuticular outgrowth (Pit III) (26 µm in diameter) rather similar in shape to the ones found in D. cornuta. Its distal end lacks the outer ridges or the central cuticle fold, instead there is a line which seems to divide it in two symmetrical halves (Fig. 7d). It is widely distributed on the carapace margins, anterior side and eye orbits.

The fourth type of outgrowth, Pit IV, has a chrysanthemum-flower shape of 12 µm in diameter. These protude from a hollow in the cuticle leaving a distance of 9 µm between the base and the top of the outgrowth. The distal part of the structure is clustered with tube-like projections which become more scanty at one third of the base (Fig. 9a). These projections are very similar to the papillae found in the unique papillate sensillum of Tenebrio molitor (Bloom, et al., 1982). These tube-like projections seem to be less numerous also in the center of the outgrowth (Fig. 9b). They delineate specific patterns along the dorsal side and edges of the carapace where they are abundant (60-100 approx.) (Fig. 9 c, d). These outgrowths do not project out of the cuticle, on the contary, they are level with it but maintain an upwright position. They do not occur on appendages or on the ventral side and are specific to juvenile instars. This type of outgrowth was present on the Decapoda: Dorippidae Dorippe lanata.

The last group of pits V, VI, VII, VIII specified in Table 2 correspond not only to cuticular outgrowths but also ingrowths. Type V is a single, round (39 µm in diameter) and unrimmed outgrowth whose cuticle folds towards the center (probably drying artifact) forming an

intricate pattern (Fig. 10a). Type VI is a single ingrown structure composed of four cuticular strip-like extentions. The above outer rim is 35 µm in diameter and well defined (Fig. 10b). Types VII and VIII are composed of paired bell-shape domes projecting from a depression of 7.6 µm in diameter (Fig. 10 c, d), while type VIII is 11 µm in diameter. Type VII is widely distributed on the dorsal and ventral surfaces of the thoracomeres while type VIII occurs as a pair on the dorsal surface of thoracomere IV (Fig. 10 e, f). The above described pits were found on the copepoda, Monstrilla longiremis.

Scale plates are uncharacterized cuticular outgrowth, with a rosette shape of 46 µm in diameter and formed by 20-30 scales whose tips split as a pectinate border (Fig. 8 a, b). They superimpose on each other giving a tumid appearance. They are approximately 30-40 on the rosettes pe incubatory plate (oostegite), randomly distributed and standing proud of the surface (Fig. 8 c, d). At the base of each scale, there is a pocket-like cavity which contains a central cone or pimple. This arrangement has a great resemblance with the plate-pits found on Decapoda (further explations in the text) found to have a sensory nature. This outgrowth was found on the female of the Isopoda: Pseudione hyndmani.

3.2 Trichoid Sensillum Occurence among Decapoda: Brachyura, Anomura, and Macrura Larval Urosome

While studying the setal armature of Crustacea:Decapoda larvae special attention was given to types and frequency of occurence. Observations on the integument, body and appendages, revealed the existence among others of a common hair: sensillum trichoidea on the Brachyura, Anomura, and Macrura larvae. One limitation of SEM mapping studies of sensilla (apart from the preparation quality) is the difficulty in analysing body areas due to the angular nature of the surfaces involved. Consequently the urosome was selected, as appendage indicator of setal development, because of its rather common configuration among the groups studied and its suitability for serial photographic recordings. Features such as number of segments and frequency of occurence according to the developmental instars are summarized in Table 3.

In the Brachyura: Maiidae, Hyas cornutatus zoea I, the urosome is formed by 5 segments with a forked telson. Each segment bears four tipped tapering trichod sensilla (22 µm long and 4 µm basal diameter) placed dorsally, one pair at the segment distal and the proximal

Table 3. Trichoid Sensilla Occurrence on the Urosome of Larval and Post-larval Decapoda Instars

	SPECIES						
	Brachyura *Hyas cornutatus*		Macrura *Homarus gammarus*		Anomura *Porcellana longicornis*		
Urosome Seg.	ZI	MI	LI	LIV	ZI	ZII	ZIII
1	4	4	12	40	0	0	0
2	4	12	28	56	0	0	2
3	4	12	28	56	0	0	2
4	4	12	20	36	4	6	6
5*	2	4	32	50			
6		2					
7**		2	48	108***			

* Telson Larval Instar (ZI-LI)

** Telson Post-larval Instar (MI-LIV)

*** Approximate numbers through drawings

end respectively (Fig. 11a). In the megalopalinstar I, the sensilla are longer (approx. 55 µm) and more numerous, totalling 48 rather than 20 present in the zoea instar I. Their distributional pattern also changes with ten hairs at the distal margin of segments 2, 3, and 4 (Fig. 11 b, c). The telson, however, has only two hairs as observed on the zoea instar.

In the Macrura: Nephropoidae, Homarus gammarus larval instar I, the urosome is formed by 5 segments which end up in a triangular anchor-type telson. The segments are characterized by the presence of horn-like extensions (Fig. 12.I a), two of which border the lateral sides of each segment with a third placed along the urosome middle line, with the exception of segment 5 which contains two. The two lateral horns lack setae whilst the central horn acts as a division line for the hair sensilla distribution. Therefore the pattern followed by the sensilla is symmetrical towards the sides of each central horn, with eight to ten hairs approximately lined up in a row (Fig. 12.I b). Four paired sensilla occupy the dorsal side of each segment (Fig. 12. I b arrow). Another group of four sensilla are placed close to the lateral horn, three of them in a line whilst a fourth hair is placed apart, close to the horn base (Fig. 12.I b dark triangle).

As can be seen in Table 3, the trichoid sensillum reaches its maximum distribution on the telson. As mentioned earlier the telson of H. gammarus appears as a strong triangular appendage with two central ridges which run along the whole telson length. The distance between the two ridges is relatively small proximally but increases significantly distally forming a V-shape. This difference of distance between the two ridges leaves a concave surface where the sensilla are placed (Fig. 12 I a, c). Regarding the sensilla arrangement on the telson, they form double rows of eighteen to twenty sensilla and there are preceded by five hairs in a single row on each side (Fig. 12 . I c). The hairs have length of 80 µm, taper tipped, and placed in a depression. Another six sensilla border the upper end of the ridges resembling a semicircular arrangement (Fig. 12 I . c arrows). Hair sensilla do not occur on the ventral side. During larval stage IV (post-larval I), there is a considerable increase in sensilla numbers and consequently changes in the distributional pattern (Fig. 12.I d; 12 . II). In general, the sensilla tend to be arranged in rows of between three to eight hairs. Segments 2, 3 and 4 bear a high number of sensilla but the maximum number is found on the telson (Fig. 12.I e).

In the Anomura: Galatheidea, Porcellana longicornis, the urosome has a length of 1.2 mm and is formed by 4 segments ending up with the rhomboid telson. During zoea stage I no sensillum is known to be present on the urosome segments. The telson, however, bears two pairs of trichoid sensilla approximately 30 µm in length. One pair is located at the very edge of the telson and the second pair is 90 µm above the first pair; thus the two pairs are parallel to each other (Fig. 13a).

During the zoea stage II, the urosome has a length of 1.3 mm with the same number of segments as in stage I. Regarding the sensilla arrangement, a new pair of sensilla appears in the telson above the second pair (Fig. 13b). This new pair is placed in a parallel position with respect to the former sensilla pairs, and another pair is present at the distal edge of segment 4. During the zoea stage III, the urosome reaches a length of 1.5 mm with the same number of segments as in previous stages. There is no increase in sensilla around the telson but a new pair appears on segment 3 (Fig. 13c). Unlike the former pair present on segment 4, this new pair of sensilla is placed close to the middle line of the urosome.

There are, however, some other body areas on the larvae which can be followed as indicators of setal development. For example, the dorsal surface of the head in P. longicornis zoea stage I exhibited two pairs of trichoid sensilla close to the joint of the rostral spine with the head itself; one pair placed anteriorly and the other one posteriorly to the joint, respectively. At this stage, the rostral spine lacks integumental structures, looking rather smooth along the whole surface. During stage II there is no change in trichoid sensilla numbers on the head side; with the difference that the rostral spine is completely covered by unrimmed scale-like projections bounded by minute pores (1 µm in diameter) (Fig. 14a). Despite their dimensions these pores have a well defined cuticular rim which projects out of the cuticle (1 µm long) (Fig. 14 b insert.). This pattern of a scale-pore, is continuous along the whole rostral spine surface. During stage III a new pair of trichoid sensilla is placed in line apart from the first pair towards the rostral spine edges (Fig. 14c).

3.3 Setal Variation on Larval and Juvenile Instars of Hyas cornutatus (Brachyura:Maiidae)

In this species was observed a remarkable change in setal types, occurences, and distributional patterns, some of them being specific for a particular instar of development. In general, during the zoeal stages, the integument has a limited number of sensilla, but some cuticular outgrowths seem more abundant here than those observed on later stages. The trichoid sensillum is present on the urosome (already described); one pair is placed on the head dorsal surface neihbouring the posterior spine.

On the urosome, however, there are two lateral knobs on somites 2 and 3 (Fig. 15a). They display a prominent outgrowth (2 µm in diameter approx.) containing a minute pore (0.4 µm approx.); they are two per knob, one close to the knob base and the other one more distal towards the knob apex (Fig. 15 b, c, d). Two occur dorsally alongside each trichoid sensillum on the urosome somites.

Another group of outgrowths is present on the dorsal and ventral side of the telson and somite 5. It consists of a group of tiny cuticular extensions (13 µm long) arranged in regular and irregular rhomboids (Fig. 16a). Another outgrowth is present on the rostral spine, a

thorn-like type (7 µm in diameter; 8 µm in length approx.) widely distributed along the whole surface (Fig. 16 a, b). Also on the telson the two unarticulated lateral spines and forked ends are covered by minute hair-like extensions which describe a rather elaborate and continuous hexagonal patterns distally, but less organized proximally (Fig. 16 c, d, e).

During the megalopal instar (Fig. 17a), there is an increase in trichoid sensilla numbers (see urosome) and in length. On the dorsal surface of the head are 20 hairs (27-29 µm in length approx.). The rostral and posterior spines lack cuticular outgrowths, instead scattered trichoid hairs can be observed on the dorsal horns (not counted). On the distal segments of the walking legs, particularly the dactylus, occurs a sensillum which may represent the earlier form of the so-called campaniform sensilla (Shelton and Laverack, 1968) or the funnel-canal organs (Gnatzy et. al., 1984) on adult specimens of Carcinus maenas. It appears as a single pore (2 µm in diameter) in the cuticle which contains a minute central pimple. There are three distinctive regions to the sensillum: an outer rim, an inner moderately flattened region and a central pimple. There are not more than 12 and these are concentrated distally towards the epicuticular cap (absent on it)

(Fig. 17 b, c, d).

Another sensillum is present along the inner side of pereiopods 1 to 5. There are five to seven in number per segment and taper tipped, slightly curved distally and 60 µm in length approximately. They have a basal annulus which is bordered by setules (10 approx.). The setules are also present along the setae surface forming more than three rows. Similar setae were found by Factor (1978) and classified as "triserrulate" on larva lobster mouth parts (Fig. 17 e, f).

In the case of C. maenas megalopal stage, the first described type of sensillum also occurs on the posterior pereiopds but placed more towards the limb tips (Fig. 18 a, b); less evident at the tips of the first pereiopds (Fig. 18c) but more developed at the first juvenile instar (Fig. 18d).

The integument of the first crab stage is striking in having a load of different types of setae which were completely absent during the two previous instars (Fig. 19a). Basically there are three distinctive types: 1) the pappose setae (b2 according to Factor, 1978), 19 µm in length and 2 µm in basal diameter, distributed in groups of two or three or placed individually (Fig. 19

b, c). 2) the plumodenticulate (c1 according to Factor, 1978) 6 µm in length, single hair and widely distributed on the carapace with slightly curved apex (Fig. 19 b, c, d). 3) Setae with nodules (Fish, 1972) 25-30 µm approximately with a third of its length bent, widely distributed along the whole carapace (Fig. 19 b,d). The trichoid sensillum was not observed in this instar, at least on the carapace. There is an abundant number of a stout cuticular outgrowth without articulation with a nipple-like shape (Fig. 19 c, e).

In general, the carapace surface can be described as irregular with some areas more prominent than others where the sensilla can be found forming groups; also it is sculptered by numerous tiny scale-like extensions distributed uniformly. The pappose setae were found to be present on the central and lateral pore of the X-organ in the eye-stalks (Fig. 19f). Thomas (1970) reported the presence of similar pappose setae, more delicate and with thin walls, in the statocysts of the adult crayfish Austropotamobius pallipes. Similar changes on the integumental sensilla were also observed in the anomuran P. longicornis, where the zoeal instars are almost glabrous (Fig. 20 a, b). Once the first post-larval stage is reached the carapace becomes furnished with V-shaped cuticular outgrowths (Fig. 20 c,

d, e) at the rim of long trichoid sensilla (Fig. 20f).

3.4 On the Occurrence of the Dorsal Organ among Larvae of Decapoda

3.4.1 Topography and External Features

The SEM mapping studies of the Decapoda larvae integument indicated not only the presence of sensilla and cuticular out/ingrowths, but rather unusual associations of the same integumental elements (e.g. pores and pits) which may represent the external components of organs or more complex-network systems placed beneath the cuticle.

This is the case of a dorsal organ present on a prominent dome lying medially, posterior to the level of the eyestalks. Among the groups studied, the dorsal organ was observed in the embryo, pre-zoea, larval and post-larval instars of the Brachyura; the larval and post-larval instars of the Anomura and Macrura. It was not traced on the juvenile crabs. Information on the occurence of the dorsal organ among larval instars of Decapoda is summarized in Table 4. The size of the various components of the dorsal organ varies according to the stage of development, and the species studied are

Table 4. Occurrence of Dorsal Organ among Larval Development of Crustacea: Decapoda

Species	Zoeal Instars	Megalopal Instars	Juvenile*
Macrura:			
Homarus gammarus	+	+ (VI)	NO
Nephrops norvegicus	+	+	NO
Anomura:			
Galathea strigosa	+	-	NO
Porcellana longicornis	+	-	NO
Porcellana platicheles	+	-	NO
Brachyura			
Carcinus maenas	+	+	-
Cancer pagurus	+	+	-
Ebalia tuberosa	+	+	-
Hyas cornutatus	+	+	-
Macropipus depurator	+	+	-

\+ = Present
\- = Absent
NO = Not observed specimen

to the stage of development, and the species studied are shown in Table 5.

In the Brachyura, H. cornutatus, the dorsal organ shows changes in form and size of its components during development. In the zoea stage I, the central pore has an approximate diameter of 1.4 µm which increases to 2.9 µm during the megalopal stage. The plate pits are characterized by three areas: an outer rim, and inner one containing a central pimple or cone. All these components are placed more less on the same flat plane (level with the cuticle) (Fig. 21 a, b). In contrast, during the megalopal stage, the inner area of these plate-pits is concave with a more prominent pimple placed in the center of this cavity (Fig. 21 c, d). They range in diameter approximately from 5.5 µm to 6.3 µm between the two instars.

Both larval and post-larval instars have, within the area of the central pore and four plate-pits, four diminutive pores (0.5 µm approx.); one pair at each side of the central pore (Fig. 21 b, d small arrows). Similar features were observed on C. maenas. Juvenile Brachyura observed possess a conspicous dome in the position of the dorsal organ with elaborate cuticular outgrowths (scales, etc) but pores and plate-pits are not

Table 5. Comparative Dimensions of Dorsal Organ Components among Crustacea: Decapoda Larvae

Species	Zoeal Instar I		Megalopal Instar I	
	CP	P	CP	P
Hyas cornutatus	1.4	5.5	2.9	6.3
Cancer pagurus	2.6	5.5	3.6	5.9
Porcellana longicornis	1.1	4.1	1.6	–
Homarus gammarus		5.4*		6.0** 8.0***

CP = Central pore diameter (μm)

P = Pit diameter (μm)

– = Absent

* = Larval Stage I

** = Post-larval Stage I

*** = Post-larval Stage II

tuberosa zoea stage I, were observed and the plate-pits found to be similar to the two previous species but lack the central pore; instead a prominent square-like area is present (Fig. 22 a, b).

Larval and post-larval instars, and juvenile crabs have a slit-like opening (19 µm long) placed vertically on the dorsal side of the head and posteriorly to the dorsal organ region (Fig. 22 c, d). During the juvenile stage the openings are positioned horizontally with no significant change in dimensions (Fig. 22e). In the case of Dorippe lanata juvenile specimens, these openings are more round in shape than the common slit-like type (Fig. 22f).

Zoea and megalopa stages, in the Brachyura, share another rare dome in the posterior part of the carapace behind the posterior spine bordering as such the first abdominal somite (Fig. 23a). Basically, it consists of two pores surrounded by a number of cuticular irregularities, oustanding and depressed areas, randomly distributed around the pores. They are not observed on juvenile forms (Fig. 23 b, c, d).

Within the Anomura larvae studied, the dorsal organ reveals some features which are specific for this group. For instance, the organ has one (P. longicornis 1.1 µm in diameter), or two central pores (P. platycheles 1.5 µm) and G. strigosa (0.7 µm) (Fig. 24 a, b, d). In the Porcellana species, the plate-pits have the same characteristics observed in the Brachyura zoea I, reaching a maximum diameter of approx. 4.1 µm. No plate-pits were found in G. strigosa. In general, observations of the dorsal organ in this group were very difficult due to the flat nature of the area where the organ is positioned. In the absence of a prominent dome, as in Brachyura and Macrura, the organ was visualized using the integumental marks; one left by the joint of the rostral spine to the head, and the other one adjacent to the first pair of trichoid sensilla on the head region (Fig. 24c). Another specific feature of this group, is that the dorsal organ could not be traced during the first post-larval instar, but in P. longicornis only the central pore was observed (Fig. 24 e,f). Post-larval specimens of the two other species were not available for observations.

In the Macrura studied, H. gammarus and N. norvegicus the dorsal organ is a depressed circular area with no pore and surrounded by the four plate-pits (Fig. 25 a,f). These plate-pits vary in diameter from 5.71 µm in first, 6 um in the second to 8.67 µm in the fourth larval instar, whilst the central area remains a constant size. In both species the dorsal organ is placed on a prominent dome as found in the Brachyura (Fig. 25a arrow).

There is, however, an important change in the morphology of the pits, as in the larvae I they appear as discs with no pegs (Fig. 25b), cones or pimples but by post-larval stage I they are minute pegs numbering 3 or 5 and forming a diminutive pore-plate. These pegs form a row on the medial side of each pit with the lower ones being slightly larger than the upper ones (Fig. 25 c, d). Each pore-plate projects out of the cuticle, bearing two rims containing the inner one a peg. This peg seems to be taper tipped but never reaches the integument. There is one peg per pore-plate.

At the post-larval instar III, the dorsal organ is still present showing no significant change in size dimensions but only four pegs were counted. The pore-plates are not as well defined as observed in the post-larval stage I (IV); the outer rim is not present looking rather abraded, which may indicate a type of degeneration. The pegs can be observed still beneath the inner rim (Fig. 25e).

3.4.1.1 Light Microscopy

Located among the integumental epidermal cells, the dorsal organ dome appears to be formed by two areas: a central one contains a large cell with a highly stained cytoplasm, where only a nucleus is visible placed at one side of the cell. This cell seems to open apically via a central pore (Fig. 26 a, arrow). In longitudinal sections, the dorsal dome occupies a position above the dorsal aorta, and is surrounded by dense cell-pockets laterally (Fig. 26b). There is the central area with an apparent single cell framed by a group of cells, pyramid-shaped with the base in contact with the haemocoel and no signs where the plate-pits are present (Fig. 26c). A continuous band of ordinary epidermal cells can be observed to form the region after the dorsal

dome (Fig. 26d). While under a light microscope the organization of these units cannot be established and only an ultrastructural study could disclose the differences which exist between the two units and their complexity.

3.4.1.2 Ultrastructural Morphology:TEM Observations

Even at low magnifications, the dorsal dome can be seen to consist of between four and six epidermal cells investing a central glandular unit which contains three cells: one secretory, one canal or ductule cell and two supporting cells; in addition to the eight sensory cells enclosed within the plate-pits (Fig. 27).

The Secretory Cell:

The single secretory cell is pear-like in shape with the base resting on the basement membrane and reaching the cuticle via a duct or canal which constitutes the central pore of the organ (Fig. 27). The most conspicuous characteristic of the gland cell is a highly increased basal cell surface, and a broad microvillous apex (Fig. 28 a, b). The secretory cell is connected to the two supporting cells by septate-type junctions. In the basal cell membrane there are arborescent

invaginations of extracellular spaces forming a continuous labyrinth (10-12 µm wide) (Fig. 28 b). The cell is separated from the haemocoel by a loose extracellular basement membrane joined by a few hemidesmosomes.

The cell has a large nucleus 6.5 µm in diameter with dense clumps of chromatin adjacent to the nuclear membrane, and has a lobed surface which is less prominent in older specimens. The free ribosomes and the granular endoplasmatic reticulum (ERG) are few; the Golgi complexes are more abundant and placed towards the outer side of the cell. The mitochondria are large-sized and very abundant around the nucleus and microvillous apex. The cytoplasm lacks secretory granules which are neither electron-lucid nor fibrillar-type.

The central side of the cell is lined by microvilli closely adhering to each other and protruding randomly with a rather bulbous appearance, which form the reservoir or storage chamber (Fig. 28c) enclosing a central lumen (Fig. 28 d, e). Each microvillus seems invested with a dense glycocalyx and there are fine filaments running parallel with the axis of the microvillus (Fig. 28 c, f triangles). In this case the secretory products are not clearly recognized in the

electron micrographs. There are, however, numerous electron lucid and coated vesicles observed at the base of the microvillous border besides, with affixed microtubules.

Ductule Cell

This cell possess a long (2.3 µm), cuticular canal or ductule (Fig. 29 a, b) which penetrates the center to reach the reservoir area. According to Sreng (1979) the ductule can be described as: 'canalicule recepteur' for the part within the reservoir, and 'canalicule conducteur' for the part leading from the reservoir to the cuticular surface (Fig. 29 a, b). The structure of the ductule, consists of two distinct areas: a thin outer layer, which is electron dense and limits the cavity, and a thicker fibrillar inner layer. The latter has fibrils which show a slightly curved orientation (cross sections) and they may represent epicuticular filaments (Fig. 30). The cuticular structure of the receptor canaliculus varies according to position. For instance, immediately inside the reservoir (Fig. 30a) the outer epicuticle, is intercepted by radially distributed microvilli, and the inner epicuticle both end and fibrillar projections become less defined (Fig. 28d). There the calibre of the canaliculus reduces in diameter to 0.35 µm in

contrast to 0.95 μm at the cuticle level. The ductule becomes more cylindrical (Fig. 30 b, c, d) towards the cuticle level; once the cuticle is reached (Fig. 30 e, f), the electron dense outer lamellae present around the ductule until that level are not observed.

In the Brachyura: H. cornutatus, the gland cell revealed the presence of membrane boundaries (Fig. 31 a, b) with desmosome-like junctions (Fig. 31 c, d), indicating the possible presence of more than one secretory cell, but their nuclei were not found in more proximal section. These membrane boundaries resemble greatly the ones present on the scent scale organ of the Lepidoptera: Caligo eurilochus brasiliensis, and characterized as secretory niches (Wasserthal and Wasserthal, 1977). In this case, however, there is very little space between the membranes to be considered a secretory niche. These membrane boundaries were not observed in older animals, such as zoeal stage IV (cf. Fig. 29 a, b). In general, during early larval stages, the cell gland microvilli are arranged in well define strip-like aggregations. This feature was not observed in later stages. Consequently, this characteristic might indicate an initial change in cellular organization.

Supporting Cells:

These are two cells surrounding the glandular cell and having a particular columnar form. They are linked on one side to the cuticle and, on the other, to a flattened epidermal cell which can be located on the external side of the gland. Besides mitochondria, the cytoplasm also contains numerous microtubules which cross the cell over the entire distance of its vertical range (Fig. 27; 31a).

Plate-Pits: Sensory Apparatus, Dendritic Sheath and Enveloping Cells.

Each of the four plate-pits on the dorsal dome has a sensory cuticle formed by two zones: an inner one highly electron dense, granular with filaments or tubules and approximately 3.5 µm in diameter and an outer one which encircles the above mentioned, also granular but less electron dense approximately 1.5 µm in diameter. Through longitudinal sections it can be observed that there are four dendritic endings centrally placed within the electron dense matrix (Fig. 32a). This material is not present beneath the cuticle and it may represent the cap formed by extracellular material surrounding the top of the sensory cilia (Fig. 32b).

Each of the plate-pits examined in serial sections was innervated by two bicilіary sensory cells. Two dendrites from each cell extend into the dendritic channel with no apparent branching, and terminate beneath the pit pimple or cone lining by the dense matrix (Fig. 32 c). The distal dendritic segments are irregular in cross section distally (Fig. 32 d, e, f) but they become more uniformly cylindrical and thicker nearer the ciliary apparatus, where they develop a 9x2+2 or 9x2+4 microtubule arrangement (Fig. 33a). Just before this segment inserts into the larger proximal one it becomes embedded in a ring of dense material (Fig. 33b). At the proximal segment one microtubule of each doublet acquires a dense core and projecting arms (Fig. 33 b,c) with a 9x3+0 microtubule configuration. Both basal bodies are placed in the same plane. From each basal body a single rootlet extends up to 1.6 μm proximally, well developed, and showing banding with a diameter of 0.13 μm (Fig. 33 d,e,f). There are mitochondria, microtubules and coated vesicles alongside the terminal part of the proximal dendrite. Proximally the ciliary root becomes surrounded by a palisade of microtubules describing a well developed desmosome junction between the two inner sheath cells and the proximal segments of the dendrites (Fig. 33 a, b, c, d).

A dendritic sheath encloses the sensory cell along the distal segment of the dendrites. This dendritic sheath is in general very thin, becoming even less distally, where it looks like compartmentalized (Fig. 32f). The receptor lymph cavity extends proximally far between the inner dendritic segments and is delimited by the inner sheath cell (Fig. 33a). A series of sheath cells enclose the dendrites, the inner most does not overlap and is cylindrical in nature, shared by the two dendrites and envelops not only the outer but the inner dendritic segments as well. It encloses a small ciliary sinus with a relatively electron-lucent liquor. Two intermediate sheath cells surround the inner one and these in turn are bounded by one large sheath cell (Fig. 33 c, e) which is infolded and whorled. The intermediate and inner cells in the basal region are characterized by the presence of sparse granular endoplasmatic reticulum (GER), rounded mitochondria, vesicles and randomly distributed microtubules. Desmosomes and septate junctions are well developed, lack elaborate cytoskeletal elements, such as microvillate or filament bundles (Fig. 34a). More proximally axon, bundles and associated wrapping glial cells can be observed limiting the secretory cell basal invaginations (Fig. 34 c, d, e).

As was pointed out before, the general topography of these plate-pits varies greatly when the animal moults to the first post-larval stage (SEM observations). In the distal end there are six dendritic endings per nerve cell; consequently an additional sensory cell is present at this stage. The dendritic sinus changes in shape and diameter according to position. Distally the six dendrites are arranged in a line (Fig. 35 a, b); surrounded by a thick dendritic sheath which is well developed, electron dense and continuous. Two more enveloping cells are observed, neurotubules are abundant, longitudinally orientated and randomly distributed, and coated vesicles (Fig. 35 c, d). These two elements were less numerous in the zoea stage I plate-pits. The dendritic canal becomes more cylindrical close to the ciliary end, and microtubule doublets appear at this level, while in the distal end one, two or three microtubules are present per ending (Fig. 35 e, f). At this level an interesting feature is observed thus four dendritic filaments are placed at the center, leaving the other two filaments aside. The last two filaments become involved by the thick dendritic sheath individually (Fig. 35 d, e). This unexpected change in dendrites dimensions seems to indicate the presence of two bipolar sensory cells. Longitudinal sections of the proximal

segment reveal the presence of dense ciliary roots (Fig. 36 a, b). In a moulting animal it can be observed that the distal dendritic filaments end beneath the plate-pit pimple or cone; the outer sheath cell limits the whole sensory structure. The distinctive cuticular regions forming the plate-pits and the thick nature of the cuticle itself (Fig. 36c) could also be observed. These electron micrographs seem to indicate that the plate-pit matrix constitutes part of the sensillar sinus (Fig. 36 a, d).

Transitional Secretory Products of the Gland Cell in the pre-zoea stage

Examinations of C. maenas pre-zoea specimens indicated the presence of secretory droplets absent in the gland cell in later stages. On the basis of their appearance the secretion droplets in this cell can be roughly categorized into two groups: the first type are opaque droplets bound by a single membrane and their content consists of an amorphous matrix, usually measuring up to 3.6 µm (Fig. 37a). The second type are smaller, appproximately 1.6 µm in diameter, containing a dense amorphous matrix embedded in small aggregates of vesicles (Fig. 37 a, b). Both types are distributed towards the apical side of the cell, and might represent

lipid droplets. The supranuclear cytoplasm is equipped with moderately dilated cisternae of rough ER which extend up to the apical membrane. Golgi complexes are numerous and have a very elaborate organization with a prominent internum (Fig. 37 a, c, d). This maximal development of the Golgi complex has been associated with the high activity of intracellular digestion in zymogenic cells and engaged in the active synthesis of some secretory protein in Pogonophora integument (Gupta and Little, 1970). Due to fixation limitations it was not possible to observe the secretory granules at the end of the Golgi stalks. The cell nucleus is large with prominent nucleoli which occupy a basal position. The cytoplasm is interspersed with Golgi dictyosomes which are also large, in groups of 4 or 5 and composed of 15-20 fenestrated saccules (Fig. 37d). They are associated with a rich population of vesicles. Round mitochondria are also abundant around the nucleus and at the apical end of the cell.

By comparing a number of electron micrographs from different specimens, the centrally placed microvilli with the secretory lumen and ductule were not observed at the pre-zoeae stage. This absence leaves open the question of how the secretion droplets are released; exocytosis into the subcuticular space might be an alternative,

helped through the cuticular pores which are known to be present. Other cytoplasmic components not present at this stage are the basal membrane invaginations which are an important cell feature of later stages. The opaque secretion droplets in ordinary epidermal cells, which apparently arise in the Golgi regions, are related to fibrous or collagenous components of the cuticle (Gupta and Little, 1970). These opaque secretion droplets were also observed in the advanced embryos of this species whose cuticle has an incipient development. The sensory apparatus of the plate-pits seems to contain roughly the same components present in the larvae (Fig. 37 e,f). One distinctive feature is the presence of a well developed dendritic sheath.

3.4.2 On the Occurrence of the Dorsal Organ in the embryos of C. maenas

Observations were made on the growth of embryos in order to establish the presence of the dorsal organ. Owing to the minute size of the embryos of this species much difficulty has been experienced in making accurate observations on their structure through light microscopy.

Egg size was found to vary according to the stage of development and ranged from 0.4 mm up to 0.98 mm. The eggs were yellow in colour and contained a large number of oil droplets. The development can be summarized into the following seven stages: 1) Early cleavage stages, prior to the formation of the germinal disc. All cells are pigmented. 2) Development of the germinal disc. 3) Formation of the caudal furrow and appearance of appendage rudiments (mouth parts). 4) Segmentation and setation of the appendages, and occurrence of the dorsal organ (strip of less coloured cells on the head region), stages IX-X (Scheidegger, 1976). 5) Appearance of red pigment in the eye region; heart, limb, and gut movements; chromatophores on the urosome. 6) Development of the posterior spine, as a tube with projecting central spine. 7) Egg hatching, emergence and moulting of the pre-zoea.

Information on the dorsal organ using whole embryos was difficult to obtain despite the fixation and staining methods employed. The cells of the dorsal organ were unrecognizable from those of the adjacent blastoderm by their size or differential staining nature. However, their position and arrangement were important features while tracing the organ. The light microscope study

reveals the organ (Fig. 38 a, b) as a thickening of enlarged blastodermic cells which never were observed to intrude into the underlying yolk (Fig. 38 c arrow). This sac contains approximatelly ten cells, with two slightly different cells placed centrally: the first one characterized by a large nucleus neighboured by another one whose nucleus was smaller (Fig. 38 a, b arrow). The organ was never found as "invaginated cells with narrow necks which become transversally striate" (Anderson, 1970), or as mushroom-shaped outgrowths (Tiegs, 1940).

The present observations indicate that the dorsal organ develops more as a cup-like group of ectoderm cells in front of the brain as found by Shiino (1950) in Panulirus japonicus. The organ lacks the elaborated and long filamentous outgrowths extending from the component cells as observed by Tiegs (1940) in collembolan insect embryos. In advanced embryos, the clump of cells is slightly in the same position but the cells are less in number, without signs of disruption, vacuolization, or becoming enclosed within the developing mid-gut (Fig. 38c). These observations are very significant considering that the majority of early embryological reports ascribe to the organ a degenerative character in mature or ready to hatch embryos.

The first SEM observations of the organ were obtained from embryos of C. maenas, stage IX-X according to Scheidegger (1976) (Fig. 39 b, d). The four plate-pits are minute with a diameter of 0.64 µm containing the central cone. There is a constriction in the area corresponding to the central pore but the open surface was not observed (Fig. 39 a, c). The fine structure study indicates the presence of the secretory cell with the typical pear-like shape having a basal polyploid nucleus surrounded by numerous clear vesicles, rough endoplasmic reticulum, and glycogen-type granules. Round and dense secretion droplets are present, limiting the nuclear area (Fig. 40 a, b). In the apical side of the cell, clusters of microvilli tend to converge at one point without describing a definitive structure as the reservoir of the cell.

The sensory apparatus of the plate-pits reveals, in stage IX-X embryos, the same structural elements found in the larval forms. There are two biciliary sensory cells per plate-pit (Fig. 40c). The dendrite sinus extends further, the basal body region. Rootlets are 3.1 µm long, well developed and banded, enclosing proximally numerous microtubules and round mitochondria. The cell body contains large mitochondria, rough endoplasmic

reticulum, glycogen-type granules and clear vesicles (Fig. 40 d,e,f). The dendritic sheath is continuous until the rootlet system where it becomes less uniform. Four enveloping cells are found bearing incipient desmosome-like junctions. At this stage, the granular and electron dense matrix lining the dendritic ends was not observed due to the lack of a three-layered cuticle. This fact might indicate their linked formation.

3.5 On the Embryonic and Pre-Hatchling Setae of C. maenas

While studying the development and occurrence of the dorsal organ in the embryos of C. maenas, attention was given to the embryonic setae and their origins. In general, setae buds are present as early as stages III-IV (Scheidegger, 1976).

For instance, on the telson margin, six setae buds, conical cuticular outgrowths with no socket, appeared at stage III which are replaced by long plumose setae at stage X. Both oral appendages, antennules and antennae, are the next to display these thick setae buds. At stage X plumose and acuminate setae are present on all mouth parts. Each seta is enclosed by a transparent cuticular (Fig. 41 discontinuous line) capsule whose apex is

surrounded by a second crenulate membrane (Fig. 41 dotted area). This whole unit projects itself into a second cavity of the same constitution as the first one bearing setule-like extentions distally. This set of membranes is shed after hatching to the zoea instar but still is present at the pre-zoea. The fine structure reveals that this transparent capsule is composed of a flocculent content which is fibrillar and granular. No typical cytoplasmatic components were found. On the contrary, the apparent undeveloped setae show a completly differentiated sensory apparatus, dendritic sheath and enveloping cells.

A brief survey of the embryo posterior spine and some mouth parts (antennules, antennae, and maxillipeds), with particular reference to the setae ultrastructure, is given below.

Posterior Spine

In stage X embryos, the posterior spine has a length of 95 µm, folded anteriorly towards the head region (Fig. 42a). SEM observations indicate the presence of tuft hairs randomly distributed along the whole spine surface (Fig. 42b) which tend to concentrate at the spine apex. The light microscopy study reveals two

areas: an inner one which constitutes the spine main body with an extracellular space between it and the outer area. The latter is formed by ectodermal cells (Fig. 38 b, arrow).

The fine structure of the inner region discloses a "sensory core" of numerous single bipolar sensory cells (Fig. 42 c, d), each with a thick and well developed dendritic sheath and a 9x2+0 microtubule arrangement in the ciliary region; four or five microtubules are present at the dendritic distal end and four sheath cells enclose the structure. The outer sheath cell contains abundant round mitochondria and scattered microtubules. Desmosomes and septate juntions are less conspicuous (Fig. 42 e, f).

The Antennules

This appendage is observed at stage V to consist of a small segment beneath and aside the optic lobe. At stage X, the appendage extends as a rudimentary stump and carries five or six flat and long setae at its distal end. Of the five setae (Fig. 43a) examined by transmission electron microscopy, 2 were innervated by approximately nineteen, 1 by nine, 1 by three and 1 by one sensory cell (s) respectively (Fig. 43b). The last

two sensory cells have a 9x2+0 microtubule arrangement in the ciliary segment and a scolopale-like matrix in the proximal segment (Fig. 43 b, c). They also have four sheath cells with typical cytoplasmic components. Gurney (1939) refered as a common feature on the Decapoda larvae stage I to have five antennular setae classified as: two long seta, a short slender seta and two aesthetacs. According to the fine structure information available there were found three potential aesthetasc hairs with multi-innervating sensory cells (Fig. 43 d, e, f).

The Antennae

This biramous appendage is characterized by a long branch, the exopodite, with two long and flat setae at its distal end, and a short segmented process, the endopodite, which forms the flagellum (Fig. 41). The spinous process was not traced. No TEM information on these hairs was obtained.

The Maxillipeds

The first and second maxillipeds are armed with four long and equal length setae (Fig. 41a). Four of these hairs were examined in cross section by TEM. Two were innervated by one sensory cell with branching cilia; and

two by two bipolar sensory neurons (Fig. 44 a, b, c). Both types have a thin dendritic sheath, but not compartmentalized, and four accessory cells. The inner one encloses a small ciliary sinus with a relatively electron lucent-liquor. The last and the intermediate cells are rich in microtubules, clear and coated vesicles. The outer ones contain round mitochondria, free ribosomes, smooth endoplasmic reticulum and glycogen type granules. Desmosomes are particularly well developed in setae type (b) in the proximal segment. Both setae lack microvillate extensions when in contact with the sensillar sinus, and therefore membranes are infolded (Fig. 44 b, c, d). The dendritic ends can be observed in the distal region with the ciliary filaments and the enveloping cells (Fig. 44 e triangles). More distally the sensilla lumen lacks the ciliary filaments (Fig. 44 f, triangles).

3.6 Dorsal Organ Role in the Decapoda larvae: Preliminary Study

The influence of particular organs on the behaviour and life of animals has been determined by many methods but especially by simple ablation experiments. Amongst Crustacea the removal of organs such as eyestalks (Costlow, 1963, 1966; Little, 1963; Skinner, 1983; Fired

et al., 1983) have revealed their importance as carrying organs responsible for growth and development. In some other arthropods, for instance, amputation of fly legs revealed the presence of a gravity receptor system (Horn, 1982); or depilation of setal blades in aquatic mites determined their essential role for swimming (Barr and Smith, 1979). In this context several experiments were designed in order to provide some information on the potential function of the dorsal organ.

Glue-blockage of the organ in Macropipus depurator zoea IV and megalopa I after two weeks observation period, indicated a 80% rate of survival and moulting in the experimental and control animals. There was not a significant change in body appearance, colour and general shape, as a result of dorsal organ blockage. Apolysis was slightly advanced and consequently their moulting time was brought forward (2 days) in the experimental animals. The animal body/volume ratio was careful observed following the Slifer (1938) suggestion of the organ in the insect embryo as being involved in some water regulation mechanism during moulting.

There was, however, one aspect of the physiology of both zoea and megalopa, which might be caused or associated with the organ blockage. Body and appendage chromatophores change in shape and in the predominant type of associated pigments in the experimental group. It is difficult to link the origin of these differences to the organ itself, knowing their intricate nature depending on light and hormone contents. The present results show that in the experimental group within the above mentioned observation period, the star-shaped chromatophores placed on the carapace laterally changed in shape considerably to a dot-like configuration (Fig. 45 a, b arrow). This agglutination of the black pigment to just a dot enhanced the presence of the red chromatophores, which at this stage are not well developed. Similar pattern was observed on the carpus of the first pair of maxillipeds. In animals which had no glue on them, during advanced ecdysis stages the same chromatophores tended to become more concentrated but never aggregated as a dot as observed in the experimental animals (Fig. 45 c, d).

Similar chromatophore behaviour was observed on the megalopa instars of treated animals; in this case special attention was given to the tip head and eyestalk chromatophores (Fig. 46 a exp; b control animals). These results do not indicate whether the blockage of the dorsal organ brings about the above mentioned changes in chromatophore organization and associated pigments, but they may suggest that certain activity, either excretory or absorptive, has been halted, producing a temporary imbalance in the animal's body, which may be reflected in the way these pigmented cells reacted. Animals were kept under the same light regime and type during the observation period, and photographed at the same time and, under identical equipment conditions.

Figure 1. Body peg sensilla. a-b, Peg I, short articulated peg with asymmetrical rim on body plates, Hyperia galba; c, Peg II, group of pegs placed on a groove on epimeral body plates, Ampellisca typica; d, Peg III, squamous short peg on the body plates, Ampellica typica; e-f, Peg IV, single and double body pegs with knob at the hair rim and surrounded by minute cuticular projections, Haustorius spp; g, Peg VI, short peg with ventrally positioned pore and squamous dorsal side, Idothea pelagica; f, Peg V, short peg with ventral, and sub-apical pore, Eurydice pulchra.

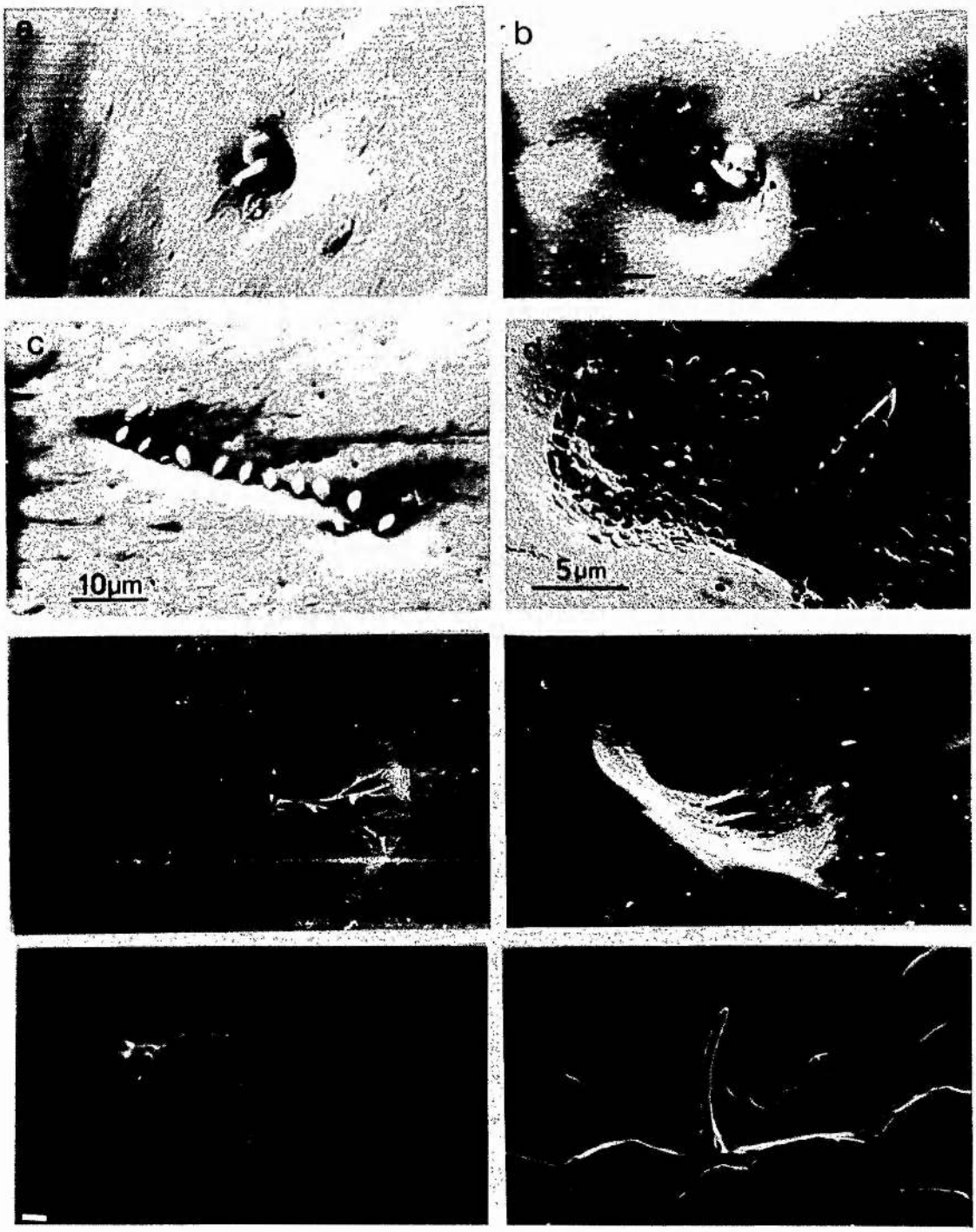
a
b
c
10µm
5µm

Figure 2. Conical sensilla on periopods of Eurydice pulchra. a, General view of the fifth periopod and rows of associated conical sensilla; b, shows the conical spine apex and the sub-apical positioned setule; c, close-up of the setule tip with ventrally positioned pore; d, position of the conical spine in the second gnathopod and body pegs (arrows).


a
100 µm
b
c
d

Figure 3. Conical sensilla on pereiopod segments of Haustorius spp. a, General position of two types of sensilla on the outer margin of the merus-carpus, and carpus-propus; b, c, d, show the blunt sensilla tip with accessory squamous setule and modified concave terminal side.

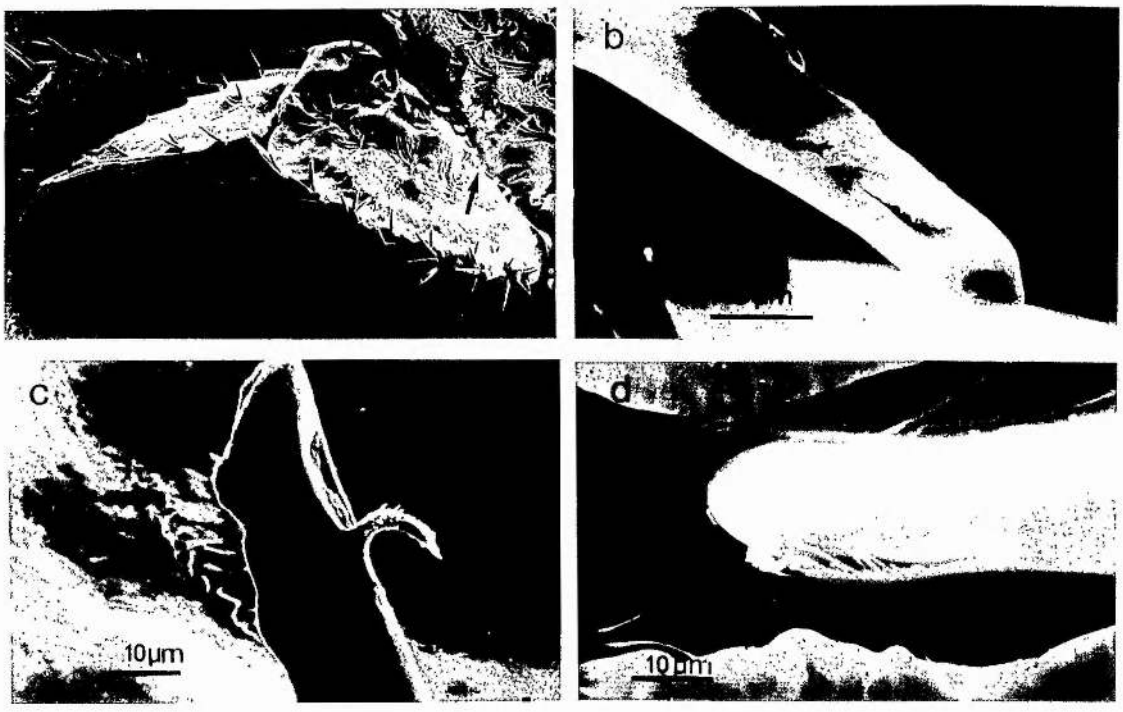
b
c
10μm
d
10μm

Figure 4. Conical sensilla on periopods of Haustorius spp. a, Tapered tip conical sensilla with and squamous setule placed at its middle length, on the inner margins of uropods 1 and 2; b, Blunted tip, robust and dorsally squamous sensilla limiting the inner margin of the carpus on periopods 5 to 7.

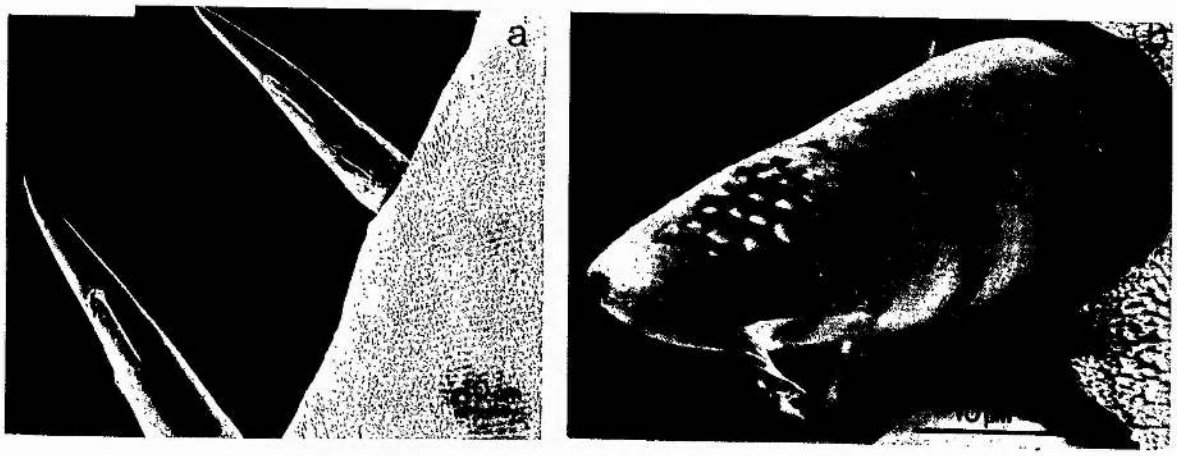
a

Figure 5. Conical sensilla with split tips of Idothea pelagica. a, Close-up of the conical sensillum with the accessory setule and ventrally positioned pore (scale bar: 5 μm). b, Position of the conical spine on the inner margin of the carpus on gnathopods 1 and 2 (scale bar: 100 μm). c, Close-up of accessory squamous setule with ventrally positioned pore (scale bar: 1 μm). d, Position of the conical sensilla with sub-terminal setule on periopods 5 to 7 (scale bar: 10 μm).

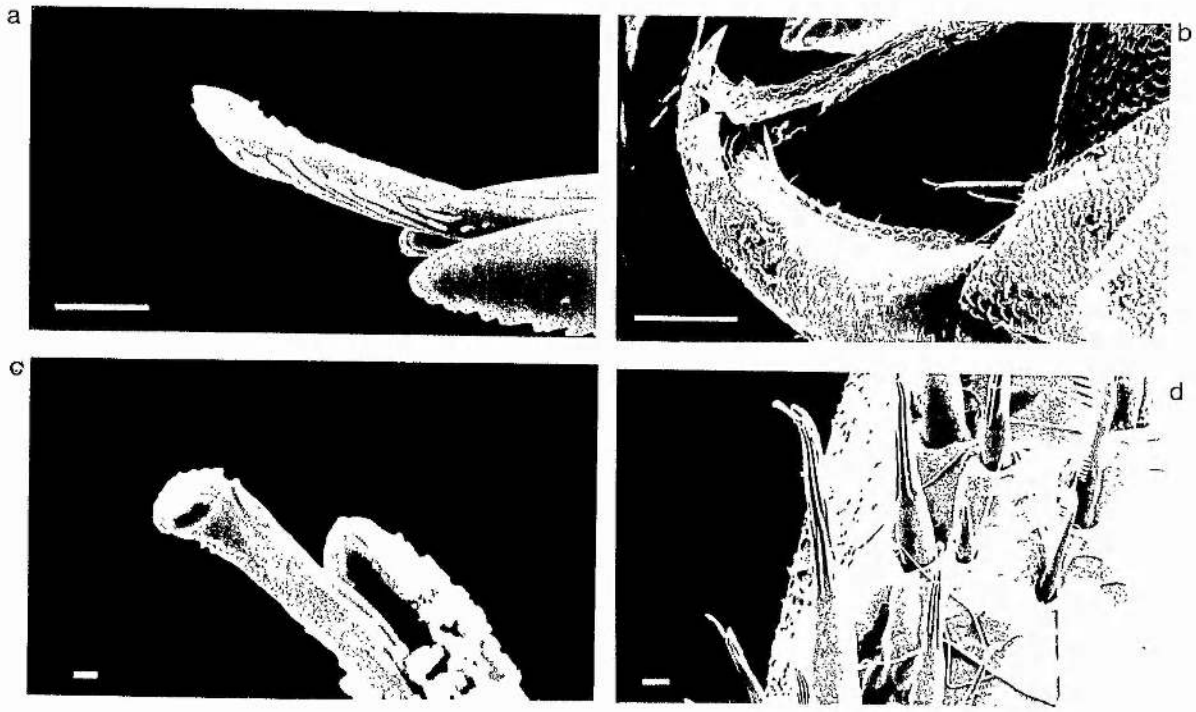
a
b
c
d

Figure 6. Aesthetasc hairs on the second antennae of the adult male Diastylis cornuta. a, Rows of eight aesthetasc hairs per annulus. b-c, Close-up of the aesthetasc tips showing the divided ends and the terminal pore (arrows). d, Aesthetasc hairs basal article (arrow).

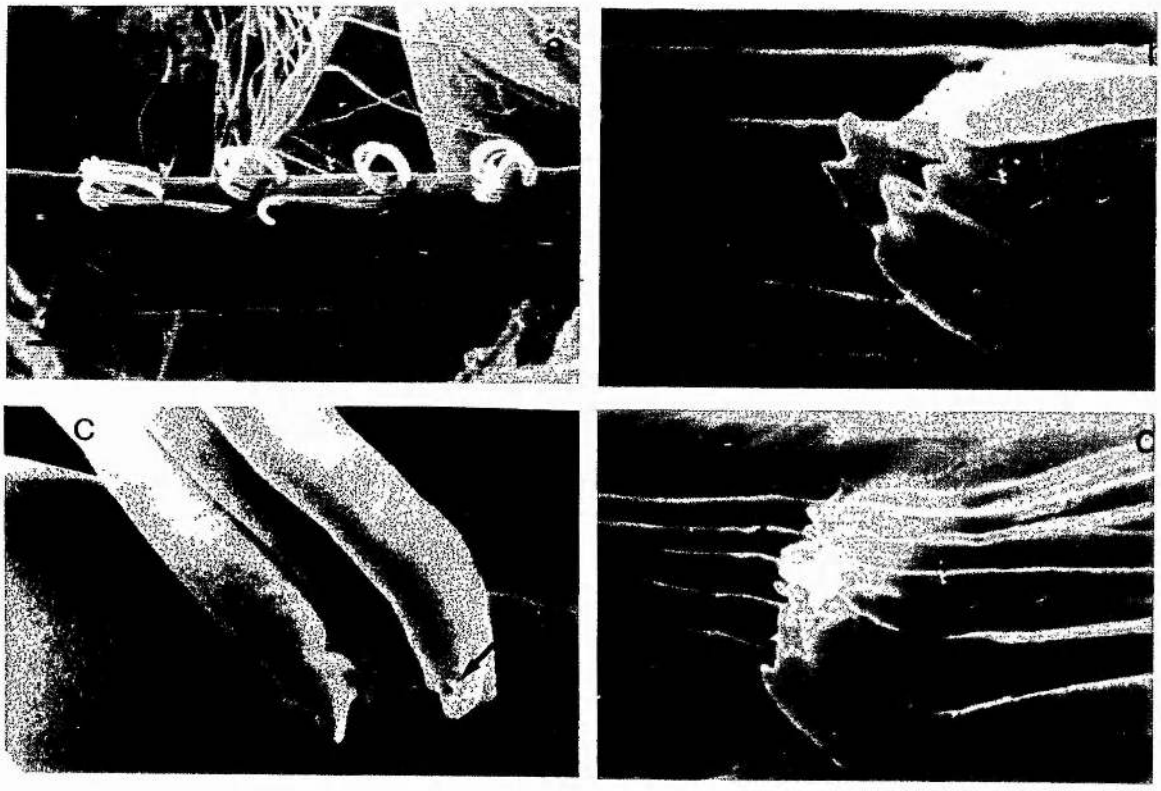
C
C

Figure 7. Uncharacterized body cuticular outgrowths of *Diastylis cornuta*. a, Pit I corresponds to blunt-like structures with central membrane folding. b, Distribution of the Pit I outgrowth describing rows on the anterior head lobes (arrows). c, Pit II, type of outgrowth less bulbous than the last type but more abundant on the head region. d, Pit III Similar type of outgrowth with central ridge on the dorsal carapace of the juvenile *Cancer pagurus*.

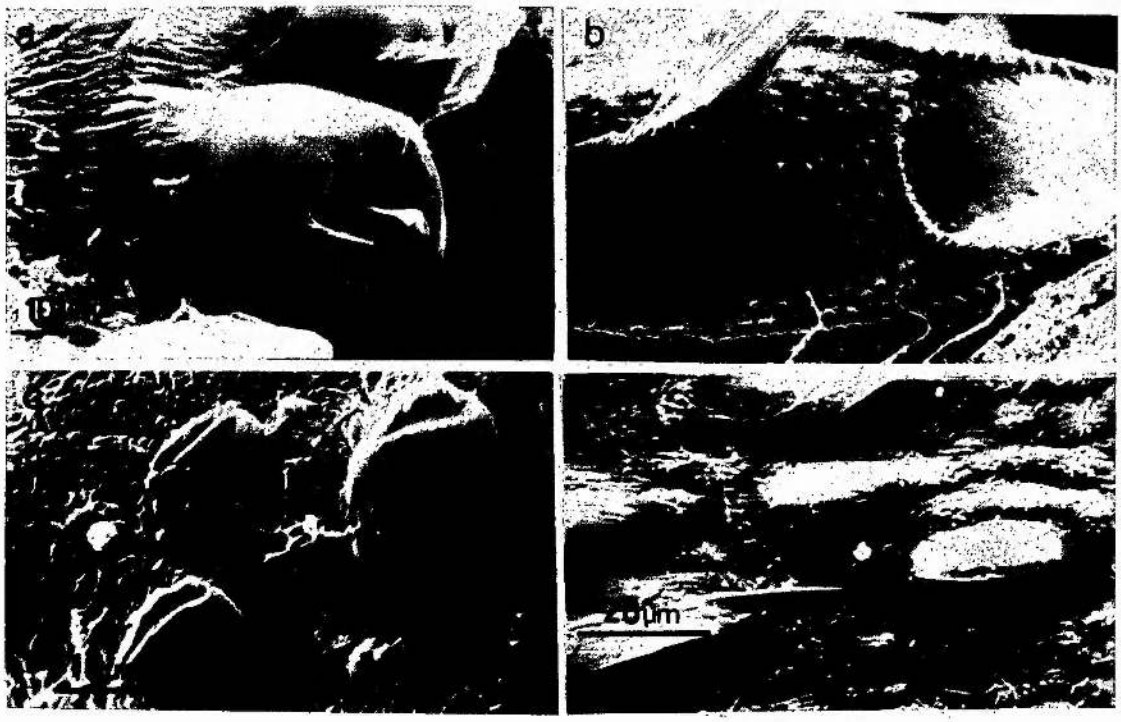
a
b
20μm

Figure 8. Scale plate-like outgrowths of the female Pseudione Hyndmani. a-b, Close-up of the rosette-like structures bearing numerous scale extentions and brush-like tips. c-d, General view of the rosettes on the dorsal side of the oostegite (arrows).

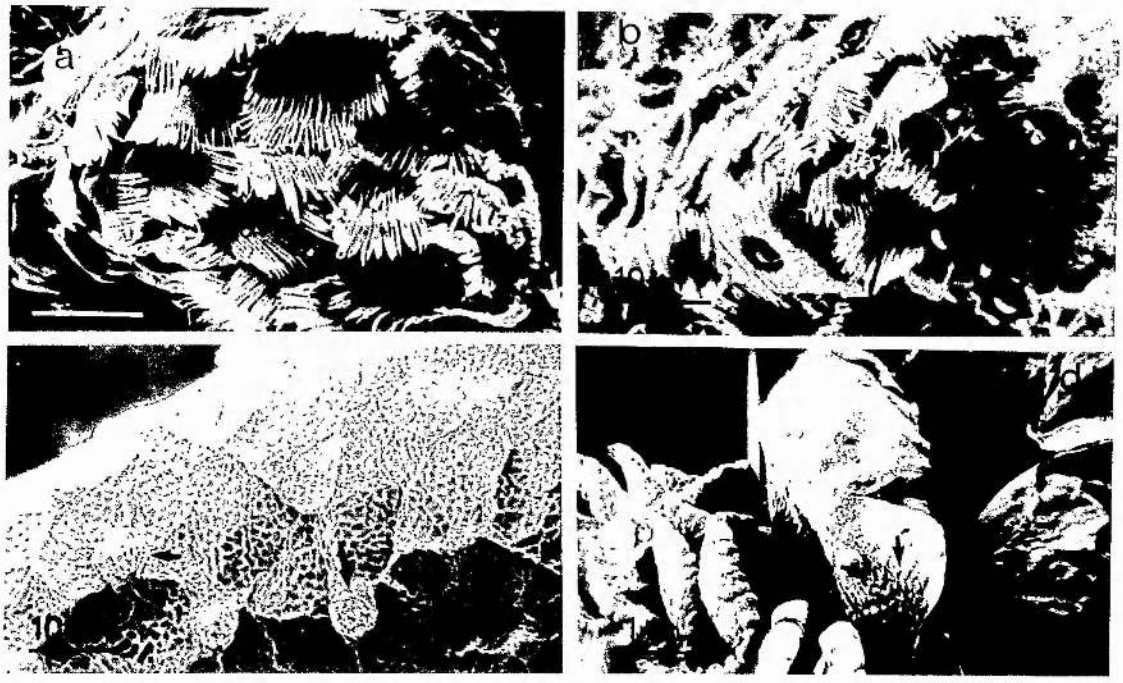
a
b
c
d

Figure 9. Flower-shaped cuticular outgrowth of the juvenile Dorippe lanata. a-b-d-, Pit IV, close-up showing their base, the abundant cuticular projections clustered towards their distal side, and the apparent central opening. c, General distributional pattern of Pit IV on the dorsal carapace (arrows).

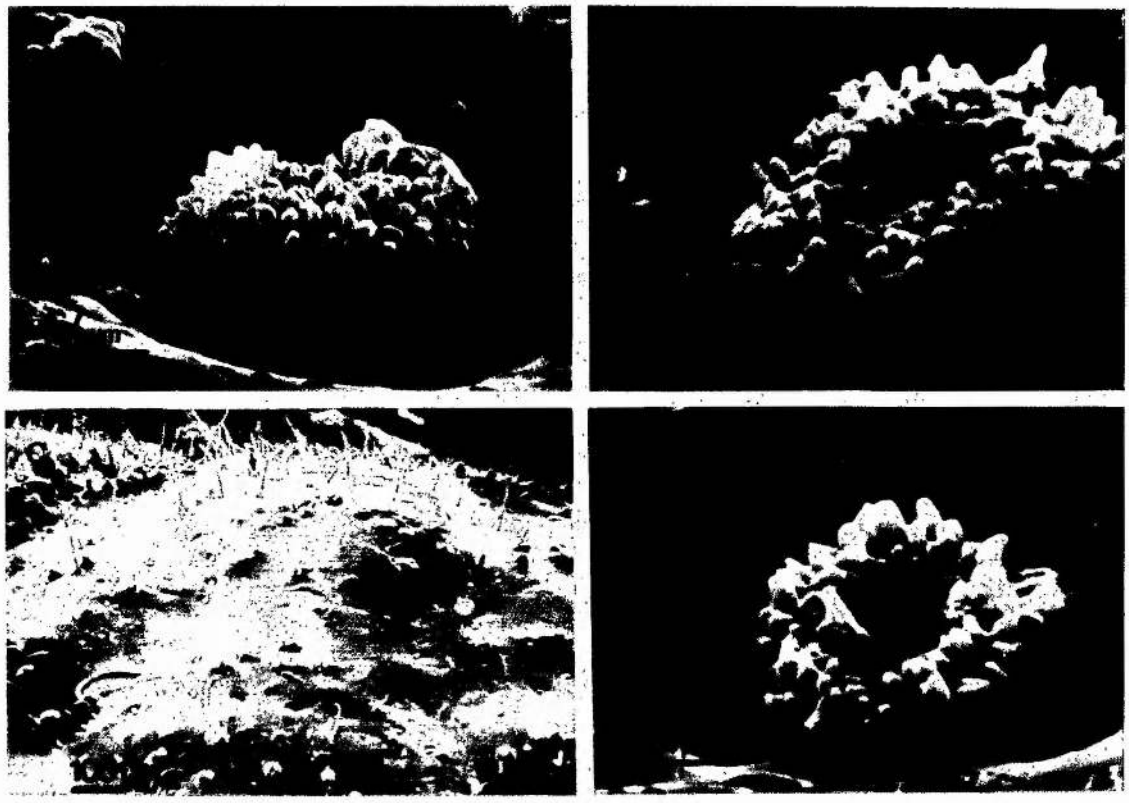

Figure 10. Out/ingrown structures of Monstrilla longiremis. a, Pit V, prominent domes with infolding membranes. b, Pit VI, ingrown structure formed by four cuticular strip-like extentions. Both types are present on the anterior lateral sides of the head region. c-f, General view of Pit VII, bell shape domes (thick arrows). d, shows the outgrowth outer rim. e, Close-up of Pit VIII and tuft hair-like projections on thoracomere IV.

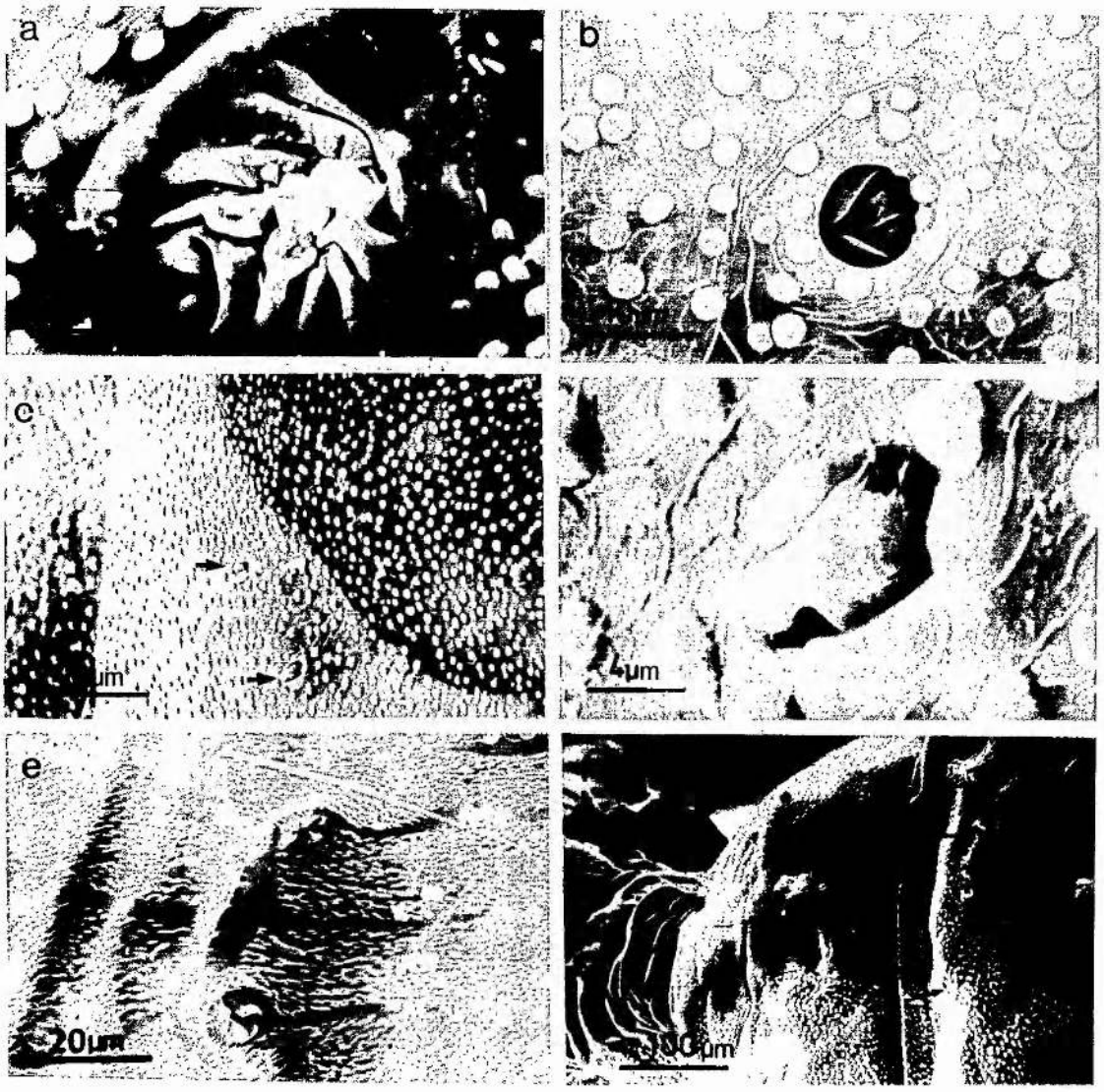
a
b
c
4μm
e
20μm

Figure 11. Trichoid sensillum on the urosome of Hyas coarctatus. a, Position of trichoid sensilla on the urosome segments (arrows) and prominent outgrowths on the lateral knobs (triangles) zoeal stageaI. b, Distributional pattern of trichoid sensilla (arrows) and absence of lateral knobs and associated outgrowths in the megalopal stage I.

Figure 12 I. Trichoid sensilla distribution on Homarus gammarus. a, General view of the anchor-type telson with rows of trichoid hairs (triangle) and long feathered hairs 8 arrows). b, Double and single rows of sensilla. c, Trichoid sensillum distribution of urosome segments on the dorsal (thick arrow and triangle), and lateral horns (thin arrow) in zoeal stage I. d, Number and distributional pattern of trichoid sensilla on the urosome and telson during post-larval stage II.


1mm
b
200um
d

Figure 12 II. Schematic representation of trichoid sensilla distribution on the urosome of Homarus gammarus. a-b-c, Dorsal and lateral position of the sensilla in the larval stage I. d, Trichoid sensilla distributional pattern in the post- larval stage II.

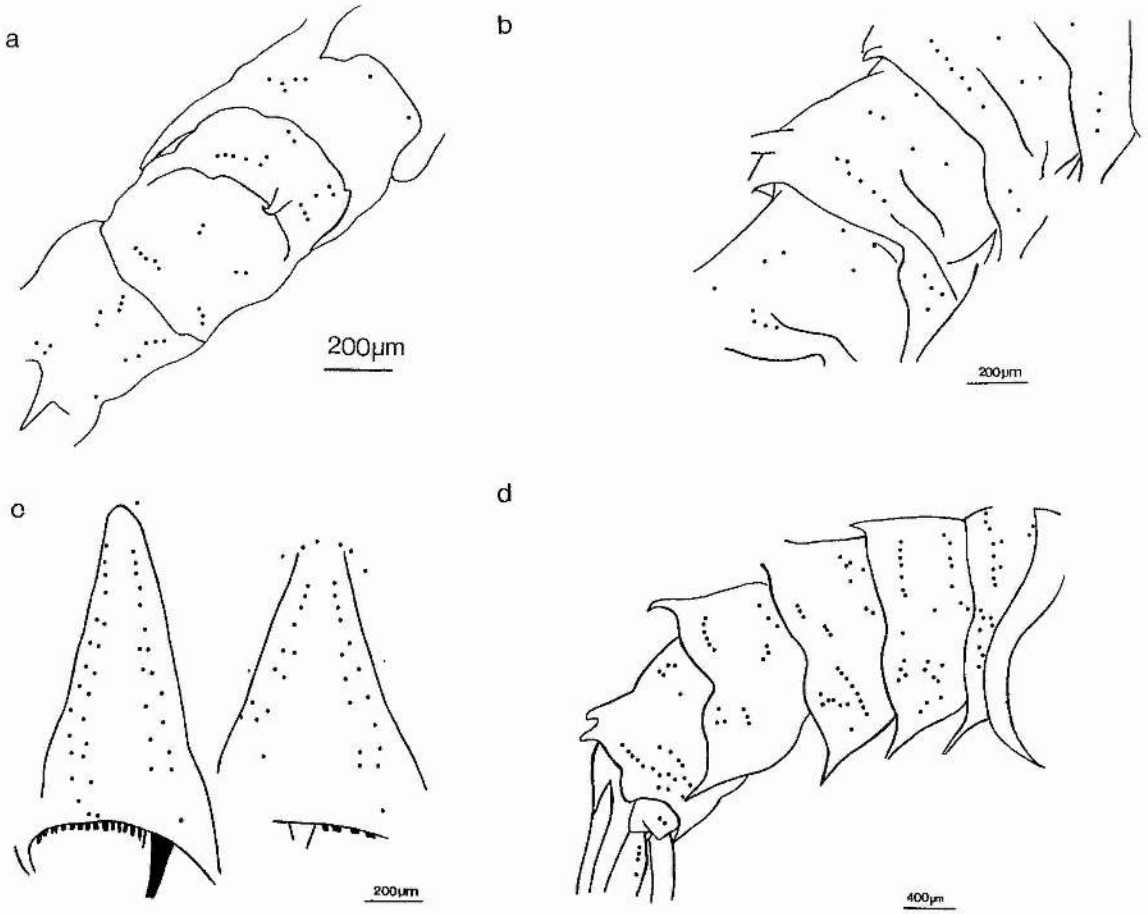
a
200µm
b
200µm
c
200µm
d
400µm

Figure 13. Schematic representation of trichoid sensilla distribution on the urosome of Porcellana longicornis during larval stages (I, II, III).

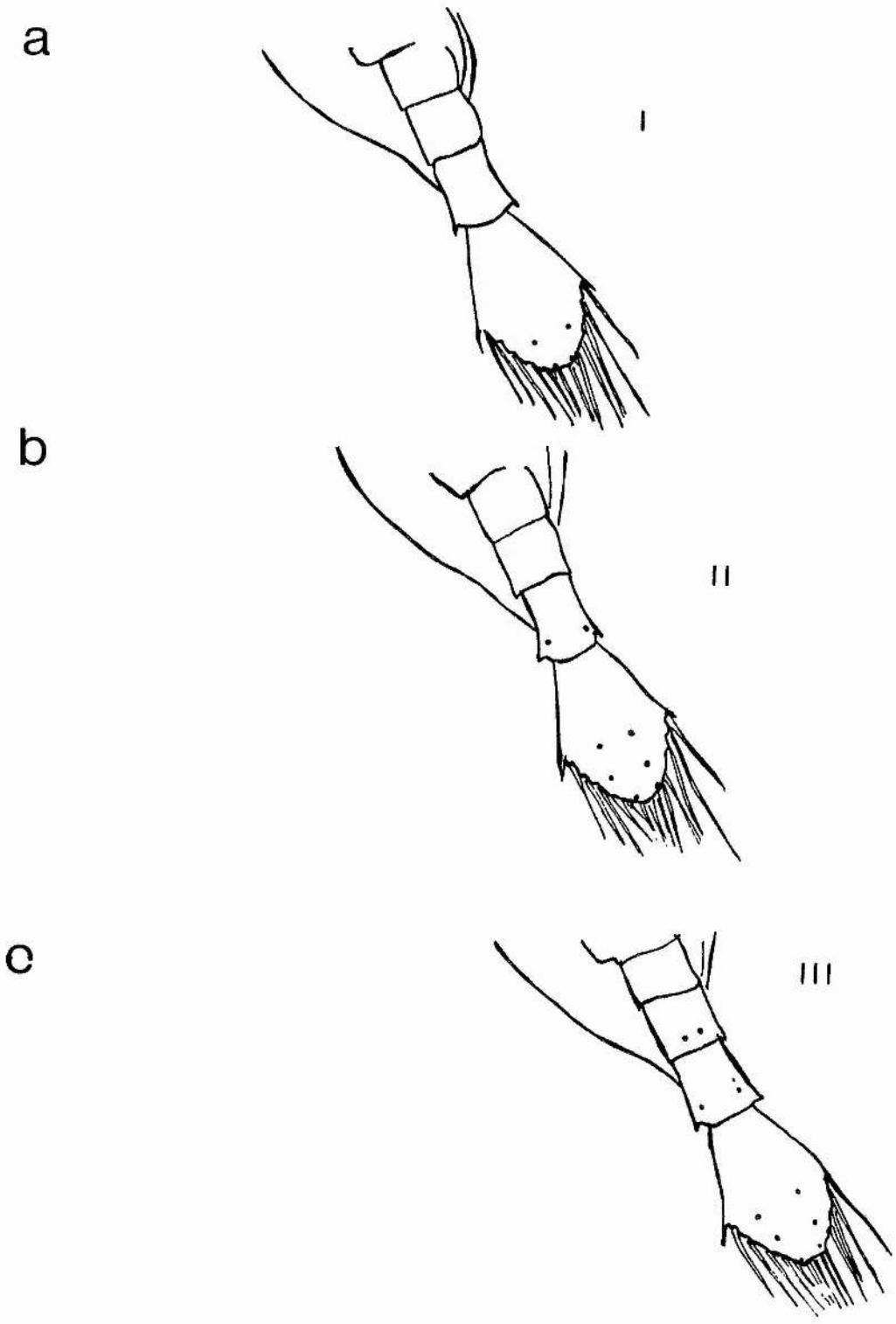
a
I
b
II
c
III

Figure 14. Cuticular outgrowths on the rostral spine of Porcellana longicornis. a, unrimmed scale-like projections bounded by minute pores. b, Scale base and protuding rim (insert). c, General view of the rostral spine and associated outgrowths.

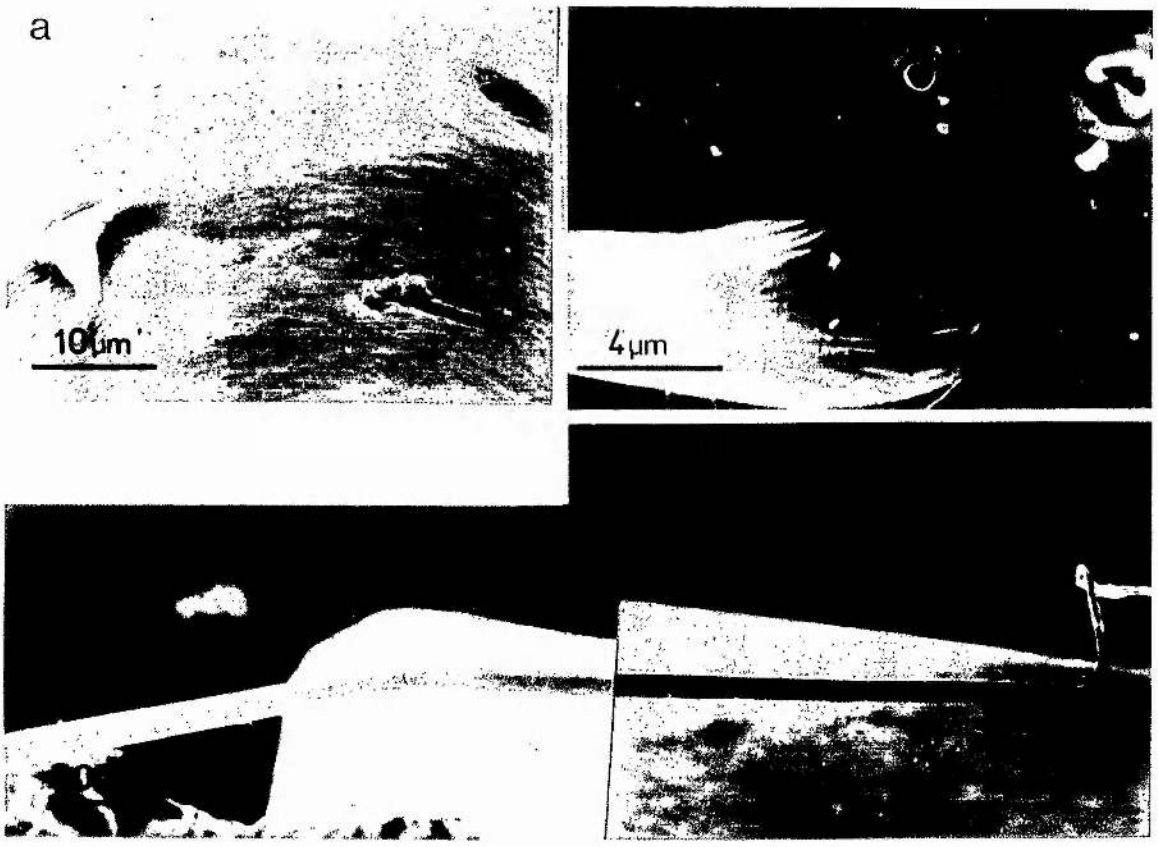
a
10 µm
4 µm

Figure 15. Cuticular outgrowths on the urosome lateral knobs of Hyas cornutatus. a-b, General view of the trichoid sensillum (arrow), and prominent outgrowth (triangles). c, Outgrowth resembling a pore-like opening. d, Same type of outgrowth but less prominent (drying artefact).


a
10μm

Figure 16. Cuticular outgrowths present on the spine and telson of Hyas cornutatus zoeal stage I. a, Tuft hair-like extensions on the telson spines describing hexagonal patterns. b, Unsocket spines on the rostral spine. c, Tuft hair-like extensions on the telson outer spines describing a less sophisticated arrangement than the telson forked spines. d, General view of scale-like projections widely distributed on the telson dorsal side. e, The scale-like projections describe a romboidal shape.


a
c
d
10 μm

Figure 17. Main types of hair sensilla on the periopods of Hyas cornutatus megalopa I. a, General posterior view of the megalopa instar. b, Basal region of the propus showing the incipient funnel- canal organs or campaniform sensilla. c, Details of the funnel-canal organs indicating the outer and inner rim with the central cone or pimple. d, Basal area of the propus showing several hair sensilla (funnel-canal organs, trichoid and triserrulated sensilla). e, Position of the triserrulated sensilla on the inner edge of propus. f, Triserrulate sensilla and accessory setules.

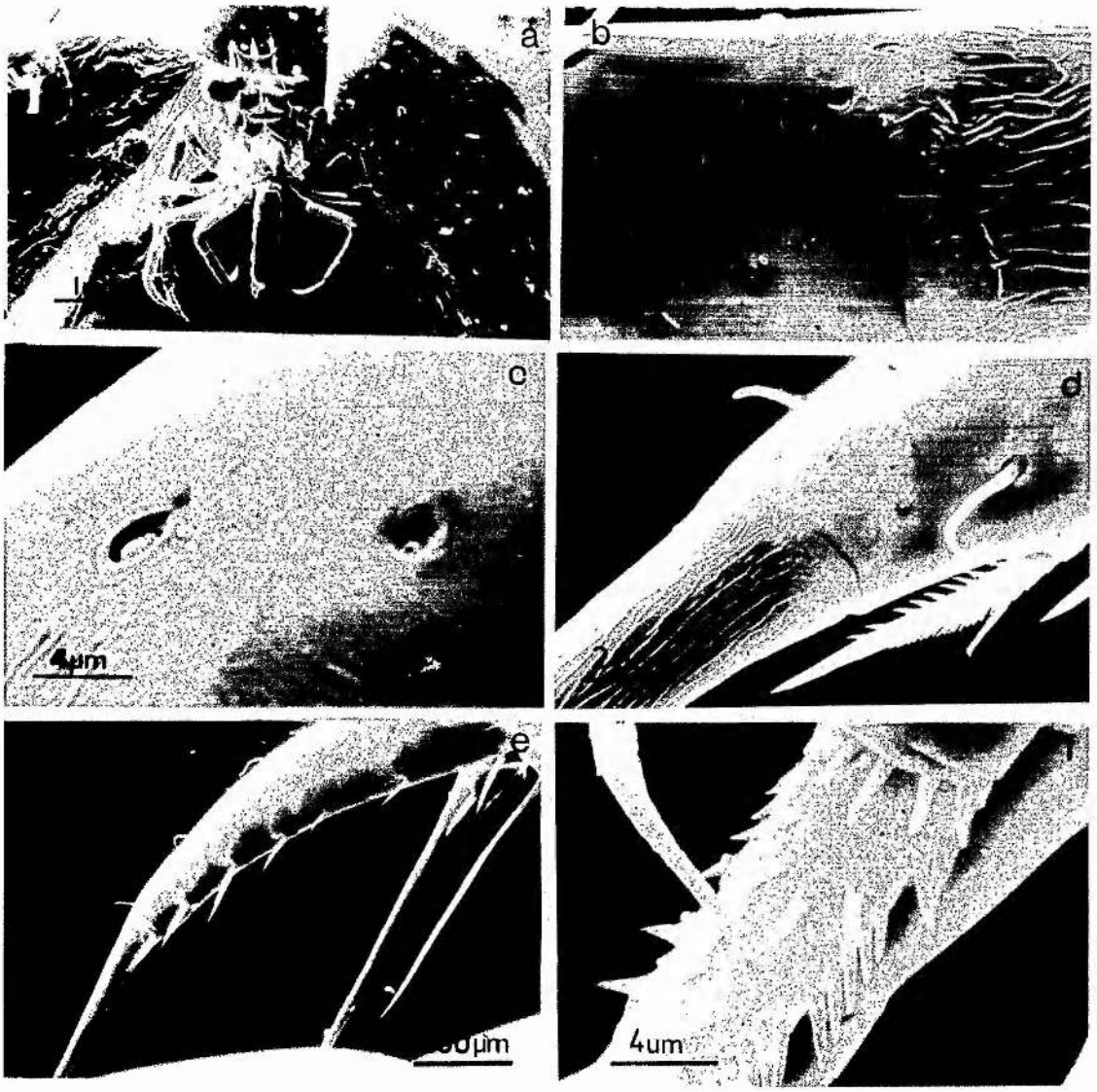
a
b
c
4µm
d
e
4um

Figure 18. Sensilla present on the first pereiopods of some Brachyura spp. a, Position of the funnel-canal organs in the first pereiopods of Hyas cornutatus megalopa I. c, First pereiopod and associated trichoid sensilla of Cancer pagurus megalopa I. d, Same appendage at the juvenile stage.


c

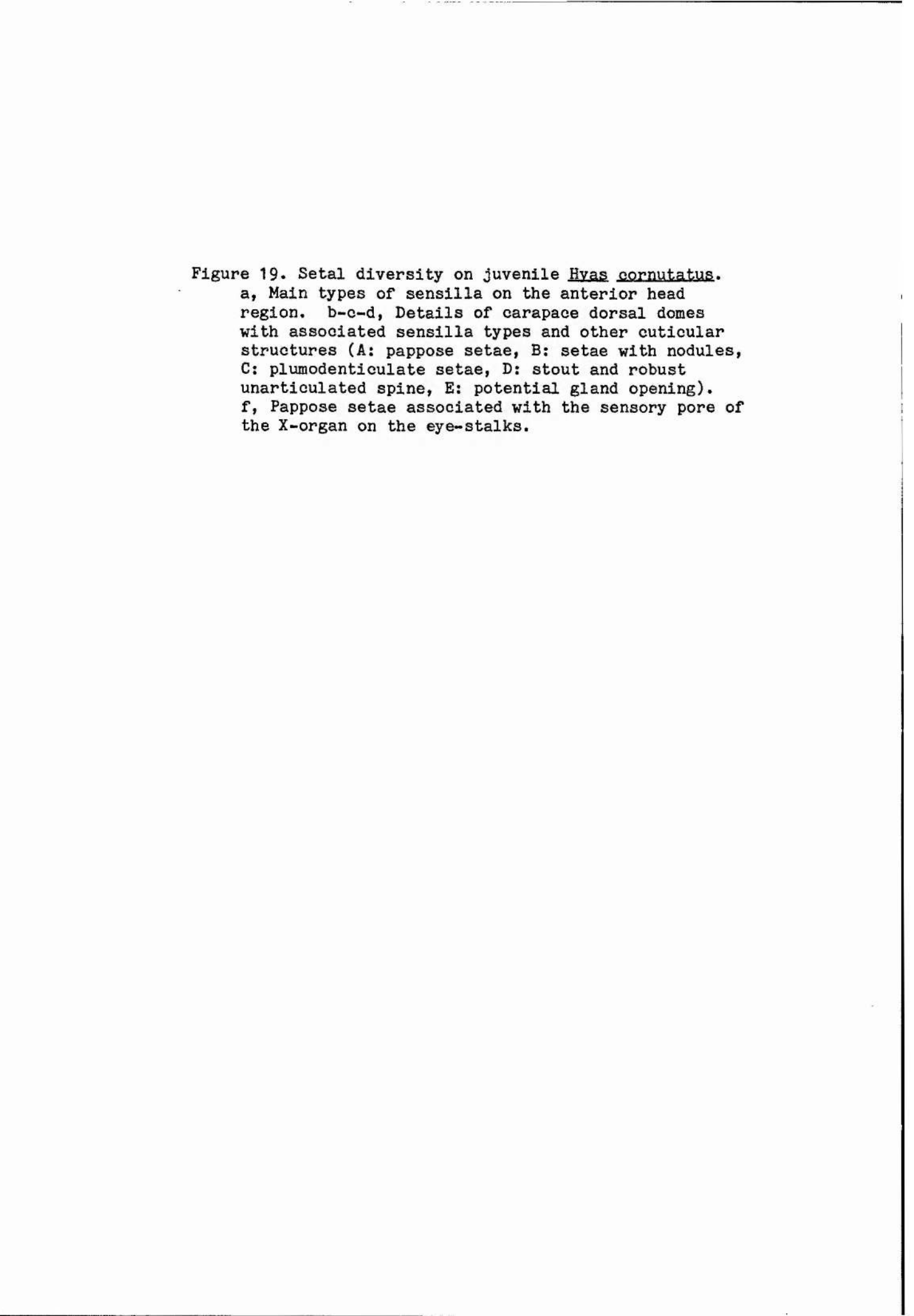

Figure 19. Setal diversity on juvenile Hyas cornutatus. a, Main types of sensilla on the anterior head region. b-c-d, Details of carapace dorsal domes with associated sensilla types and other cuticular structures (A: pappose setae, B: setae with nodules, C: plumodenticulate setae, D: stout and robust unarticulated spine, E: potential gland opening). f, Pappose setae associated with the sensory pore of the X-organ on the eye-stalks.

a
b
c
20μm
e
20

Figure 20. Setal varaiation in Porcellana longicornis developmental instars. a-b, View of the body dorsal and anterior side devoid of setae; only scattered trichoid hairs (arrow) are present in the zoeal stage I. c-d, Trichoid sensilla associated with V-shape extensions at the hair base on the carapace anterior side. e-f, Same type of cuticular extension at the hair base but with broader angles on the posterior side of the carapace edge.

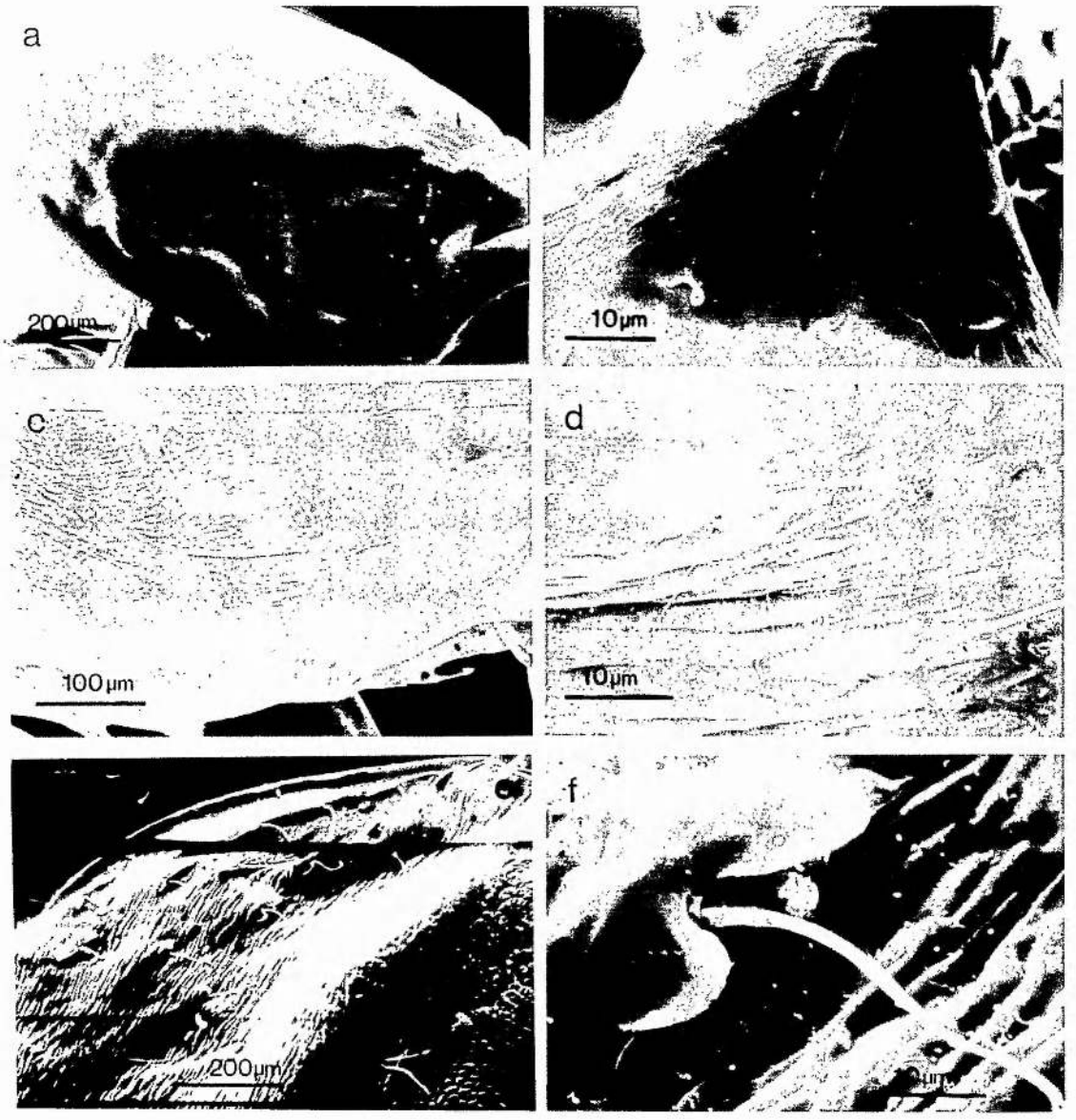
a
200µm
10µm
c
100µm
d
10µm
e
200µm
f

Figure 21. Main external features of the dorsal organ on the developing Hyas cornutatus. a, General anterior dorsal view of the zoeal stage I showing a dorsal ridge. b, Dorsal organ components: central pore and the four plate-pits (triangles) with a central pimple (long arrow), and diminutive pores (small arrows) in the zoeal stage I. c, Position of the dorsal organ (arrows) on the prominent dorsal ridge beside the dorsal horns, in the megalopal stage I. d, Changes in the main external features of the dorsal organ in this stage such as outstanding central pimple (arrow) and associated pores (short arrows). e-f, Dorsal ridge with no pores or plate-pits on the juvenile Cancer pagurus.

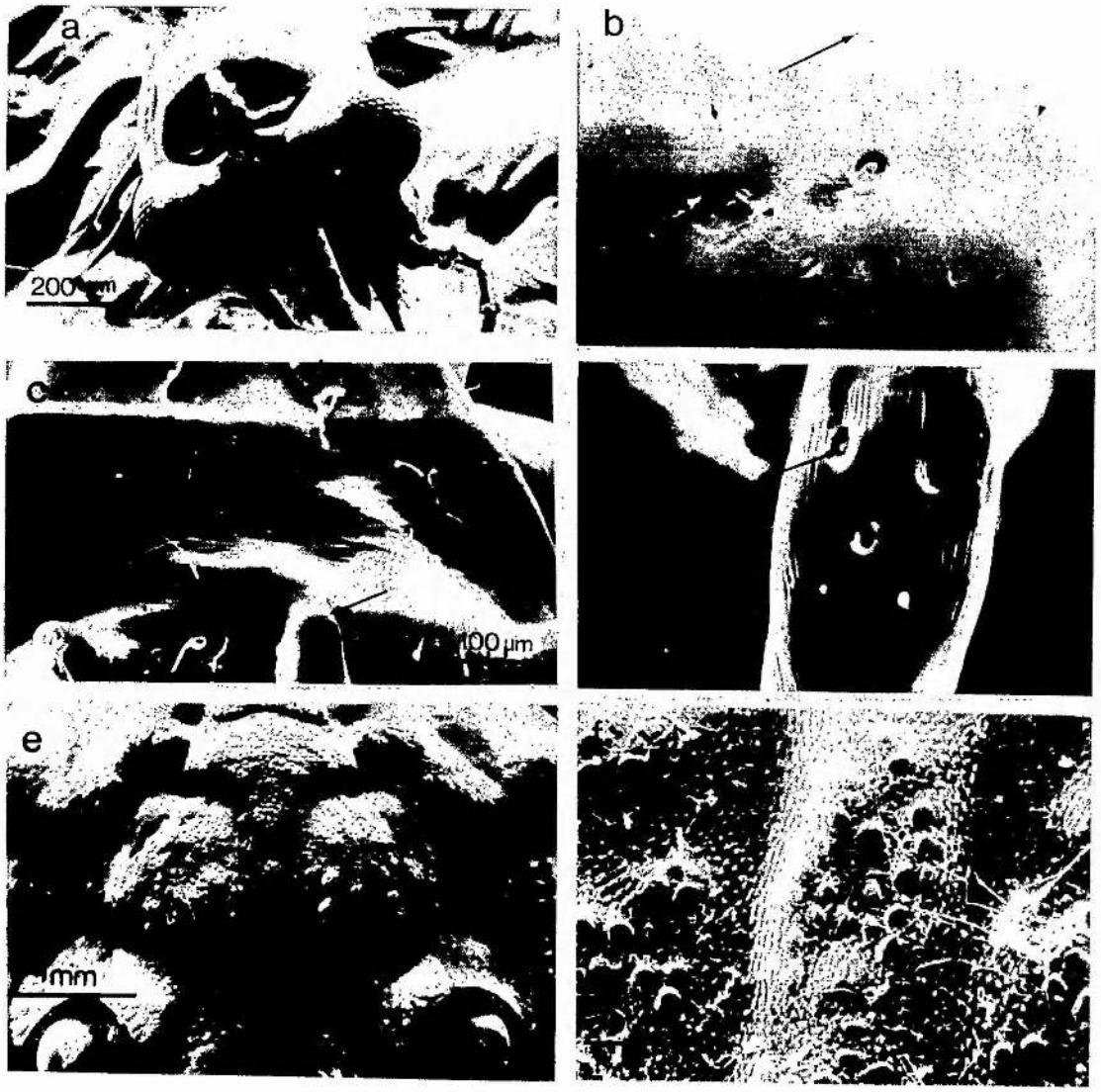
a
200 µm
b
c
100 µm
e
mm

Figure 22. Dorsal organ and other openings on the dorsal side of larvae and megalopa Brachyura. a, Anterior view of *Ebalia tuberosa*. b, Dorsal organ without central pore but containing the four plate-pits (arrow) in the zoeal stage I. c-d, Slit-like openings of *Cancer pagurus* megalopal stage I. e, Same slit- like openings of *Cancer pagurus*. f, *Dorippe lanata* (e-f juvenile specimens respectively).

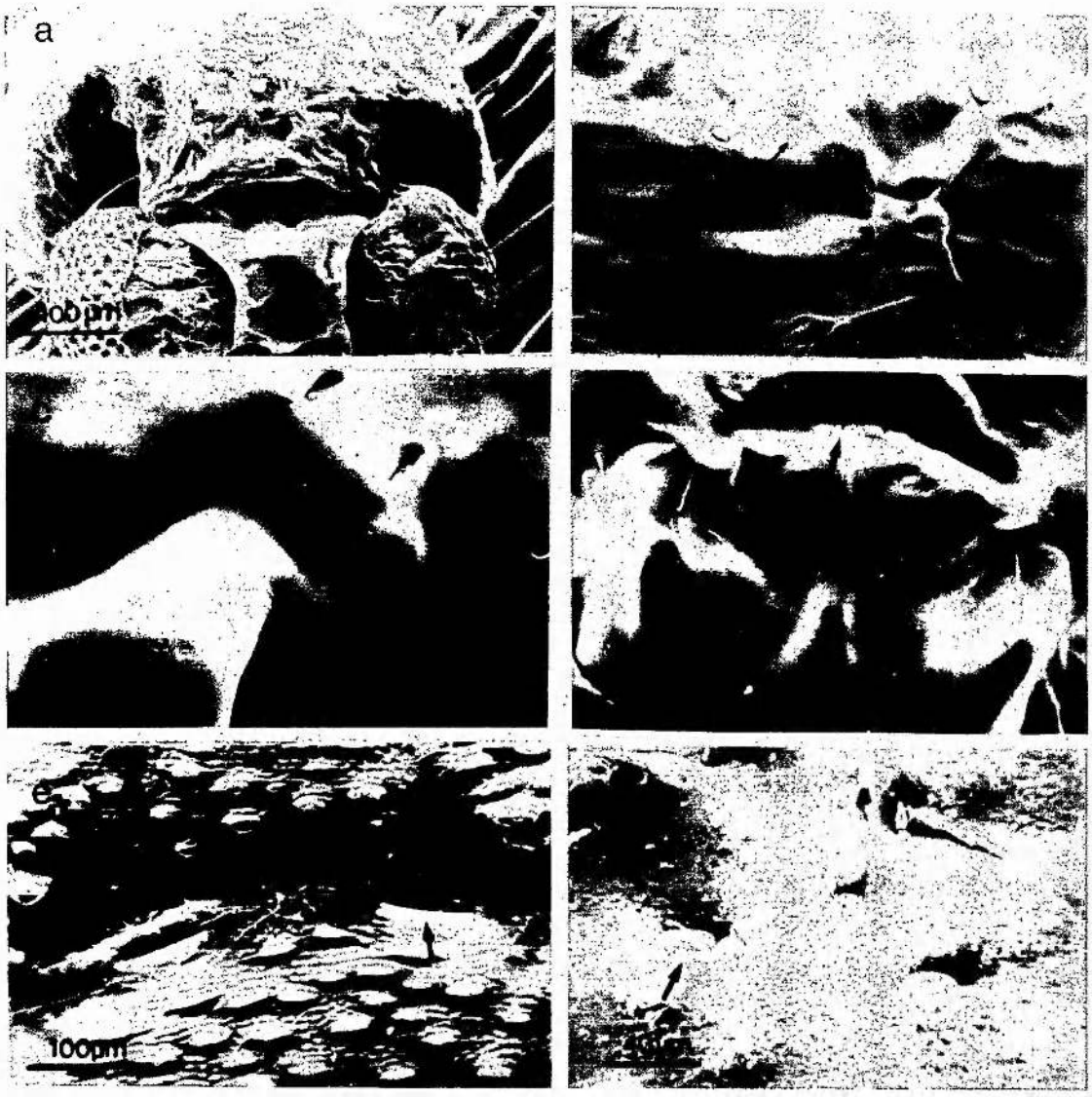
a
100μm
e
100μm

Figure 23. Posterior dome and associated outgrowths of megalopa I Hyas cornutatus. a, Position of the posterior dome (thick arrow). b-c-d-, Large pore (arrow) and small pores (triangle) associated with the dome.

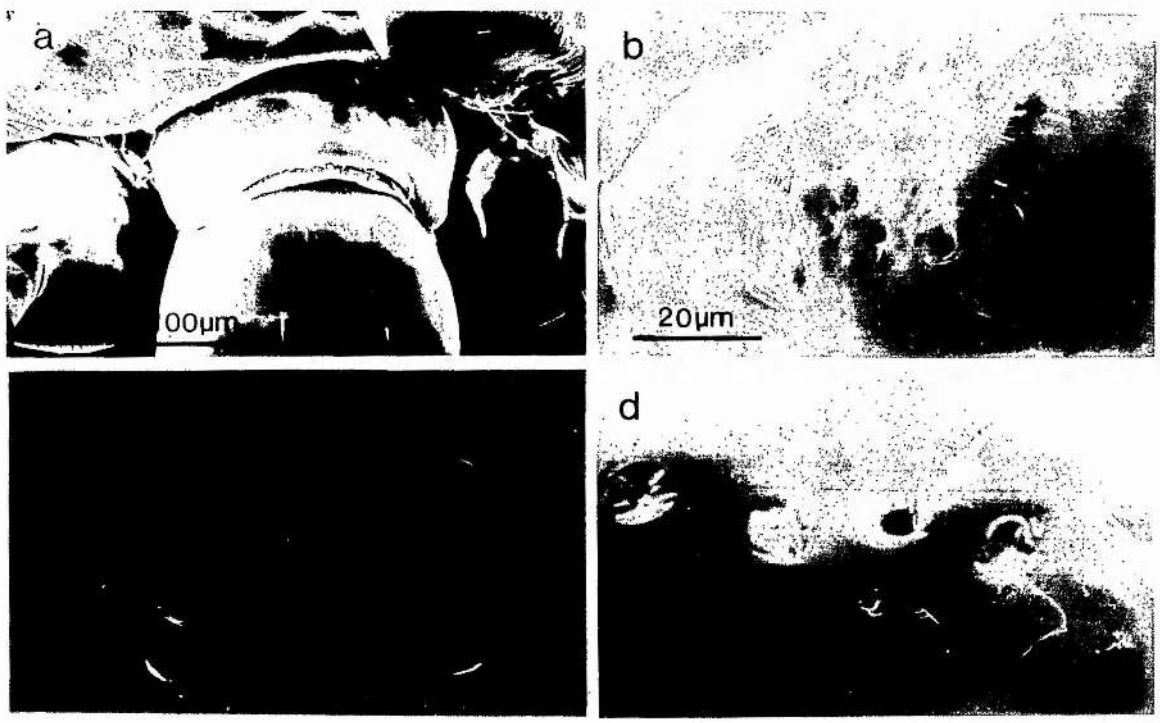
a
00μm
b
20μm
d

Figure 24. Dorsal organ main external features in some Anomura spp. a, Two central pores and four plate-pits (arrow) present on Porcellana longicornis zoea I. b, One central pore and four plate-pits (arrow) present on Porcellana platycheles zoea I. c, Position of the dorsal organ in the anterior head region (thick arrow). d, Two central pores without plate-pits on Galathea strigosa zoea I. e-f, Porcellana longicornis megalopa I showing the presence of a central pore with no distinctive plate-pits.

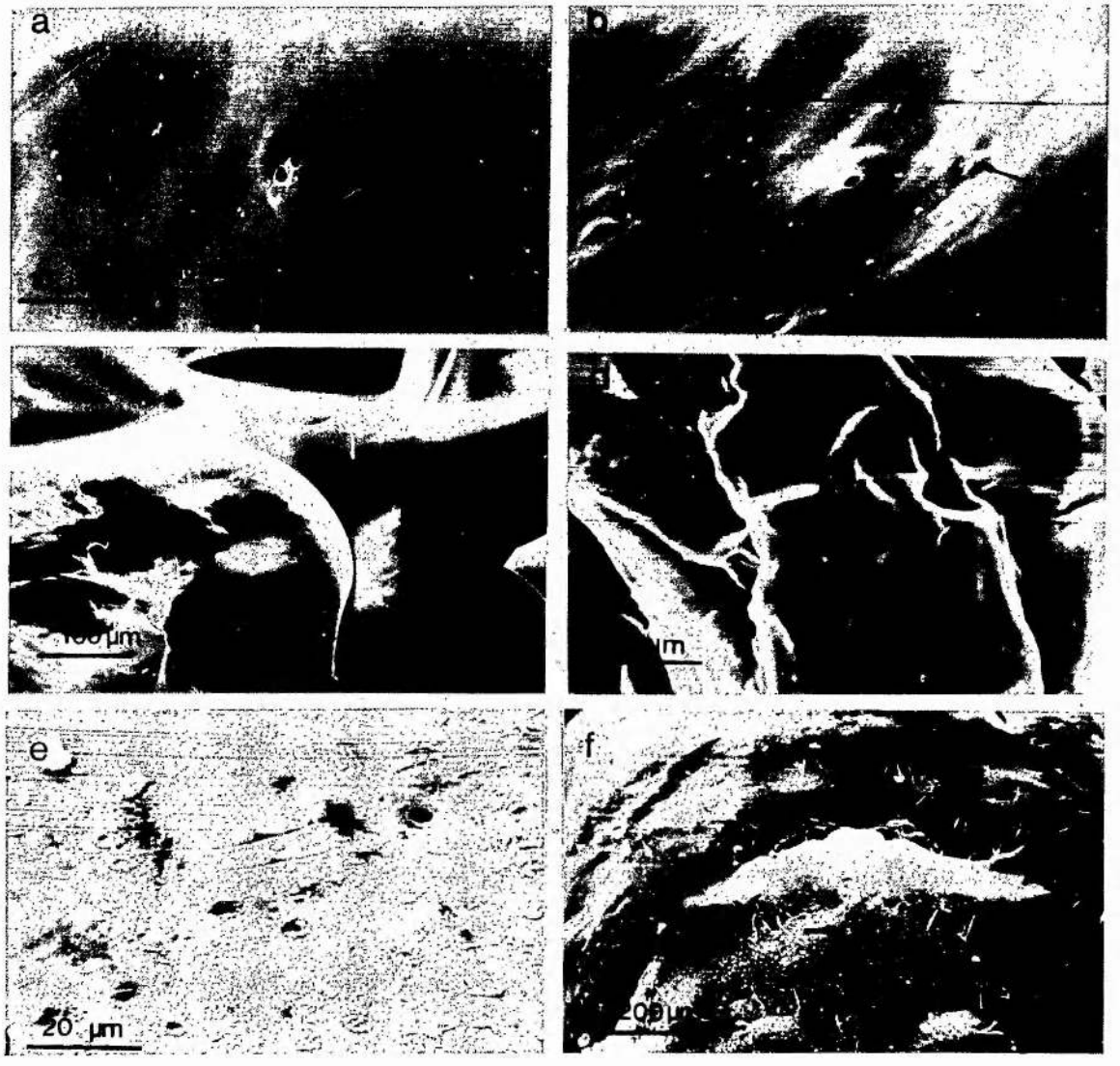
a
b
e
20 µm
f

Figure 25. Dorsal organ main external features on some Macrura spp. a, Head dorsal region showing central ridge (thick arrow) larval stage I. Homarus gammarus. b, Dorsal organ with poreless area and the four plate-pits without central pimple (arrow) larval stage I. c, Dorsal organ appearance in the post-larval stage I, arrows indicate the plate-pits containing five diminutive pore-plates. d. Close-up of the pore-plates showing each one innervating peg. e, Same plate-pit indicating abraded pore-plate in the post-larval stage III. f, View of the dorsal organ present on Nephrops norvegicus larval stage I.

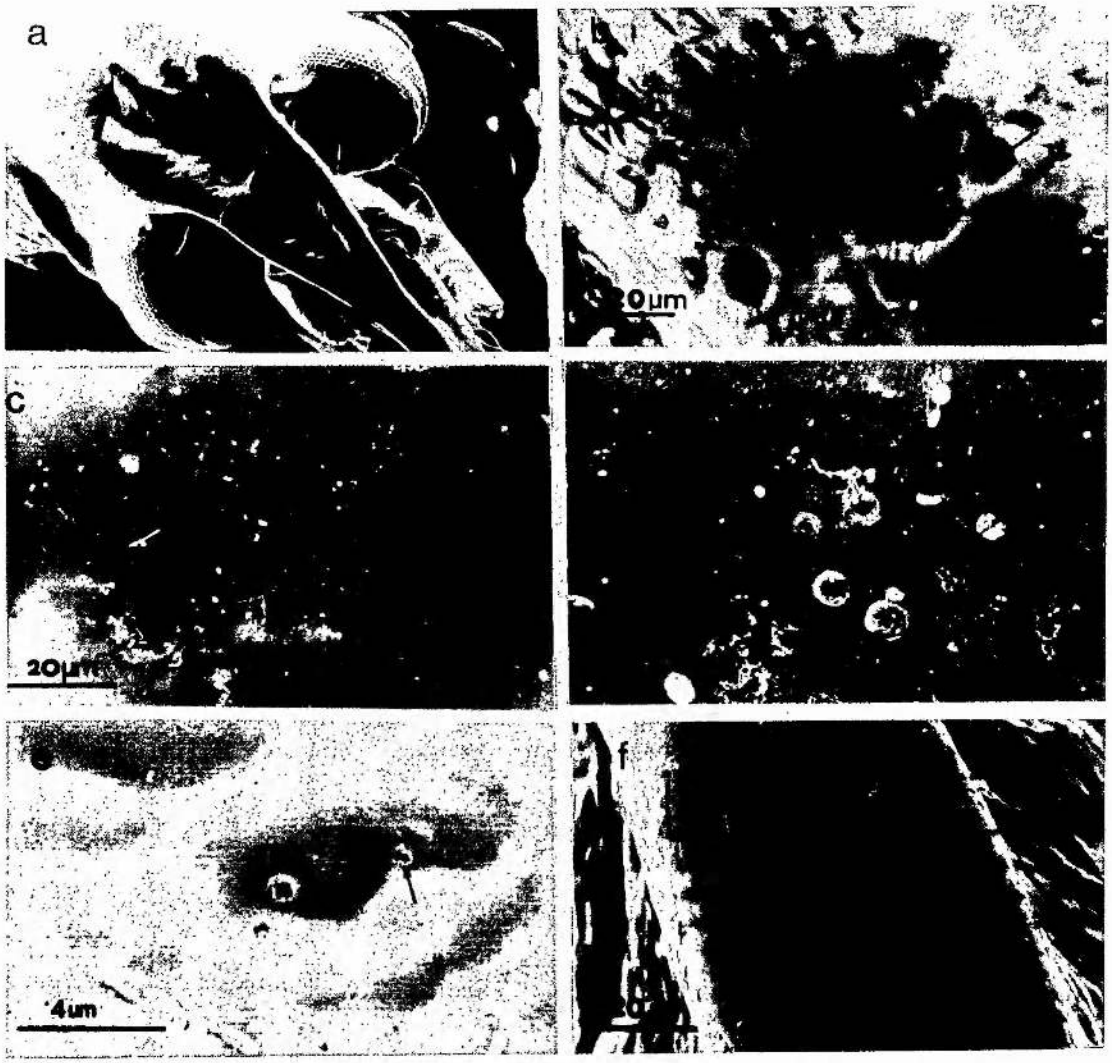
a
b
0 µm
c
20µm
4um
f

Figure 26. Light micrographs of the dorsal organ of Hyas cornutatus zoeal stage IV. a, General view of the dorsal organ components with the secretory cell duct (thick arrow) and the four plate-pits (long arrows) Mag. 160x. b, Longitudinal section through the dorsal dome and position of the aorta vessel (ao) and epidermal cells. Mag. 400x. c, Longitudinal section through the dorsal organ and associated pyrimidal mucous cell type. Mag. 400x. d, Longitudinal section of the dorsal organ posterior dorsal area showing the narrow strip of epidermal cells. Mag. 400x.

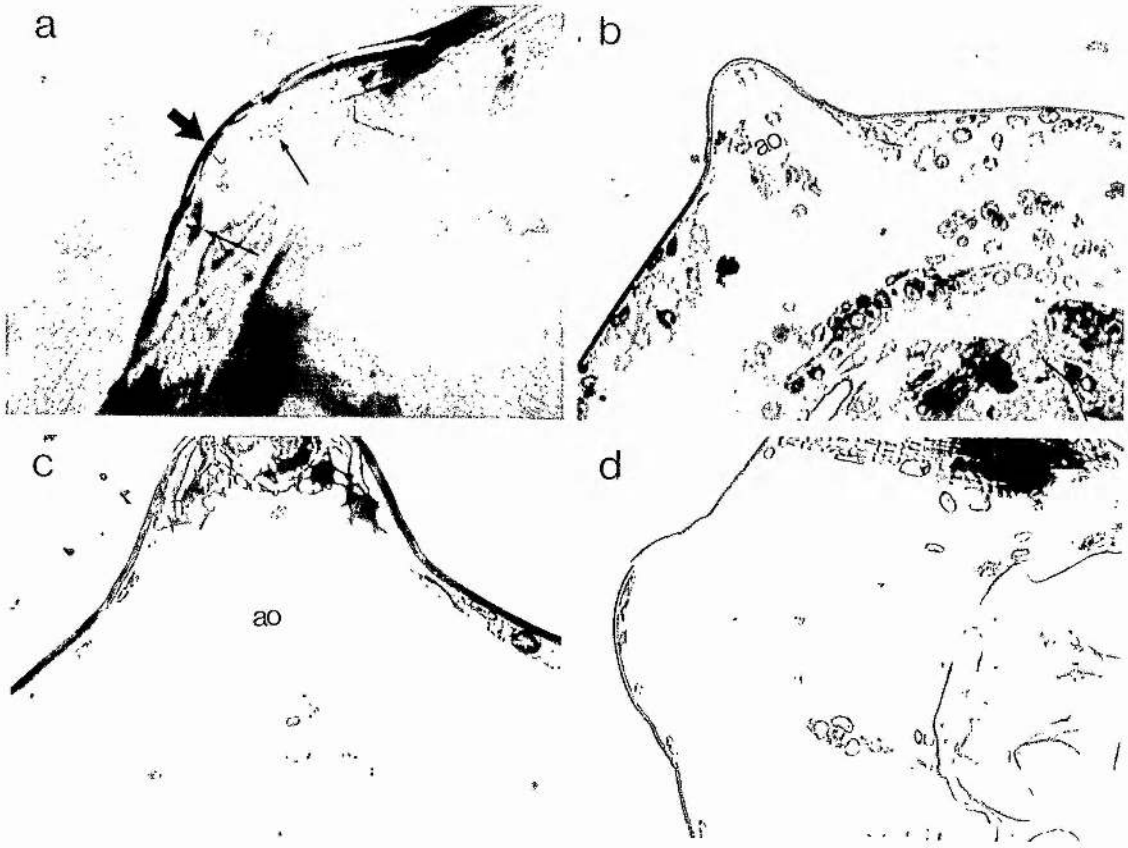
a
b
ao
c
ao
d

Figure 27. Schematic representation of the dorsal organ and its main cellular components. bb: basal bodies; bl: basal membrane; ci: ciliary segment; cut: cuticle; dc: ductule cell; ds: dendritic sheath; ep: epidermal cell; er: endoplasmatic reticulum; G: Golgi apparatus; ii: electron dense matrix (pimple); mi: mitochondria; mv: microvilli; N: nucleus; R: rootlet system; L: lumen; S: sensillar sinus; SC: secretory cell; sc: suppoting cell; sg: secretory granules; SC1: SC2: SC3: enveloping cell 1, 2 and 3; v: vesicles.

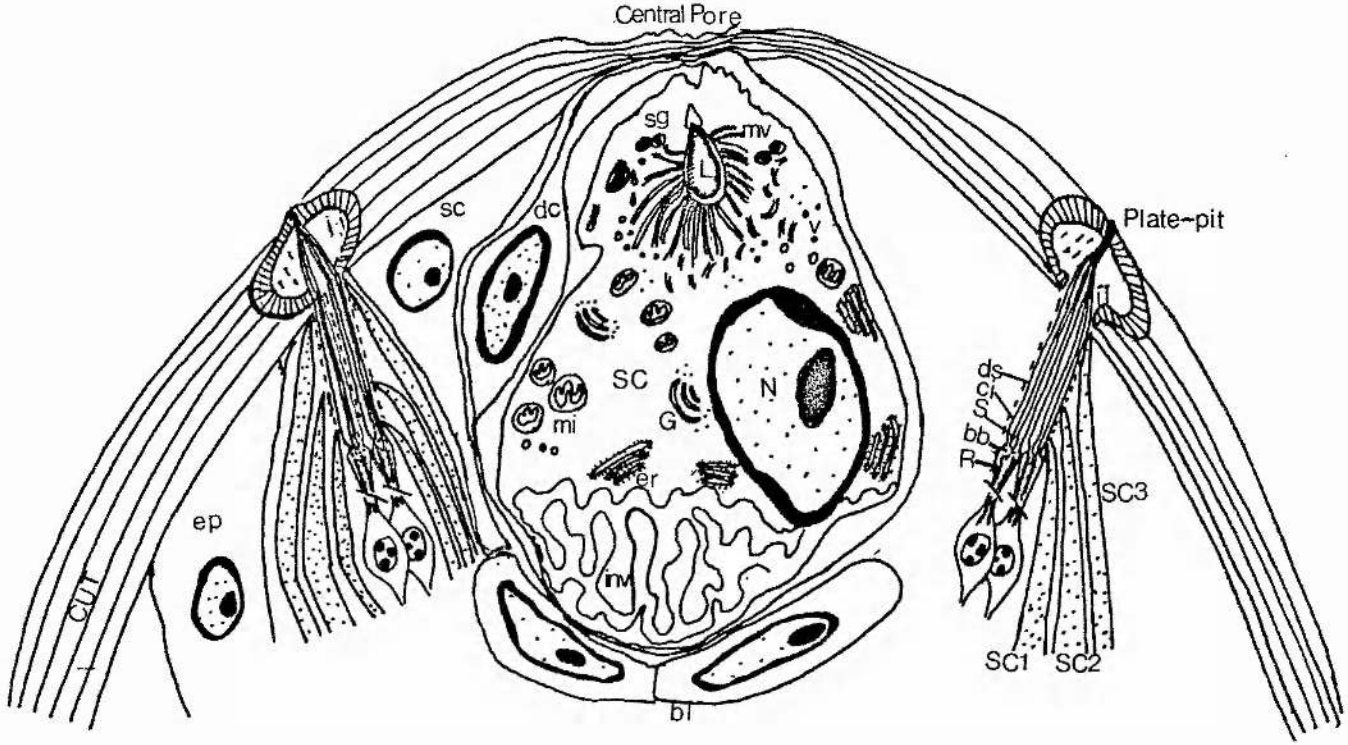
Central Pore
sg
mv
sc
dc
Plate-pit
SC
N
G
mi
er
ep
CUT
m
bl
SC3
SC1
SC2

Figure 28. Main ultrastructural features of the dorsal organ gland cell and its associated cellular components of Carcinus maenas zoea I. a, Transverse section through the secretory cell (sc) showing the reservoir (r) with the microvilli matrix (mv), basal invaginations (inv) and associated Golgi complexes (G) and endoplasmic reticulum (ER); position of four sensory cells (sec) and the basal membrane (bl). b, A large number of invaginations (inv) form a continous labyrinth all around the cell with associated mitochondria (mi) and endoplasmic reticulum. c, Details of the central reservoir which is bounded with microvilli and secretory vesicles are visible. d, The lumen of the reservoir (L) with radially placed microvilli. e, View of the glandular complex showing the voluminous central reservoir bounded with microvilli , a cuticular canaliculus (d) opens and secretory vesicles are visible (arrow) especially in the anterior part of the cell. f, a more distal section shows the change in shape of the canaliculus (L).

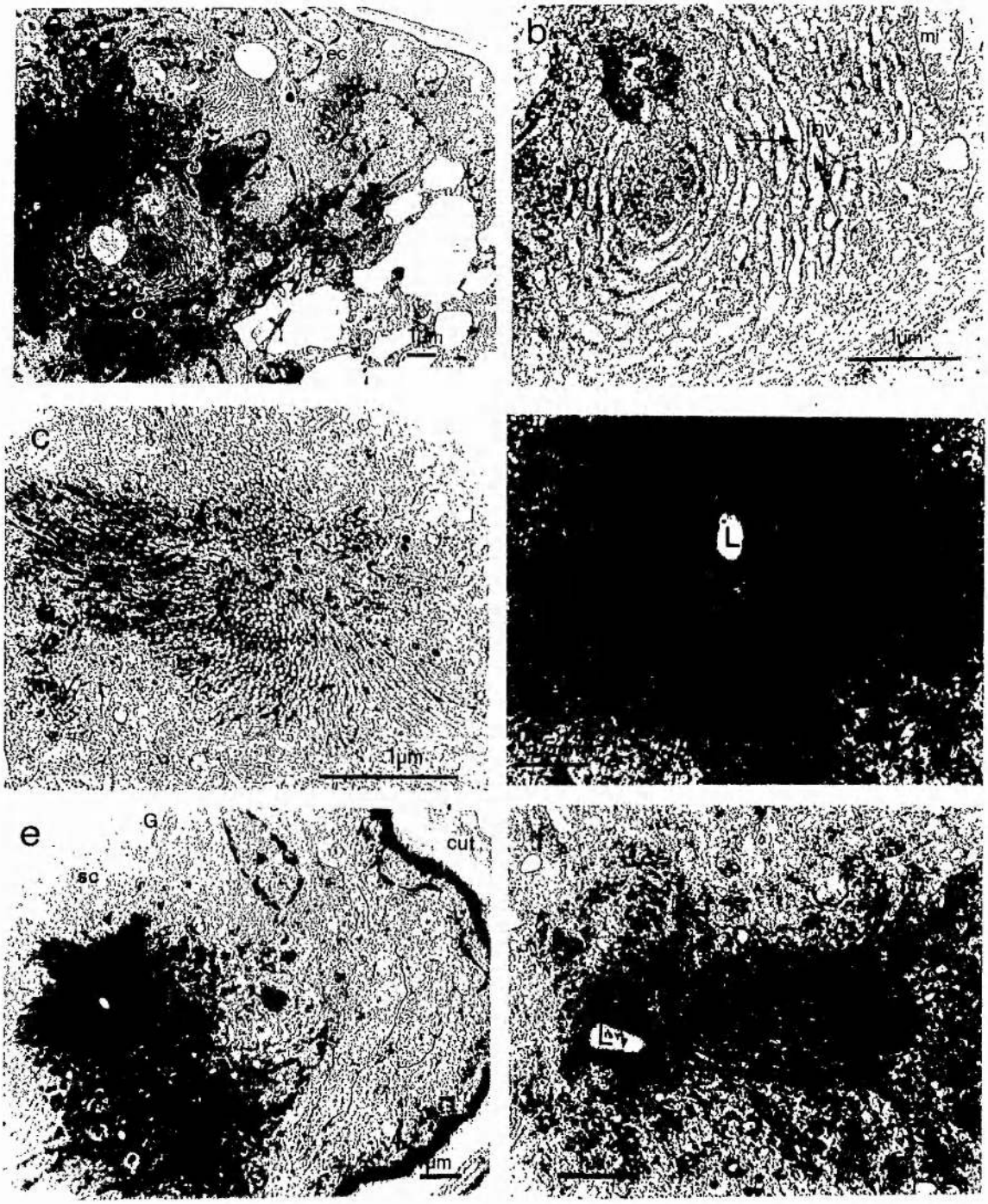
ec
1µm
b
mi
mv
1µm
c
1µm
L
e
G
cut
sc
1µm
Lv

Figure 29. Longitudinal sections of osmium tetroxide fixed specimens of Carcinus maenas zoeae I. a-b, Details of the "canalicule conducteur" (CC) and the "canalicule recepteur" (RC), position of the secretory cell (sc) and surrounded by the ductule carrying cell (dc). cut: cuticle; N: nucleus; mv: microvilli.

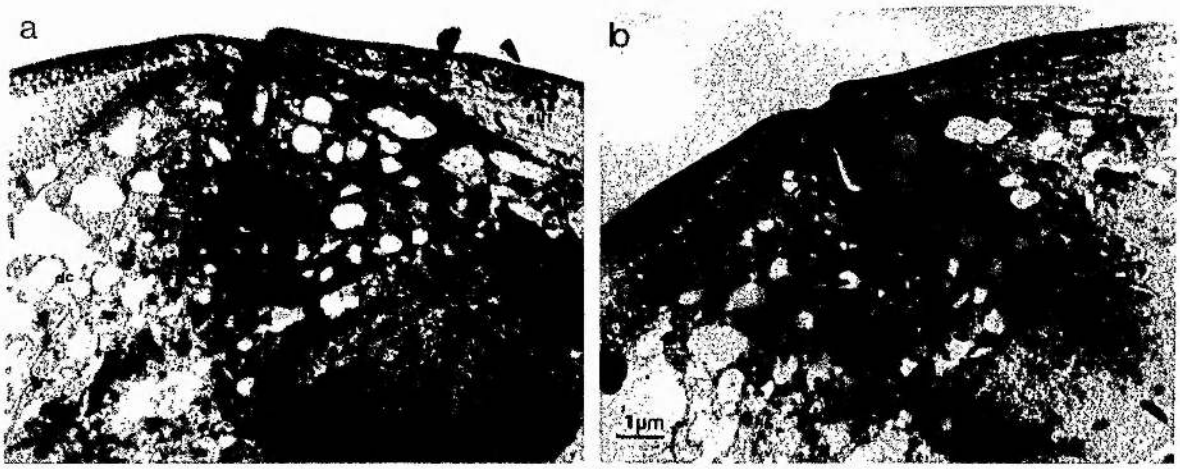
a
b
1µm

Figure 30. Main ultrastructural features associated with the position of the ductule. a, Proximal section showing a relative narrow ductule where the fibrillar projections of the inner epicuticle seems to close the basal area. b-c-d, It represents a more distal section showing the change of calibre and the occurrence of the electron dense lamellae (small arrow). e, Section at the cuticle level (cut) where the duct is cylindrical in shape. f, General view of the duct (clear arrow) and details of one plate-pit (thick arrow) and its sensory innervating dendrites (d).

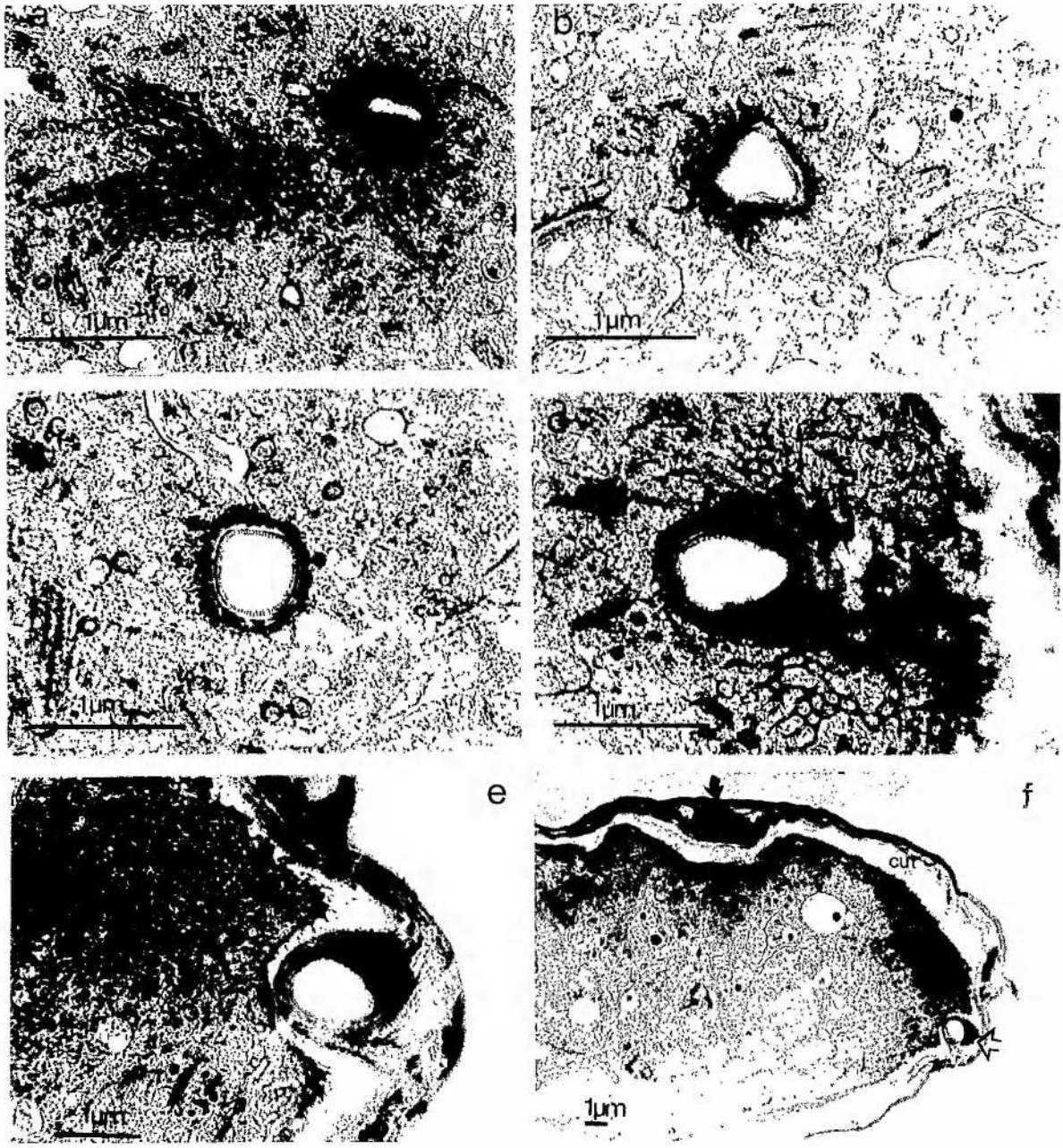
a
1µm
b
1µm
c
1µm
d
1µm
e
1µm
f
cut
1µm

Figure 31. Dorsal organ ultrastructure of Hyas cornutatus zoea I. a, Longitudinal section through the secretory cell (sc), apical microvilli (mv), sensory cell (sec), supporting cell (suc), and epidermal cell (ec) with the basal membrane (bL). b, Oblique section with the reservoir lumen (L), microvilli (mv), and cell membrane boundaries (arrows). c-d, Transverse section of the same area.

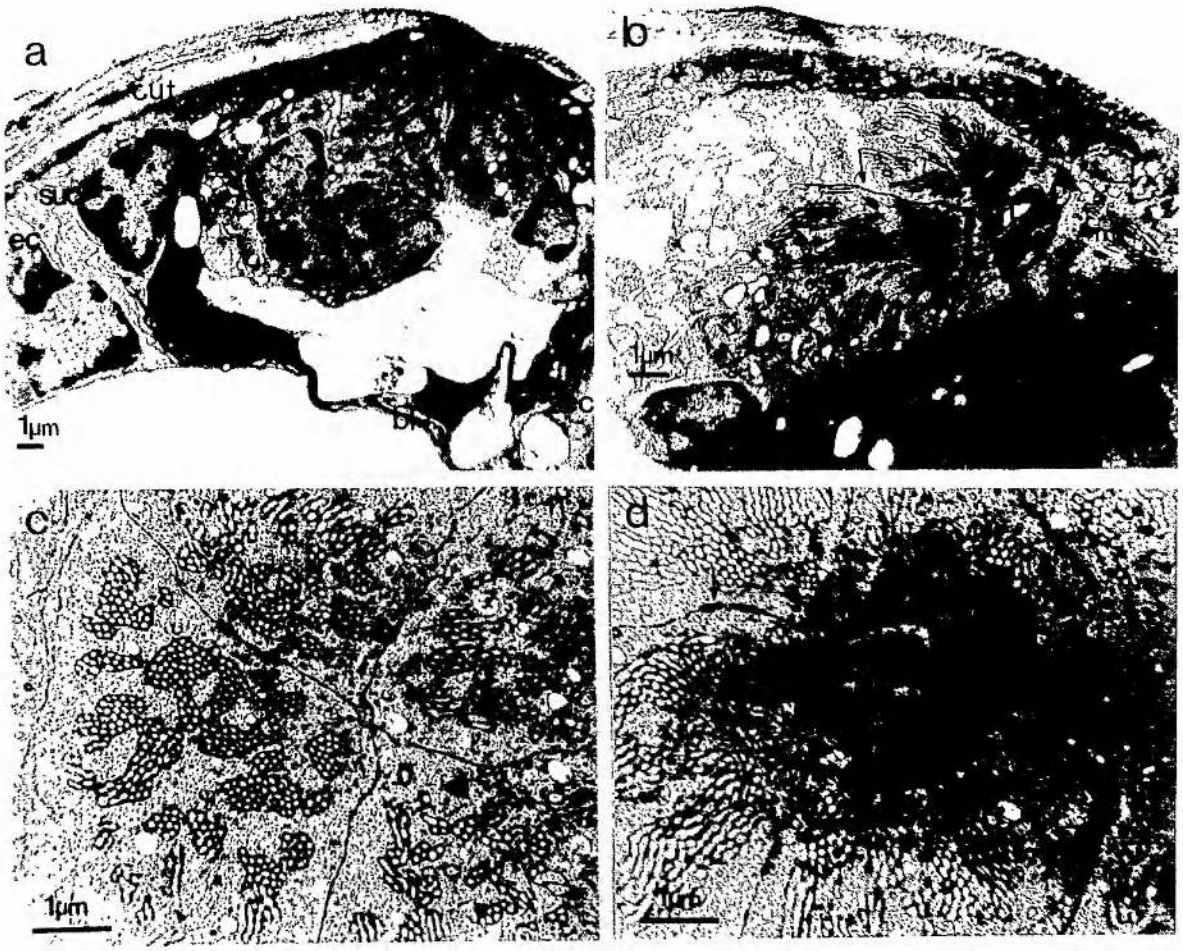
a
cut
suc
ec
1µm
b
c
b
1µm
c
1µm
d
1µm

Figure 32. Ultrastructural features of the plate-pits and associated sensory cells of Carcinus maenas zoea I. a, Transverse section through the central pimple or cone which contain four innervating dendrites (d) inmersed within an electron dense matrix (ii). b-c-d, Transverse sections of the sensillum at more distal levels. e, Transverse section through dendrites showing one enveloping or sheath cell (SC3). Microtubules (mt) are filling the dendritic sinus (s) and details of the compartmentalized dendritic sheath (ds) (arrows) indicate central filaments. cut: cuticle.

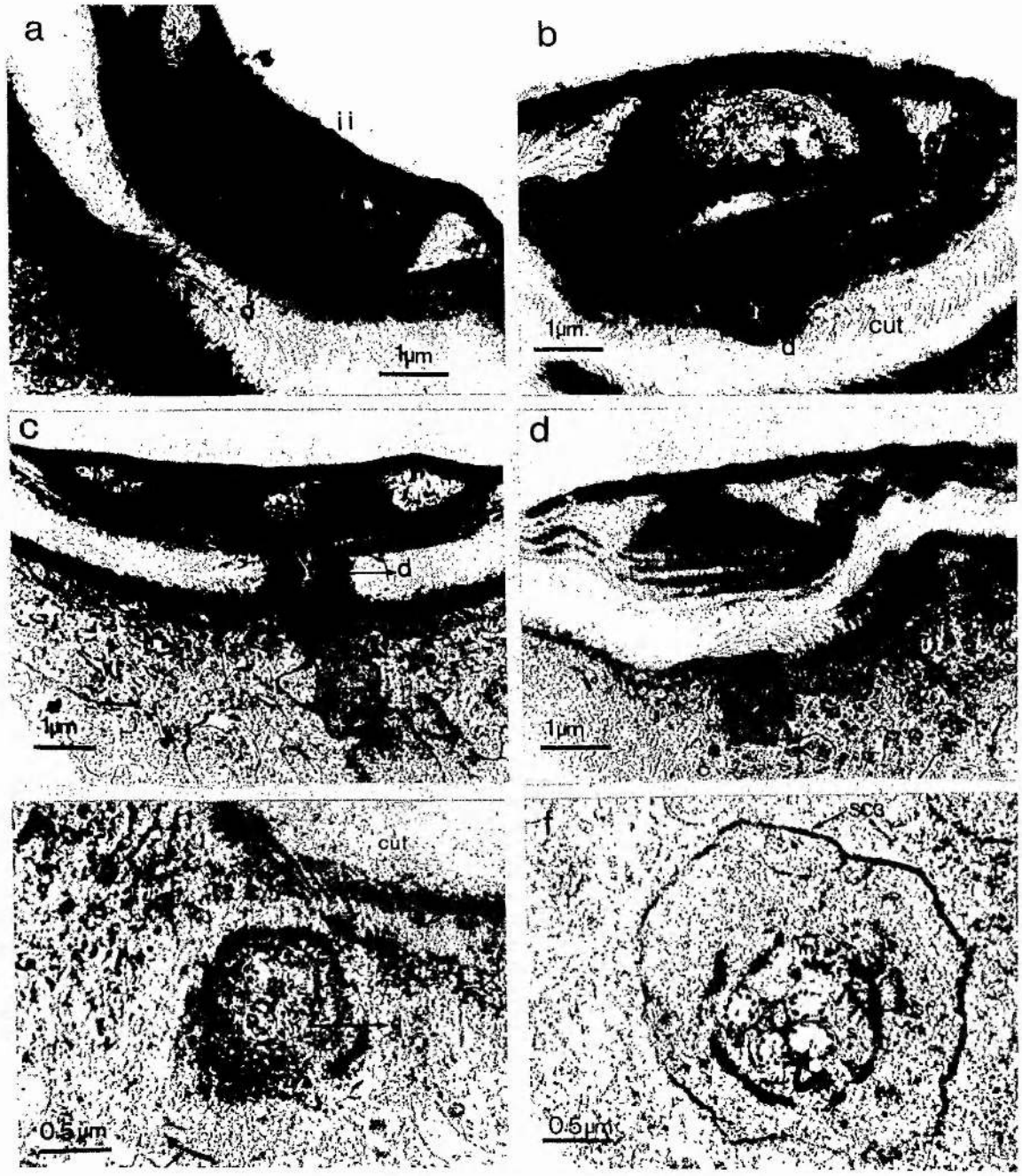
a
ii
d
1µm
b
1µm
d
cut
c
d
1µm
d
1µm
cut
0.5µm
f
scg
0.5µm

Figure 33. Plate-pits sensory cells and proximal region features of Carcinus maenas zoea I (transverse sections). a, Section through the distal ciliary segment showing details of the microtubule doublets, desmosome-like junctions (des) observed at this level, abundant number of microtubules (mt) and two sheath cells (SC2 and SC3). b, proximal ciliary segment with a tube (t) joining the inner side of the microtubule doublets, and the Y-like extentions extending from the ciliary necklace. c, Basal body segment with nine microtubule triplets (small arrows) and the inner sheath cell (SC1). d-e-f, Sections through the ciliary rootlets (R) and associated osmiophilic matrix (thick arrow).

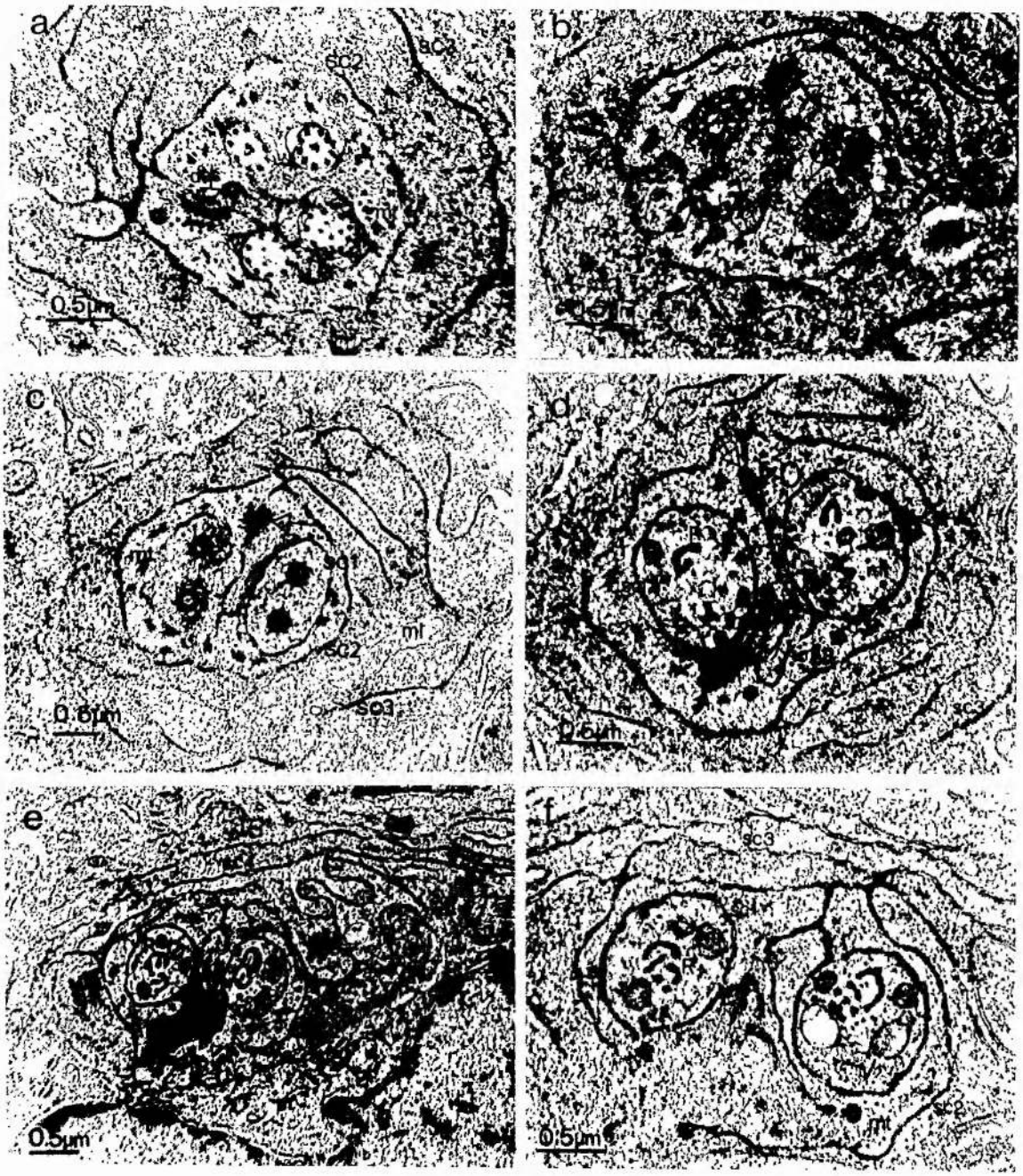
a
sc2
sc3
0.5μm
b
mt
c
mt
sc1
sc2
mt
sc3
0.5μm
d
0.5μm
e
0.5μm
f
sc3
mt
sc2
0.5μm

Figure 34. Sensory cell rootlet system of Carcinus maenas zoea I. a, A more proximal section through the rootlets. b, Cell bodies of the two sensory cells with their nuclei (N). c-d, Position of the four sensory cells, two in a more longitudinal section (curved arrow) and two in a more cross section (thick arrow) bounding the secretory cell (sc), basal invaginations (inv) and some unfixed component (?). d, Detail of a nerve ending (Ax) and two sensory cells (arrows). cut: cuticle; sc1:sc2:sc3: enveloping cell 1, 2 and 3 respectively.

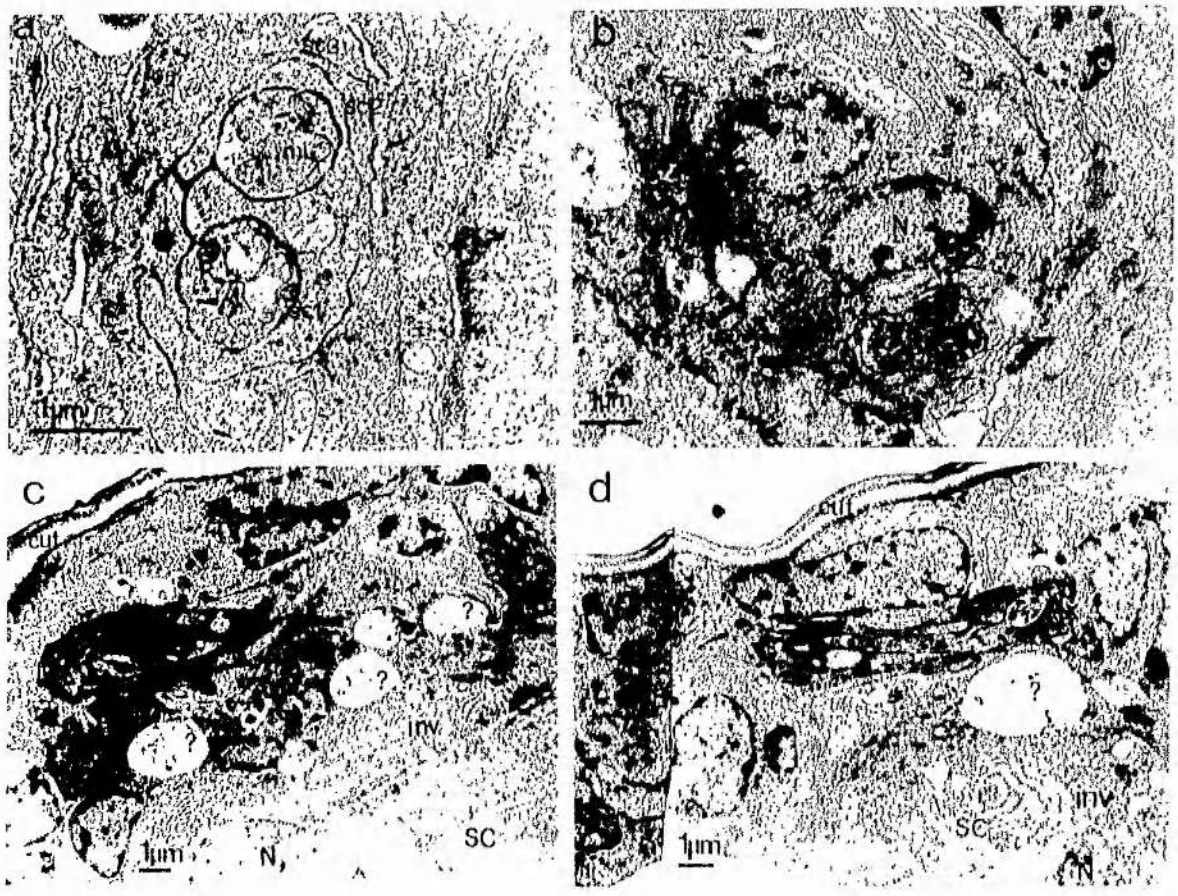
a
b
c
d
1µm
N
SC
inv
cut

Figure 35. Sensory plate-pits of Hyas coarctatus megalopa I. Transverse sections showing the thick nature of the plate-pits at this stage as well as the presence of six innervating dendrites with a thick dendritic sheath (d, arrows), and abundant microtubules in the sheath cells.

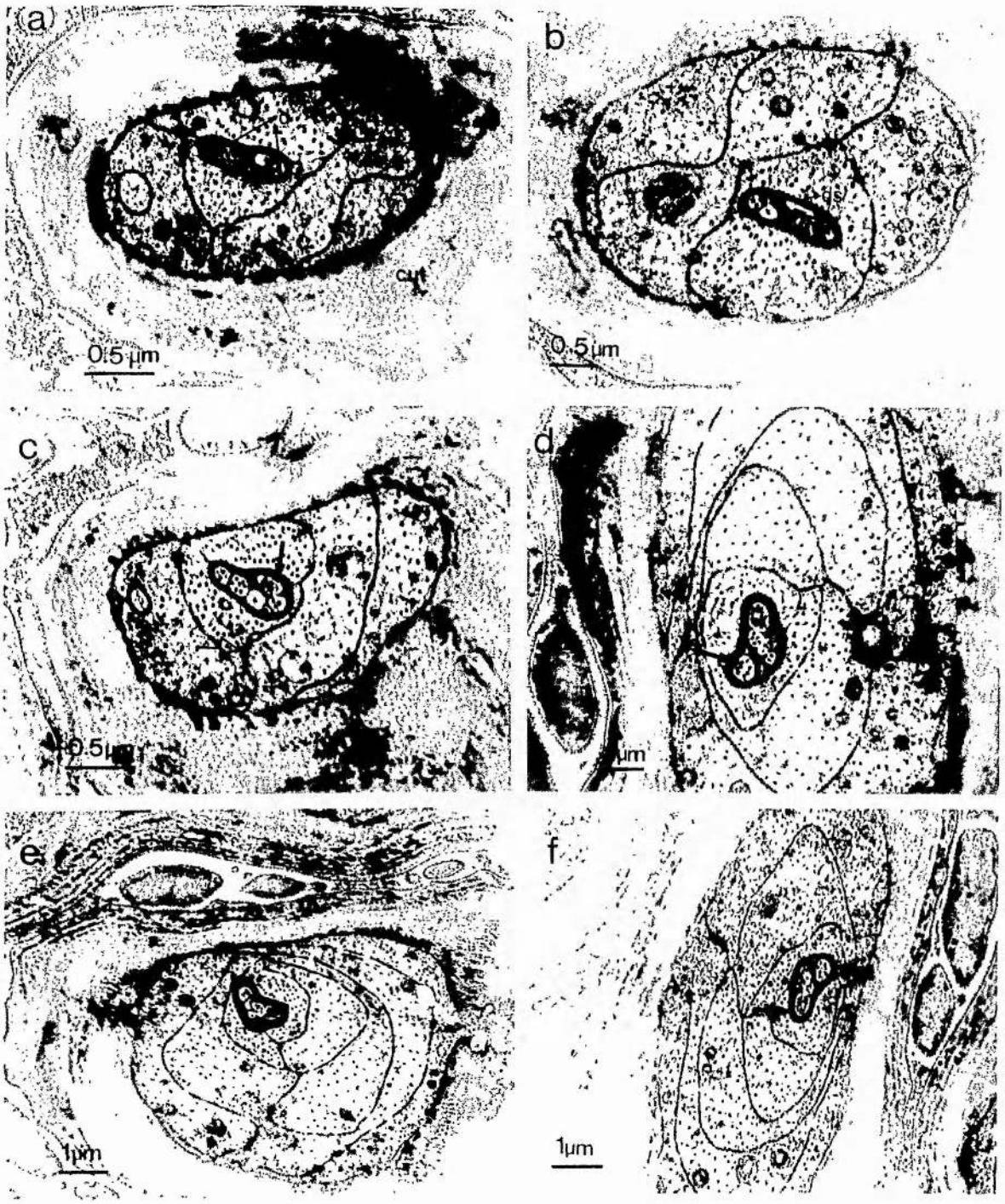
a
cyt
0.5 µm
b
0.5 µm
c
0.5µm
d
µm
e
1µm
f
1µm

Figure 36. Sensory plate-pits of moulting Hyas cornutatus megalopa I. a, Longitudinal section showing the dendrites ending beneath the central pimple. The sensilla sinus seems to fill the plate-pit inner rim area (i). b, Detail of the well developed ciliary rootlets (R) and desmosome-like junctions (arrow). c, Transverse section of the plate-pits showing the innervating dendrites and the thick outer cuticle (arrow). d, it represents an old and new plate-pit, and the potential dendrite position in the new (dark arrow), and old (clear arrow) central pimple or cone of the sensillum.

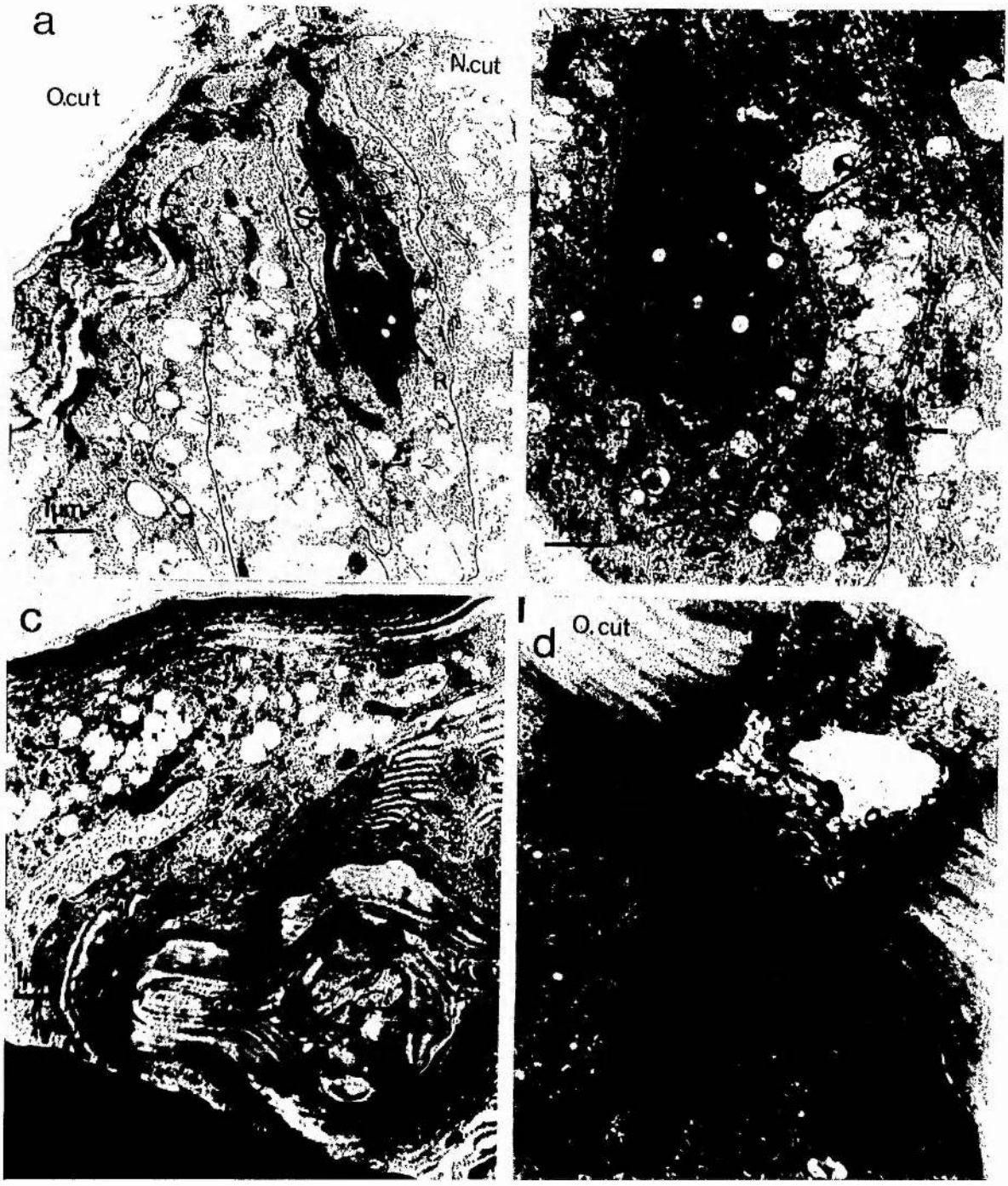
a
O.cut
N.cut
R
1μm
c
d
O. cut

Figure 37. Dorsal organ appearance in the pre-zoeal stage of Carcinus maenas. a-c, The secretory cell (sc) is packed with secretory granules (1,2), abundant and well developed Golgi complexes (G) boundaring the nuclear region ; cell membranes are indicated by clear arrows. b, Detail of the sensory cell of a proximal nerve innervation (insert). d, Golgi complexes with prominent internum and associated vesicles. e-f, Details of the dendrites (d) innervating the pits. N: nucleus; er: endoplasmic reticulum; mi: mitochondria.

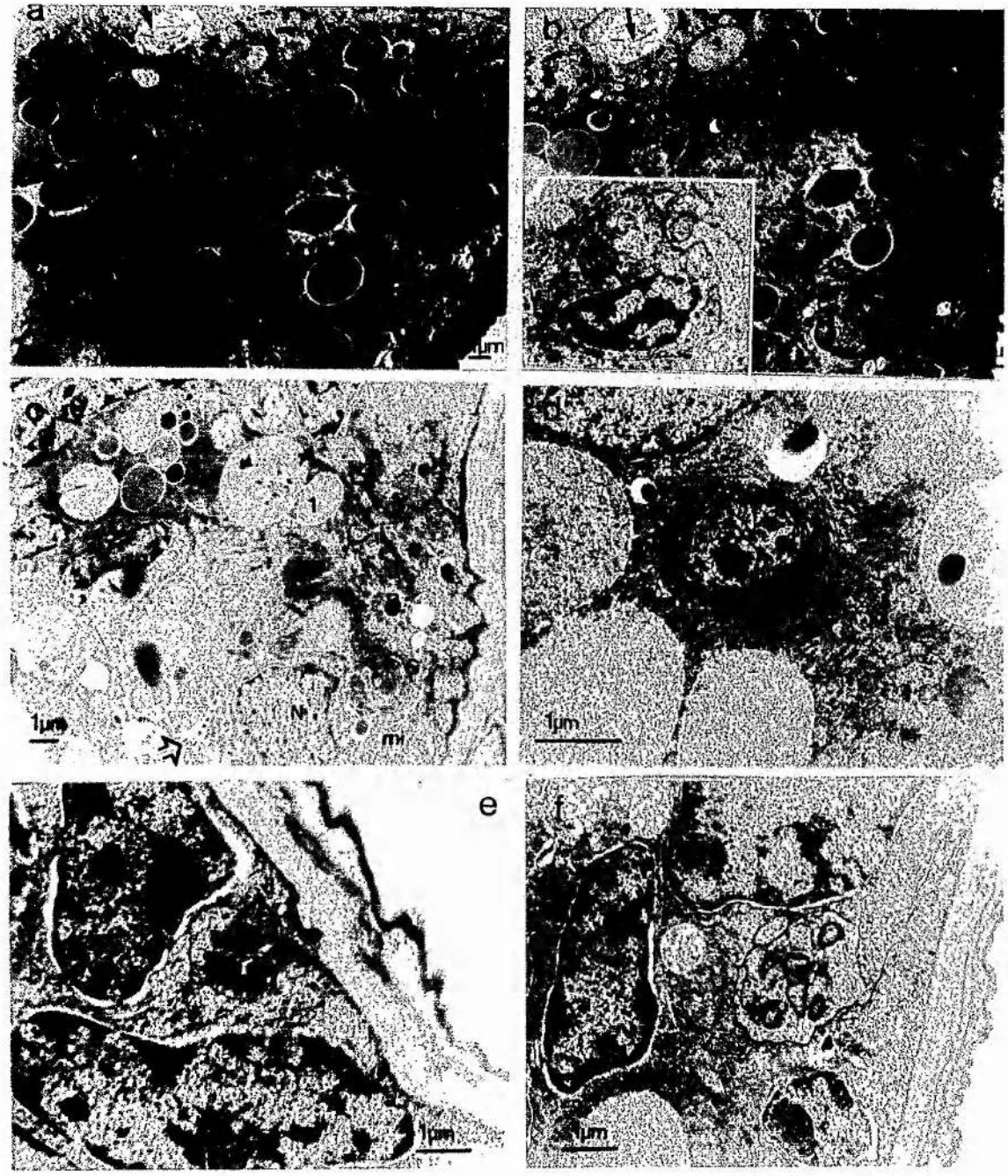
a
b
c
d
e
f
1μm
N
m

Figure 38. Light micrograph sections of the embryonic dorsal organ of Carcinus maenas. a, Detail of the blastodermic cells which form the organ (EM: embryonic membrane , B: brain) Mag. 400x. b, Transverse section showing the same group of cells. Mag. 400x. c, Transverse section showing the dorsal organ cells (arrow) which do not sink into the underlying yolk (Y), and the posterior spine placed above it (ps). Mag. 400x.

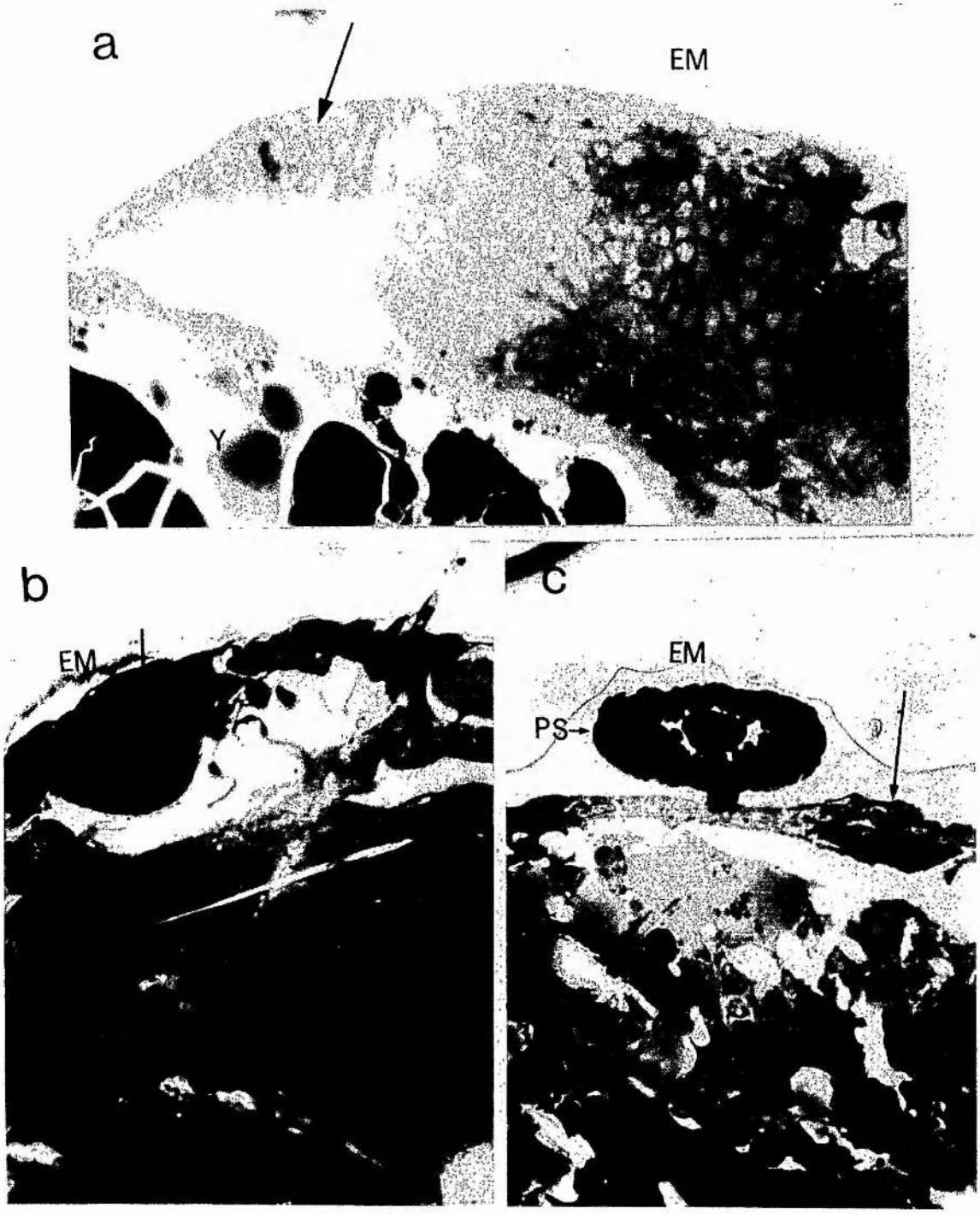
a
EM
Y
b
EM
c
EM
PS

Figure 39. SEM observations of the dorsal organ in Carcinus maenas embryos. a-c, Position of the dorsal organ (arrows) showing no central opening. b-d, General view of the dorsal organ in the head dorsal region (square). PS: posterior spine.

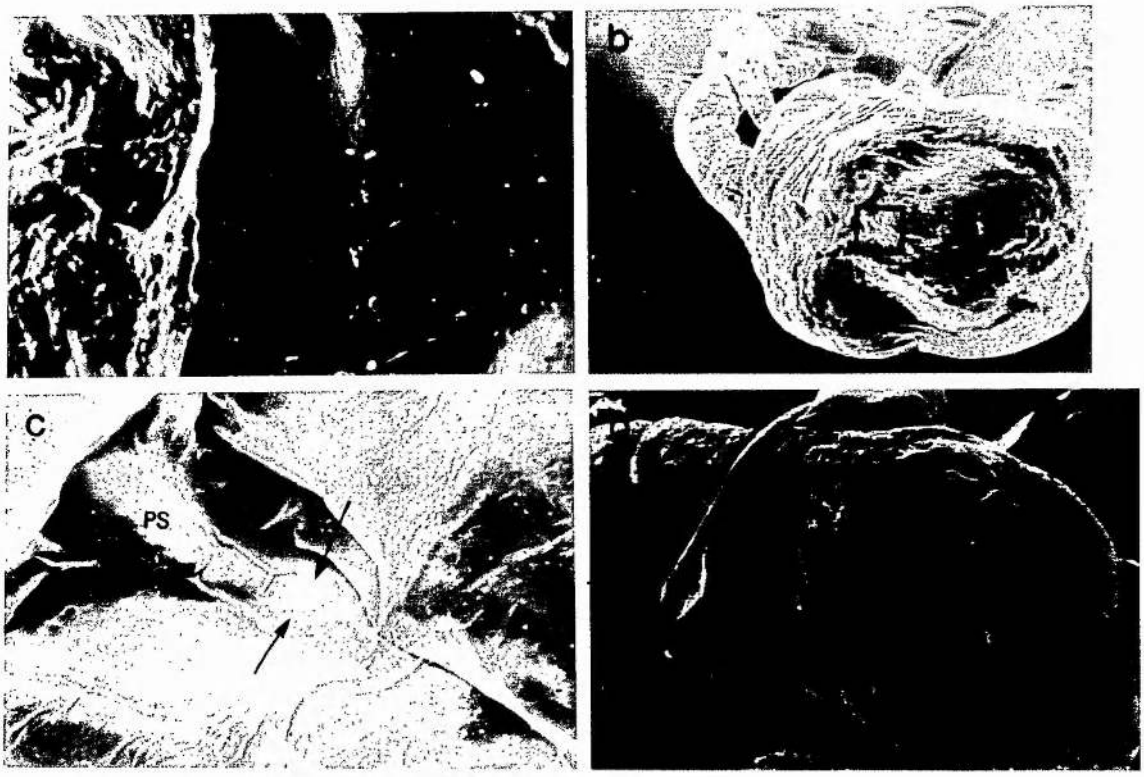
b
C
PS

Figure 40. Ultrastructural features of the dorsal organ of Carcinus maenas embryos. a, Single secretory cell (sc) with basal secretory granules (g) and potential tubular system placed apically (arrow). b, Detail of the tubular system formed by microvilli (mv); vesicles are clearly seen (small arrow). There is not defined reservoir but an incipient one might be present (thick arrows). c, Position of two sensory plate-pits (arrow) and surronding yolk (Y). d, Longitudinal section through the rootlet system (R) and sheath cells (SC1, SC2, SC3). e, Longitudinal section of the sensory pit showing the rootlets (R), basal body region (bb), and distal dendrites (triangles). abundant Golgi complexes (G), endoplasmic reticulum (er) and mitochondria (mi) are present more proximally. f, Transverse section of the same proximal segment and the two rootlet system (R) can be observed. EM: embryonic membrane.

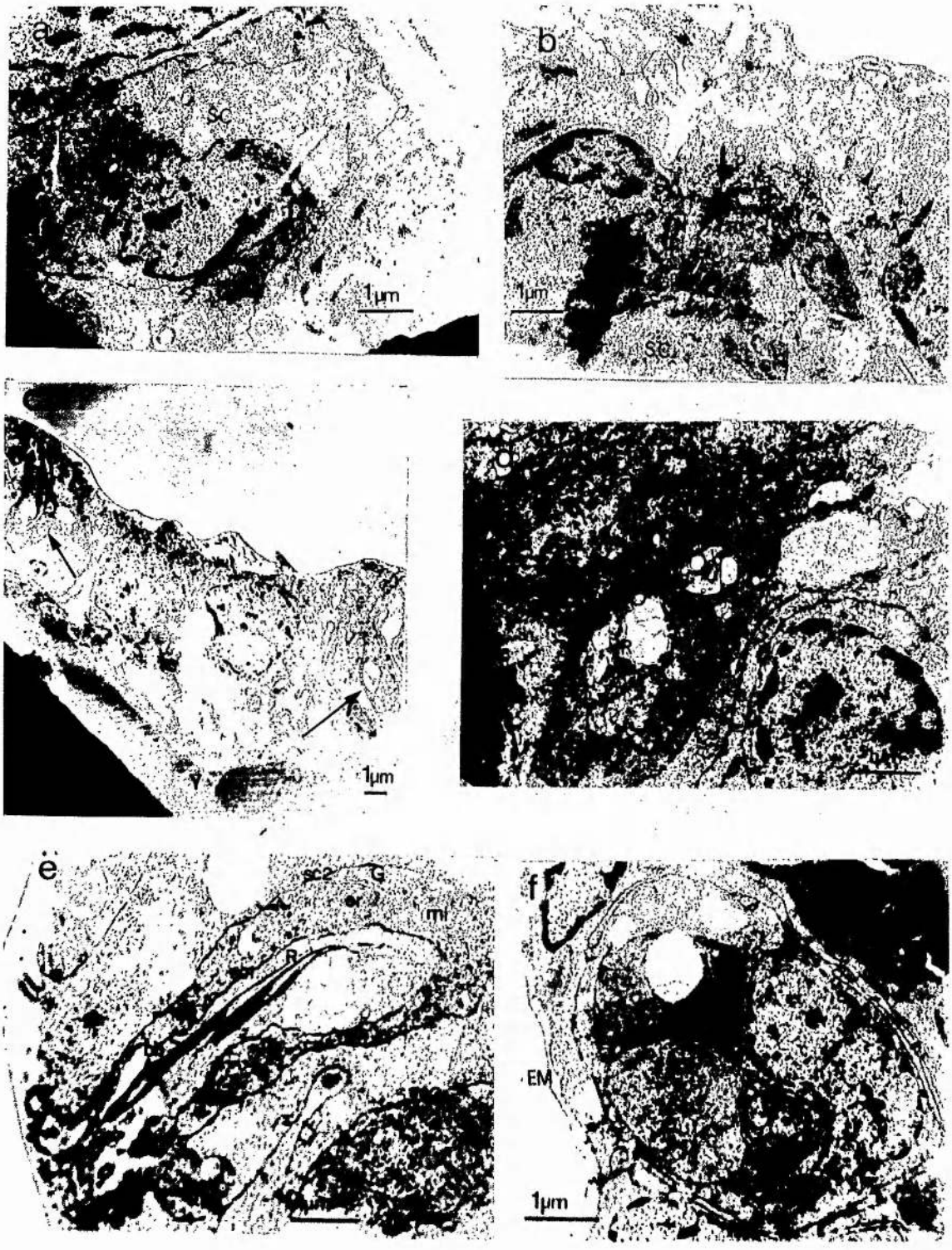
a
sc
1µm
b
1µm
sc
1µm
e
sc2
G
er
mi
R
f
EM
1µm

Figure 41. Schematic representation of the head region and associated setal appendages of *Carcinus maenas* embryos.

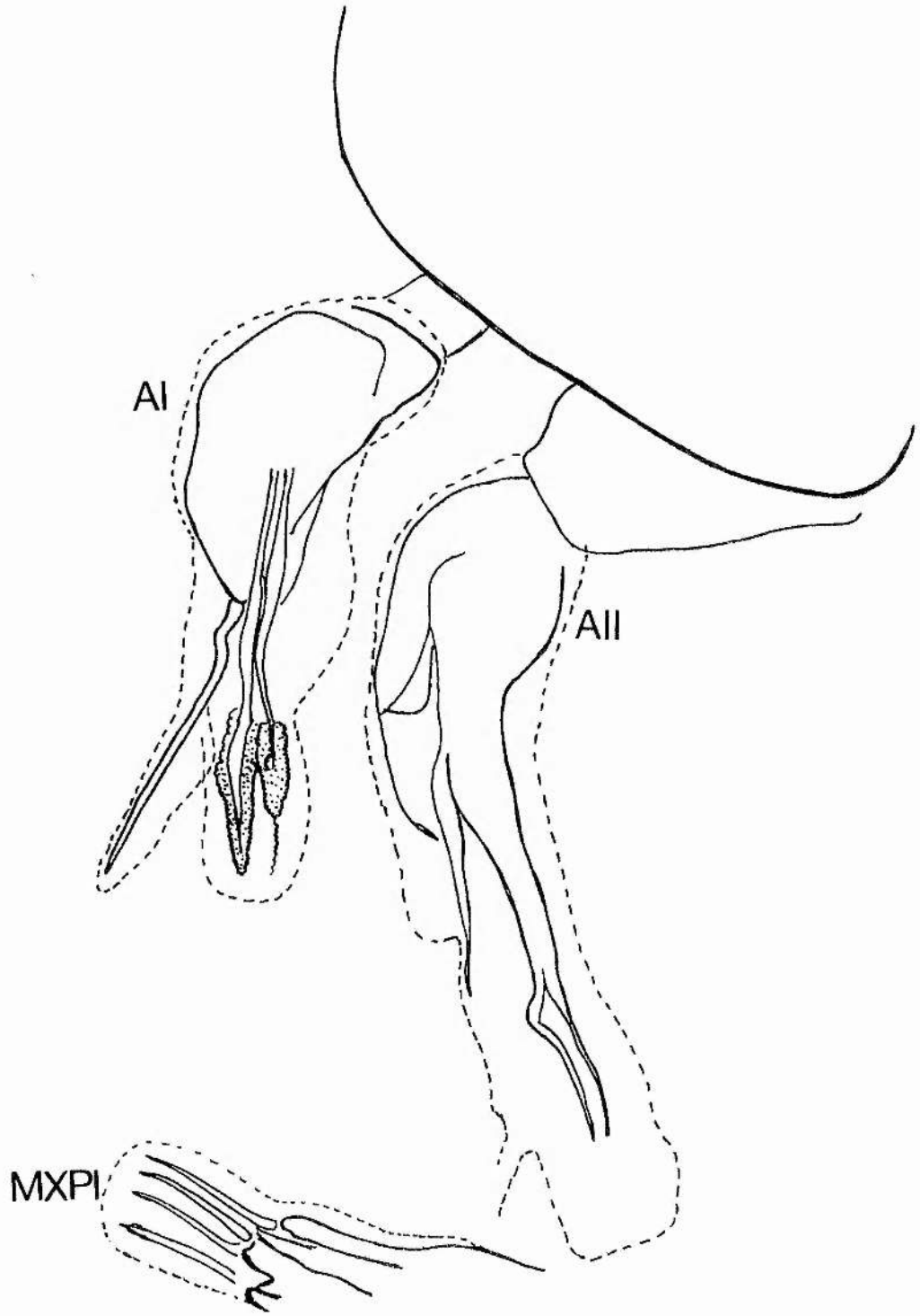
AI
AII
MXPI

Figure 42. Ultrastrutural features of the embryonic posterior spine of Carcinus maenas. a, SEM view of the anteriorly folded posterior spine (ps). b, the tuft hair-like projections (arrow), and the surrounding yolk (Y). c, Transverse section through the posterior spine main body and the tuft hair-like projections (arrows). d-e-f, Transverse sections through single bipolar neurons at different levels, and associated cell components (sheath cells (sc1, sc2, sc3) and mitochondria).

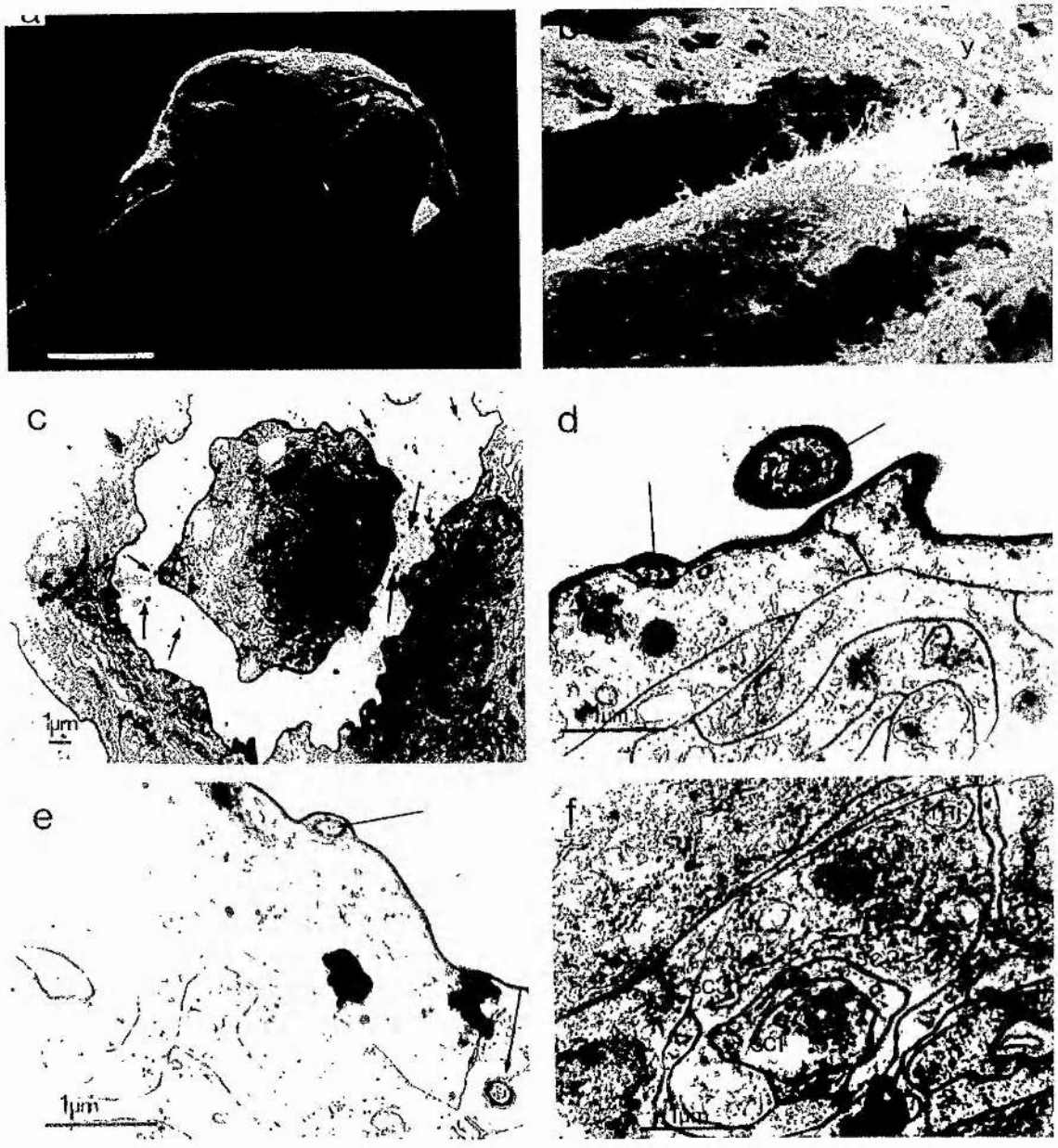
a
b
y
c
1µm
d
1µm
e
1µm
f
mi
scl
scl
mi

Figure 43. Hair sensilla associated with the embryonic first antennae of Carcinus maenas. a, General view of two potential mechanoreceptors and three chemoreceptors hairs (cd). b, Detail of the scolopale matrix of two and three bipolar sensory neurons. c, Same group of neurons and the ciliary segment. d-e-f, High number of innervating sensory cells in the potential chemoreceptor hairs.

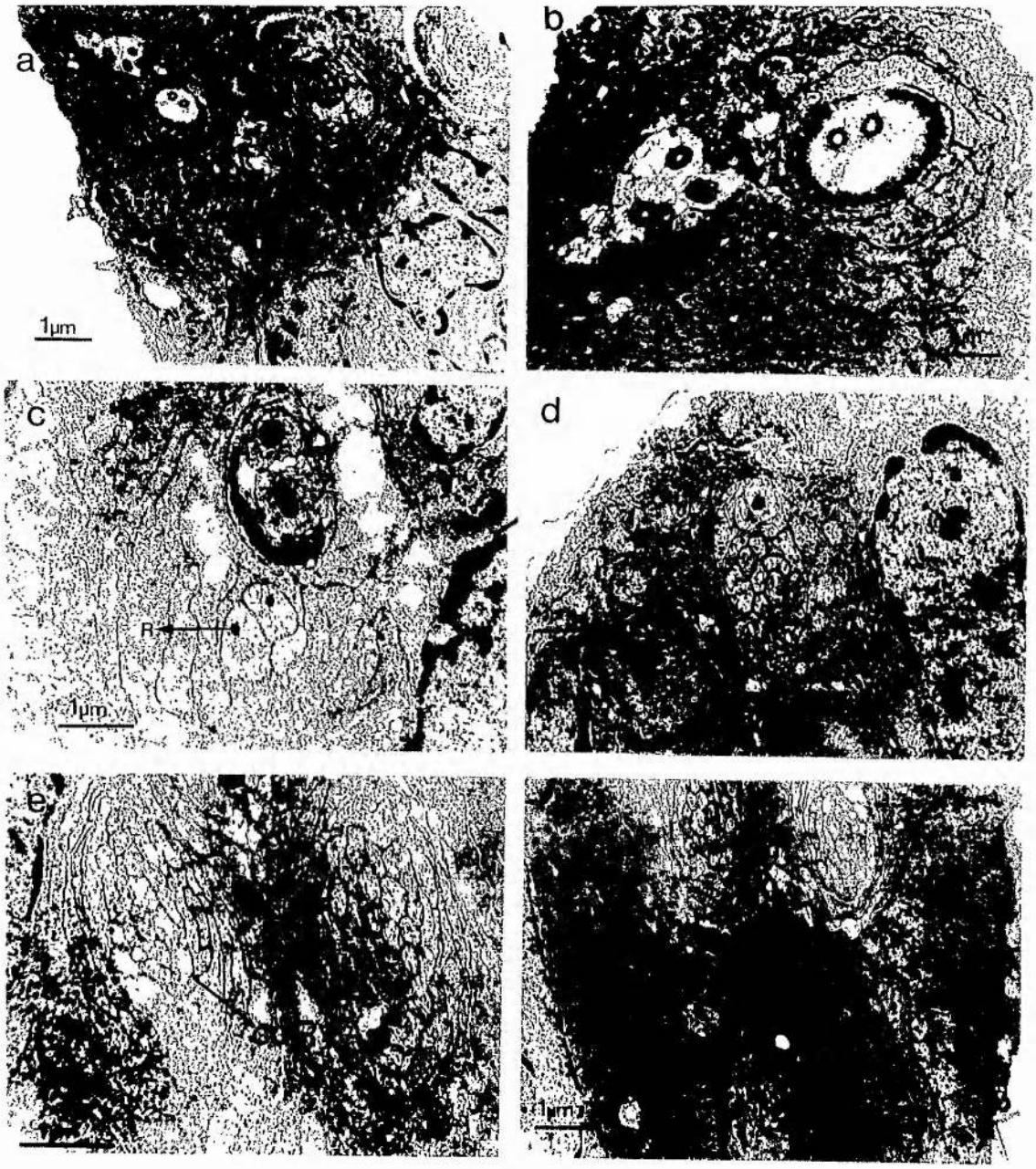
a
1μm
b
c
R
1μm
d
e
1μm

Figure 44. Ultrastructural features of the embryonic and pre-hatching maxilliped setae of Carcinus maenas. a, Four sensory hairs (arrows) are associated with each maxilliped. b-d, Details of two sensory cells innervating one hair and the corresponding cellular components. c, Potential chemoreceptor hair showing four dendrites (d). e-f, Details of the same type of hair (clear triangle) in a more distal region.

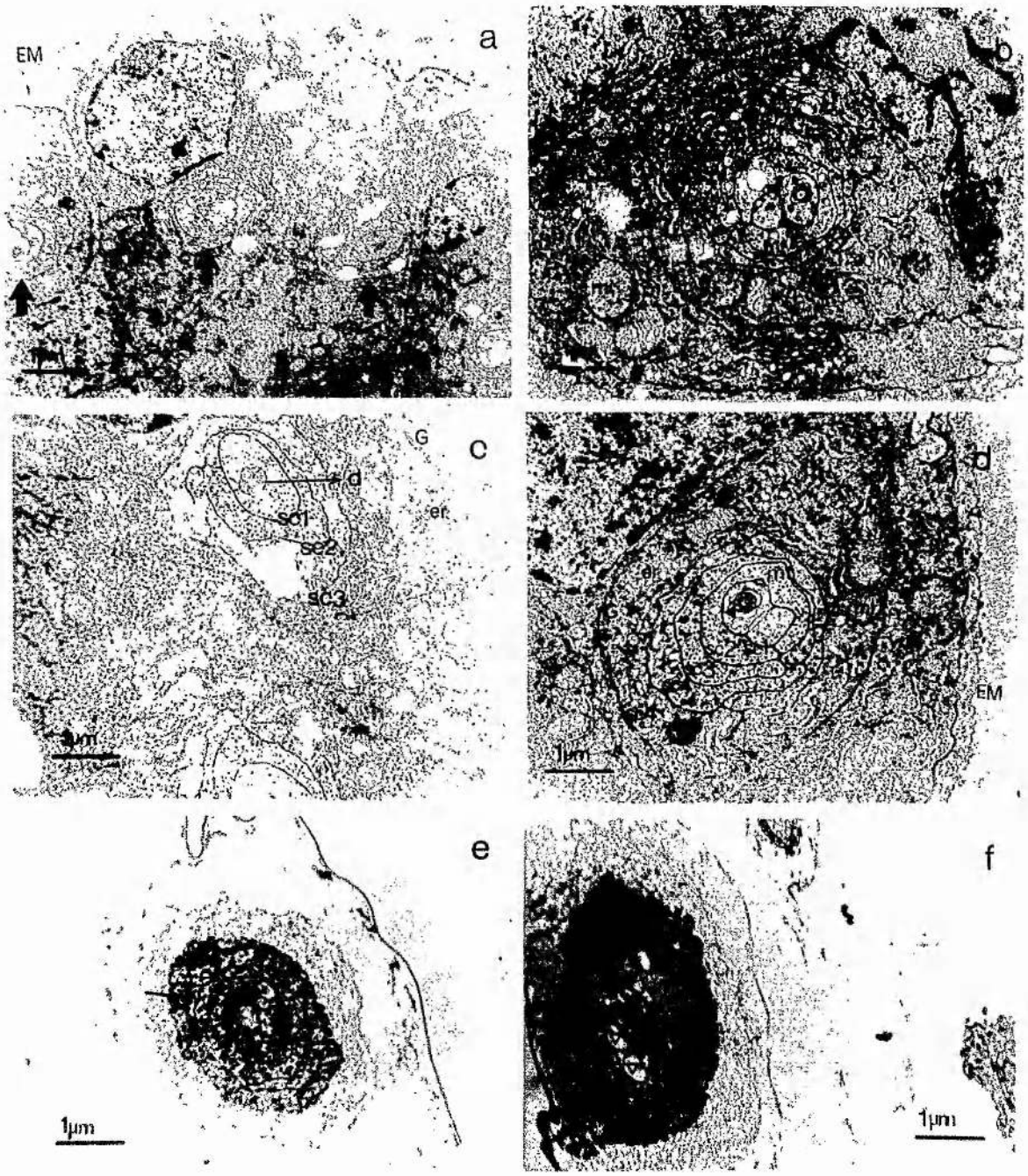
a
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Figure 45. Body chromatophore behaviour after dorsal organ glue- blockage in Macropipus depurator zoea I. a-c, Chromatophore pigment agglutination in the experimental animal. b-c, Normal chromatophore shape in the control animal.

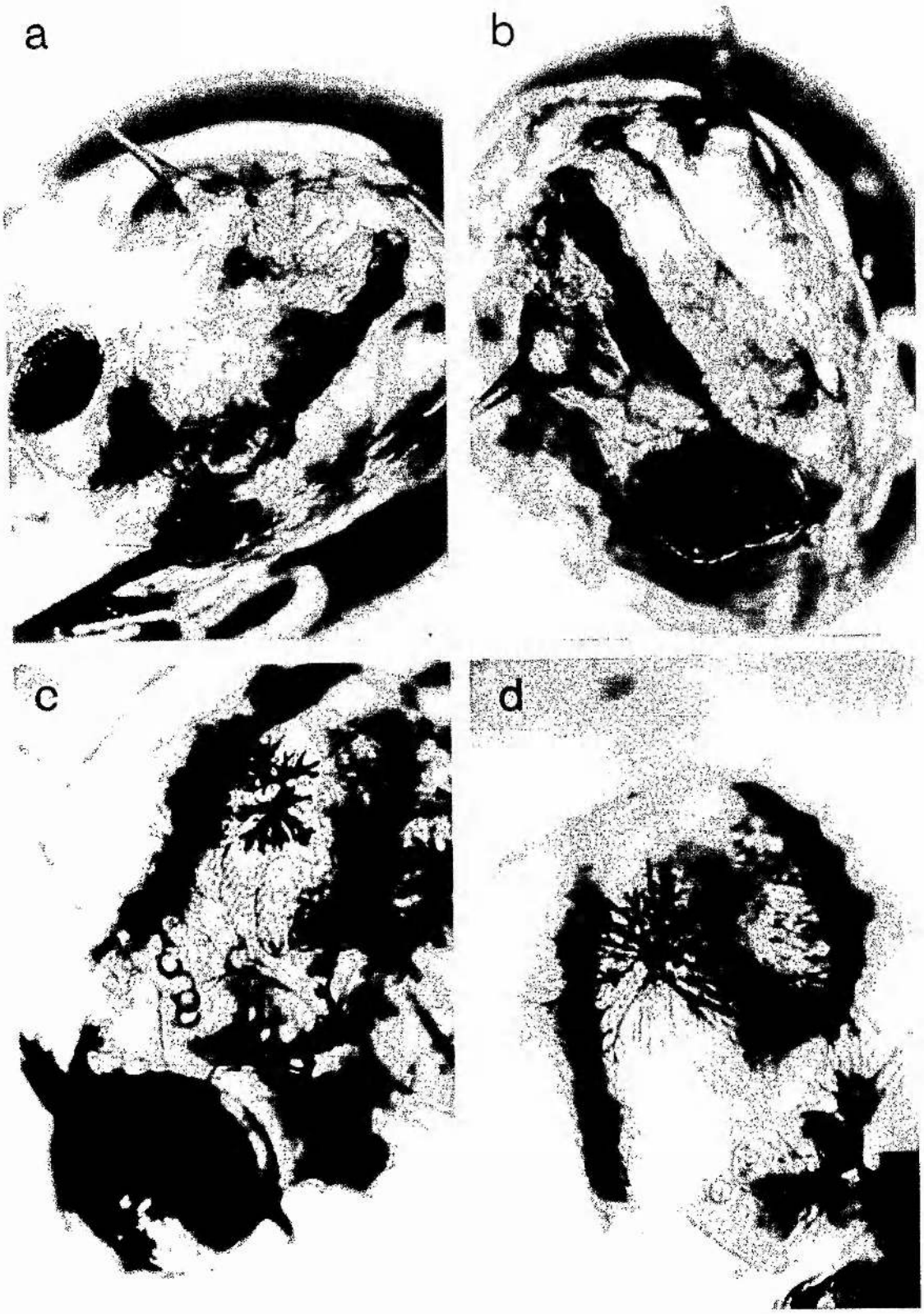
a
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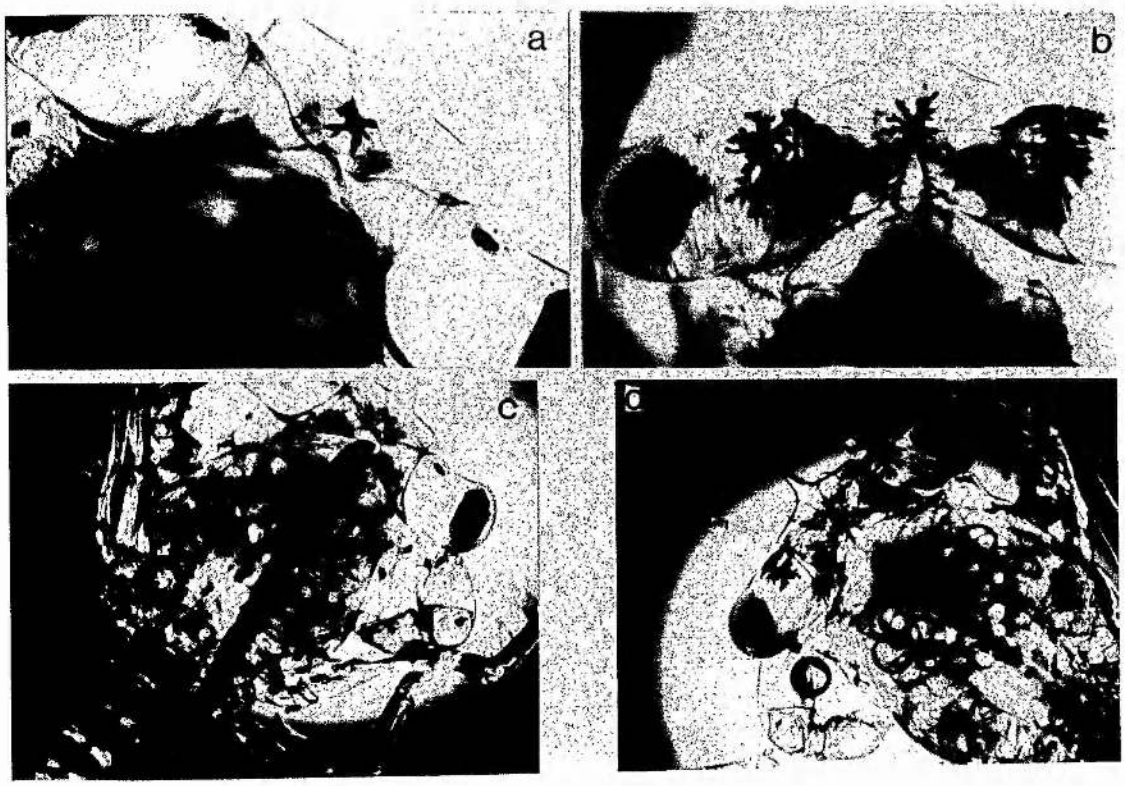
Figure 46. Eye-stalk region and chromatophore behaviour after dorsal organ glue-blockage of Macropipus depurator megalopa I. a-c, Chromatophore pigment aggregation in the experimental animal. b-d, Chromatophore pigment dispersion in the control animal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SECTION IV

DISCUSSION AND CONCLUSIONS

Little work has been done on the functional anatomy of setae on the body and appendages of crustaceans. Completed studies on sensilla are difficult to achieve, especially when dealing with problems such as setal dimensions in small forms or preparation of the animal tissue in adult forms. For a number of sensilla, however, not only is the fine structure known but their function has also been established by electrophysiological methods (Laverack, 1963; Shelton and Laverack, 1968; 1970; Hatt and Bauer, 1980; Derby and Atema 1982 a, b; Altner et al. 1983; Seelinger, 1977, 1983).

Behavioural studies have indicated that the animal is equipped with sensors which permits it to respond to the changes in its environment. Stimulii such as prey/predator approach, mate and territory recognition are important. The animal can generate a specific behavioural pattern of activity in response to the incoming stimulii. Some of the data obtained here on the fine structure of sensilla among the species of Crustacea studied will complement earlier studies (Fish, 1972; Atkinson et al. 1982) to give a better understanding of

the role of these sensilla in the activities of the animal. In other cases, the results are more difficult to relate to previous work as they represent new types of sensory or non-sensory structures. In this study, the term setae or sensilla refers to all cuticular projections which have an articulated or rimmed base. Other projections are categorized as simple outgrowths.

Sensory and Other Superficial Structures of Crustacea: Malacostraca

A comparative survey of appendages and sensilla among members of several Amphipod and Isopod families (Pontoriidae: Haustorius spp; Ampelliscidae: Ampellisca typica; Idotheidae: Idothea pelagica; Cirolanidae: Eurydice pulchra) deep and sublittoral species respectively), shows a remarkable arrangement of conical spines (spicate spines as Atkinson et al. 1982). In all these species, the conical spines have modified tips bearing sub-apical setules. For instance, spines with a sub-apical depression with adjoining squamous setule: Haustorius spp, second and seventh pereiopods (Fig. 3); setule with ventrally positioned single pore:Eurydice pulchra, third and seventh pereiopods (Fig. 2); spines with split tips bearing a setule with ventrally positioned single pore:Idothea pelagica second and

seventh pereiopods (Fig. 7).

Studies on amphipods living in soft bottoms (Enequist, 1949; Dalh, 1970, 1973; Fish, 1972; Saudray, 1972; Atkinson, 1974 a, 1982) have shown that their behaviour involves several activities including picking, stretching, swimming and crawling, to produce the complex burrow systems which they inhabit. Some of these studies have described the morphology of the pereiopods, in particular the gnathopods, and their associated setae. Atkinson et al. (1982), working on the burrows and burrowing behaviour of Maera loveni (Crustacea:Amphipoda), suggested that the disposition and structure of setae of the first and second gnathopod might indicate a dual role of these limbs in digging and grooming. These authors interpreted the position of the spicate spines along the leading edge of the dactylus and propodus (gnathopods) and their structure as indicative of a chemosensory rather than a secretory function (cf. Fish, 1972). Atkinson et al. (1982) found the terminal perforations of the spicate spine at the light microscope level but not with the scanning electron microscope.

In the present study, evidence has been found indicating that there are potential sensory endings at the conical spine tips on the amphipod and isopod species studied. The size of the pore and the lining membrane may represent a cuticular cap for the sensory endings of potential chemotactile receptors.

Interstitial amphipods apparently feed actively on sand grains to which food material has adhered (Wilson, 1966; Nicholaisen and Kanneworff, 1969). Earlier studies showed that in sand-dwelling meiofauna many species are able to distinguish between sand grain sizes (Boaden, 1962). Gray (1966 b, c), working on the interstitial archiannelid, Protodriloides symbioticus, found that it seemed to be able to select sand grains of 200-300 µm in diameter, although not all sand grains within that range were picked up. Attractiveness was found to be linked with the number and type of bacteria coating the grains. Removal of the bacteria coating using chemical and heating procedures reduced the degree of attractiveness (Gray and Johnson, 1970). The presence of a specific cocoid bacteria was responsible for the desirable grains, and linked with this was a component of the bacteria cell wall. Bousfield (1978) reported the first and second gnathopods on some species of two amphipod superfamilies,

Ampeliscoidea and Corophioidea, as being glandular and basic to the needs of burrow construction. Shyamasundari and Rao (1974) reported mucous glands in the first and second antennae, periopods and uropods, suggesting that pereiopods were not alone in having glandular units. They found no evidence of mucous secretion in the gnathopods of Talorchestia martensii (Weber) and Orchestia platensis (Kroyer).

In contrast with the stout and robust spines found on the pereiopods of the amphipod and isopod species studied here, the dorsal and epimeral body plates are furnished with a wide range of ariculated peg sensilla. These pegs describe specific distributional patterns and frequencies per body plate. In general the pegs do not differ greatly in length, ranging from 5 to 15 µm. There was species specificity, however, in the accessory elements at the hair base or hair socket.

For instance, a cuticular lip is present at the peg base in Hyperia galba, modified cuticle in the shape of extensions in Haustorius spp. and squamous surface of a peg or several pegs of the same type placed in a groove in Ampelisca typica. The last group might be related to the cuticular articulated pegs (CAP organs, cf Laverack, 1978 a, b), found at the joints of maxillipeds and on

other pereiopods of many decapods. Derby (1982) reported them in similar body areas on the lobster, Homarus americanus. These sensory pegs represent external proprioceptors, detecting the position of joints by the bending of the appendages and the extension of joint membrane (Oakley and Macmillan, 1980; Mill, 1976).

Articulated pegs, as present on Haustorius spp., resemble greatly those reported by Derby (1982) on the crusher claw of H. americanus. Similar pegs were categorized as type I hair organs by Solon and Cobb (1980). The presence of a knob limiting the rim of the peg was reported as giving a preferential directional sensitivity to deflection (Derby, 1982) and this has also been demonstrated for the hydrodynamic receptors of Palinurus vulgaris (Vedel and Clarac, 1976). The presence of an asymmetrical cuticular lip around the peg base as found in H. galba in this study illustrates the above mentioned function.

In comparison with H. galba and Haustorius spp, the isopods E. pulchra and I. pelagica also have short pegs on the body surface but with no modified rims or bases. Peg tips, however, have apparent terminal pores, ventrally positioned and half size with respect to those found in the conical spines of pereiopods of the same

species (Fig. 1 g; 1 h). These peg sensilla may respond to water vibration and touch (Laverack, 1962 a, b), and are probably involved in many other patterns of behaviour.

The antennae of the male Cumacea D. cornuta, are greatly developed and their multiarticulated flagella contain a unique type and arrangement of aesthetasc hairs. No other type of sensillum is found along the flagellum. On the basis of their external morphology, these aesthetascs represent a unique type in Crustacea, with tips bearing a ventrally positioned pore and a bifid end. Heimann (1984) described the aesthetascs of Asellus aquaticus and terminal or apical pores were not found on them. This author suggested that the name "moulting pore" following previous Gnatzy reports, may be more accurate when discussing pores of this type of sensillum. He considered that the pores and pore-channels (serving as stimulus conducting structures) in the insect sensilla are not present in crustaceans. Laverack and Barrientos (In press) suggest the potential importance of split setae tips as chemoreceptive indicators. Observation of the pores in this cumacean did not reveal the presence of any electron dense material which Heimann (1984) considered to represent a moulting plug as found in insect aesthetascs. This group

of aesthetascs was observed to be stretched out or curled up along each annulus, with their tips clustering together. This particular arrangement defines an area where the pores are less than 0.5 μm distant from each other. This organization of pores concentrated in this comparatively small area could represent an important anatomical device for stimulii detection.

Felgenhauer and Abele (1983) have indicated that the olfactory setae or aesthetascs borne on the antennules of the shrimp, Atya innocous, possess apical pores placed ventrally at the hair tips. They suggested that the cheliped fans scrape rock surfaces, and thus the pores are in direct contact with the substrate and potential food sources. These chemoreceptors may help the shrimp in detection of food in both the water column and the substrate.

It is known through antennae and aesthetasc ablation experiments that they function as sensitive chemoreceptors which elicit searching behaviour (Copeland, 1923; Atema, 1977; Devine and Atema, 1982; Gleeson, 1982; McLeese, 1974; Reeder and Ache, 1982; Wasserthal and Seibt, 1976). Details of the fine structure of these unique aesthetasc hairs awaits future investigations. On the basis of the present study it is

obvious that Heimann has overgeneralized these aesthetasc anatomical observations.

The integument of this cumacean, as well as, that of the copepoda Monstrillidae Monstrilla longiremis, exhibits a most unusual type of cuticular outgrowth (Figs. 7, 10). There is no mention of related shapes in the literature. Sars (1918), in earlier taxonomic reports on these species, referred to their coarse integuments as "strongly incrusted with squamous structures" and with "finely granular or dotted surface" respectively. At present, no evidence has been found to ascribe a sensory character to these cuticular outgrowths. Both species do possess common types of articulated peg sensilla on their body surface, these being less in number in the Monstrillidae. The presence of folded membrane domes along the lateral sides of the animal may represent potential devices for body adhesion to the host tissues (Fig. 10a). Other openings, such as those present on the last metasome segment (Fig. 10 b, e, f), could indicate the presence of integumental glands. The two blunt-sac outgrowths in the Cumacea (Fig. 7 a, c) are also unusual but their function is unknown. Probably under the same group could be included the rosette outgrowths present in the Bopyridae, Pseudione hyndmani and found on the ventral body plates

(oostegites) (Fig. 8).

Among all these unusual outgrowths, one was found to possess some morphological features which could put it in the categorization of a sensor. This is a flower-shaped outgrowth furnishing the carapace of Dorippe lanata and describing distinctive patterns (Fig. 9). The outgrowth is articulated at its base with a large surface area at the top due to the presence of thin membrane projections. Bloom (1982) found rather similar projections called papillae forming part of an enigmatic papillate sensillum with a unique sensory cuticle on the larval antennae of Tenebrio molitor. No function was ascribed to this unusual sensillum by the author. A similar type of outgrowth was found on the chelae of H. gammarus characterized as a fan-receptor involved in water vibration and movement detection (Laverack, 1962 a, b).

This rather limited comparative study of superficial structures on the integument of Crustacea indicates that a lot more research is necessary for a better understanding of the role of these presumtive sensors in the behaviour of the animals. There is a great deal of variety in size and form of setae in the Crustacea described here. There is still, however, a lot to be

morphological features, distribution and association of setae described, it is still extremely difficult to assess the potential function of the various types.

Sensory and Other Superficial Structures on Decapoda Larvae and Embryos

Examination of the decapod larval integuments indicates the presence of sensory structures and outgrowths, some of which are specific in type and frequency for a particular developmental instar. There are, however, some sensory types which represent incipient forms of the fully developed types present in the adult.

The trichoid sensilla mapping studies of the larval body and urosome show that the majority of the larvae are glabrous. Progressive increase in number and type occurs from the zoeal to the megalopal stage and completely furnished carapaces with superficial projections (sensory and non-sensory) characterize juvenile stages.

The traditional argument has been that the spines and larger feathered setae, with which planktonic Crustacea (particularly larvae) are frequently provided, may assist flotation or give protection against enemies

(Calman, 1911). Then, it seems that the argument for flotation might be a more valid one (Kaestner, 1970; Strickler, pers. comm). The presence of long spines in the planktonic forms do not imply the occurrence of sensory structures on them. This was the case in the Porcellanidae spp. provided with long body spines with no sensors on them (Fig. 14a). In this study it was observed that the larval instars displayed the least sophisticated setal armature, in terms of type and numbers. This finding was also encountered by Thomas (1970, 1973) while describing the first stage hatchlings of the crayfish, Austropotamobius pallipes. Factor (1978) suggested that the change in diet from planktonic to benthic habitat during the larval and post-larval stages of H. americanus, was correlated with the variation of setal organization and mouth part morphology. This author pointed out that the development of potential fuctional teeth on the ischium of the third maxilliped occurs at the time when the primary function of these appendages changes from swimming, in the first three stages, to feeding, in all the subsequent stages.

A common trichoid sensillum was observed in varying numbers and arrangements amongst all the larval forms studied, indicating that the setal organization and frequency may be an important factor in attempting to

account for functionality. Particularly, in lobster larvae (Fig. 12), the trichoid hairs are concentrated in rows or groups along the urosome surface, while in the crab larvae these hairs are less in number and in a simpler arrangement along the same appendage. Also in the lobster larvae, the trichoid sensilla tend to be concentrated in two double rows along the telson but during post-larval stages this hair arrangement becomes more widespread along the whole telson and uropod sides. A similar pattern was observed by Thomas (1970) in young crayfish, where the hamate setae are confined to the margins of the epipodites, while in older animals these setae have a tendency to spread over the two faces of the epipodite lobes. Seemingly, once the post-larval stages are reached, the trichoid sensilla are still present in the lobster group (with different dimensions) but in the majority of the crab larvae these hairs are replaced by a completely different type of hair, set singly or in small groups. The best example of these setal changes are the ones observed in the juvenile integument of H. cornutatus and P. longicornis. In the former species there are at least four types of sensilla clustered in each of the cuticular domes (Fig. 19c). This characteristic is also found in the crayfish, A. pallipes where, for instance, acuminate setae in the young animals are found singly while in the adult they are found in groups and

associated with pappose setae with stout setules (Thomas, 1970).

Perhaps one of the most striking findings of this larval setal survey, is the incipient form of the "campaniform sensilla" (Shelton and Laverack, 1968), or the "funnel-canal organs" (Gnatzy et al. 1984) found on the distal segments of the walking legs, particularly at the tips of the dactyl epicuticular cap, of the adult C. maenas. The latter authors suggest that the funnel-canal organs are chemo-mechanosensitive and that their distribution is parallel with the distribution of contact chemoreceptors in insects.

In the present study these structures were found in the same appendage region in the megalopal instar of H. cornutatus and C. maenas (Fig. 17). Obviously these sensory structures occur only at this stage of development because these limbs are absent in the zoeal instars. Most of the sensory studies carried out on the adults have ignored the potential existence of structures like the above mentioned in the developmental instars. This study, therefore, provides some information on the occurrence and distribution of this particular sensillum in the post-larval forms of crabs.

In the megalopal stages another type of sensillum was found along the inner edge of the pereiopod segments. It is a triserrulated hair. Bauer (1975, 1977), working on pandalid and caridean shrimps, found similar setae on their mouthparts, which he said indicated a rasping function during grooming and ascribed a chemoreceptive character to them. Equally, reports by Roberts (1968) showed that these serrate setae might be involved in cleaning processes as "cleaning brushes". Factor (1978) suggested that serrate setae may aid grooming but behavioural observations were not available to confirm this.

In the present study, however, these types of triserrulated setae (as Factor 1978; but more than three setule rows in this case) occur specifically on the pereiopods. This setal position suggests that they are more related to substratum grasping than scraping or cleaning. Animals were observed firmly attached to the bottom of a plastic petri-dish and picking them up was difficult.

A number of cuticular extensions which ornament the integument of early zoeal stages (Figs. 15, 16) are more difficult to characterize or relate to a particular function. Most taxonomic and phylogenetic studies have used integumental outgrowths and setal counts as indicators of evolutionary trends among groups of Crustacea (Gurney, 1926, 1939; Lebour 1927, 1928 a, b; Menzies, 1960; Rice, 1967; Gonor and Gonor 1973; Fleminger, 1973; Mauchline, 1977). Some of these studies have used chemical abraded integuments, and their interpretation of the integumental holes as previous sensilla may be dubious when considering the heterogeneous projections and ingrown structures (gland ducts, plate-pit, folded membranes, scales, etc.) of the animal integument.

Setal studies in embryonic and pre-hatchling Crustacea are even more scarce (Prentiss, 1901; Cheung, 1966; Thomas 1970, 1973). During the brief pre-zoeal stage, lobsters and crabs are unable to swim. Some studies have stated that, since the natatory appendages are devoid of setae, immediate moulting after hatching brings about the first free-swimming stage (Lebour, 1928 a; Thomas, 1970; Farmer, 1974). In the present study, observations (using transmission electron microscopy) of

some appendages (first, second antennae and maxillipeds) of C. maenas embryos (stage IX-X) revealed the presence of well developed (anatomically speaking) setae in these limbs (Fig. 43, 44, 45). Early studies have overlooked the fact that embryos and hatchling crustaceans do have well developed sensory hairs. These sensilla are enclosed by the embryonic membranes which are disrupted at the moment of hatching. There is no reason, however, to assume they lack sensilla at these stages or earlier ones.

Thomas (1970) described hamate setae on the margins of the embryonic epipodites three days before hatching. They are not fully formed at this stage, lacking the hemispherical basal portion characteristic of the fully-developed setae. He also pointed out that the fringe of pappose setae on the scaphognathite margin is partially developed two days before hatching when the scaphognathite itself becomes functional. He suggested that all setae present on the first stage hatchlings are those associated with the respiratory movements of the animal, during this inactive feeding stage. At the same time, he questions the fact that the hamate and pappose setae should develop so early in the life of the animal (larvae I).

In examining the fine structure of the setae associated with C. maenas embryos stage (IX-X), it becomes apparent that there is an analogy, in terms of the anatomical organization of potential mechanoreceptor and chemoreceptor hairs, with the other well-known receptors present in the adult Crustacea. There is usually an increase in sensory cell numbers and organelle dimensions, and a greater complexity in function due to the more intricate and complete sensory net-works in the adult animal. At the embryonic level, however, the genetics and the developmental biology of the animal are the modeling forces generating the future code or the sensory organization that these animals will exhibit in later stages of life. This study has advanced the knowledge of the ultrastruture of the antennal and maxilliped receptors. Sensory setae are structurally well defined in these early embryonic stages. The animal is not using them functionally speaking. It may be assumed that the sensors are non-functional in these embryos due to the egg membranes isolating the animal from the environment.

Dorsal Organ:Glandular and Sensory Unit on Decapoda Larvae

The most conspicuous structure described in this investigation is a discrete organ system lying in the anterior region of the carapace of these developing forms of Crustacea. This organ was present in the embryos of Decapoda: Brachyura (C. maenas) and the larval and post-larval instars of Macrura, Anomura and Brachyura. The dorsal organ appears as a pore or poreless central area surrounded by four plate-pits. It occurs in stage IX-X embryos and prevails in the following instars until the juvenile forms, where no trace of it was found. There are significant changes among the groups. For example, in the Anomura some species display more than one central pore. This was the case of P. platycheles and G. strigosa.

The internal organization of the dorsal organ indicates the existence of a glandular unit consisting of a gland cell and a ductule cell surrounded by a sensory complex of four plate-pits. All these components are incorporated in a dome-like structure. The nature of the cellular components of the gland cell permits its characterization as a class 3 gland cell (Noirot and Quennedey, 1974). In this complex the ductule cell secretes the cuticular ductule that is connected with the second cell, the gland cell, bearing a large central

cavity. This cavity has a well developed tubular system which consists of large and packet microvilli, arranged in serial clusters. This arrangement was more pronounced in early zoeae than in later zoeal instars, where the microvilli matrix (at the reservoir) described a more packed organization in a rather bulbous fashion. This cavity or reservoir contains the modified terminal part of the duct, the end apparatus. The other main cytological component of this gland cell is the amplified plasma membrane invaginations formed by extracellular channels of various sizes and shapes (Fig. 28). This amplification of the basal membrane taking up the greatest portion of the gland might demonstrate its importance in the functioning of the gland, facilitating exchange between the cell and the haemolymph.

In this glandular system there seems to be evidence of much synthesizing activity (mitochondria, smooth and granular reticulum and Golgi complexes), suggesting a substantial synthesis of small molecules. It was not possible to find any trace of secretion in the duct. Only a histological study could provide additional information. Noirot and Quennedey (1974) indicated that small-size molecules, which are extremely important in insect secretions, may be lost during the fixation or embedding procedures and cannot be recognized under the

electron microscope. This may be one of the problems encountered in this research work where good fixation of the vacuole contents was difficult to achieve.

The secretion products in the gland cell are probably of no more than two types. They consist of dense homogeneous secretions, found only within vacuoles of the apical cell region (Fig. 28 a, e small arrows).

The secretory products were present in a large amount at the pre-zoeal stage. There are dark and light electron dense granules placed at the supra-nuclear area. The high abundance of well developed Golgi-complexes (Fig. 37 a, d) containing "internum" and associated vesicles, and the cisterna of ER present in this region may form part of an intracellular digestive system as found by Gupta and Little (1970) in zymogen cells of Pogonophora, and engaged in synthesis of some secretory protein.

The major concentration of these secretory products was observed to occur only at this stage of development. This aspect may provide a link between the synthesizing activity peaks of this large gland cell and larval development. The present electron microscope study indicates that the fine structure of the gland cell

components could provide evidence for the above statement. Features such as the amount of secretory products which are associated with the well developed Golgi complexes, vesicles and ER at the pre-zoeal stage; the presence of microvilli clusters with dense tips and attached glycocalyx (potentially related in secretion transport, cf. Wasserthal and Wasserthal, 1977) during the early zoeal stages; and the absence of secretory products, microvillar clusters, as well as, electron dense material attached to the microvillous tips during late zoeal stages; are all examples of cellular changes and deterioration in relation to activity. According to the available SEM information, this organ is not present in the integument once the post-larval (Anomura and Macrura) and the juvenile instars (Brachyura) are reached. Internalization of the organ might be an alternative but this is also unknown.

The importance and function of the electron dense microvillus tips and attached glycocalyx (Fig. 28 c, d; 31 c, d) are unknown. In Caligo eurilochus brasiliensis, gland cells with dense microvillar tips were found associated with dense microvillar clusters in the secretory niches and both may help in the transport and orientation of secretions from the releasing vacuoles towards the centre of the glandular space (Wasserthal and

Wasserthal, 1977). These authors have pointed out that the transportive function of the microvilli has not been considered in insect glands so far (Steinbrecht, 1964; Quennedey, 1969; Pliske and Salpeter, 1971; Noirot and Quennedey, 1974) despite their constant occurrence among class 2 and 3 gland cells. The alternative to the transportive function by microvilli is the reabsorption of some components in special compartments. This is the case of a kidney-shaped organ in the reservoir of the scent gland of Dysdercus spp. which suggests an absorptive rather than a secretory function (Schumacher, 1971).

Much attention has been given to endocrine systems in the larvae and adults of Decapoda, but rather fewer studies have been done on their excretory systems and these have been restricted to the antennal glands (Robertson, 1949; Parry, 1955; Gross and Marshall, 1960; Riegel and Lockwood, 1961; Malley, 1977a) and gills (Koch, 1954; Bielawski, 1964; Lockwood, 1967). In endocrine systems, in reports on the x-organ in Homarus, spp. indicates its occurrence in the embryonic stages, increasing in size and complexity through larval and postlarval development. In contrast the sinus gland does not develop until the third larval stage and its activity has been traced only at the adult stage when acidophilic

and basophilic secretion granules are present (Aiken, 1982).

The Y organ (Gabe 1953, 1954, 1956) is known to be related to moult control (Echalier 1955, 1956, 1959) and found to be larger in young crabs rather than in old animals. Both the Y-organ and the cephalic glands (Gersch et al., 1979) are responsible for secretion of ecdysteroids which seem to regulate the moulting process. By analogy with the insects, it was assumed that the moulting hormone would prove to be one of the ecdysones (Pasano, 1960), and which is known to be produced in the prothoracic or ventral (head) glands or ecdysal glands. This pair of glands, together with the Corpora Allata (CA) lateral glands (which sometimes fused into a single structure c.f. Highnam, 1967; Herman, 1968) are discrete and non-neural epithelial endocrine glands. Their target is the epidermis and their developmental role involves the control of metamorphosis, caste determination and phase differentiation. They are derived from clusters of ectodermal cells at the base of the maxillary mouth parts. Both glands, ecdysal and Corpora Allata, become vestigial after nymphal methamorphosis. As can be seen, these are examples of endocrine glandular systems active in the animal during the early stages of life.

Insecta and Crustacea do have cephalic and post-cephalic glands involved with excretory/secretory functions. This is the case of the scent glands of Hemiptera (Filshie and Waterhouse, 1969; Stein, 1969); the pheromone-secreting gland of Harpobittacus. spp. (Crossley and Waterhouse, 1969); and the terpene secreting gland of Anisomorpha (Happ et al., 1966). All these examples represent class 3 gland cells according to Noirot and Quennedy (1974). Frontal glands in insects are reported to eject alarm pheromones and are placed in a high platform in the animal's head (Blum, 1969). The nature, however, of the gland unit reported in this study is definitely exocrine. In Decapoda, the paired antennal or green glands are found anterior to the ventral portion of the cardiac stomach and open through prominent papillae (ducts) on the lower side of the basal segment of the first antennae. They are important releasers of Mg^{++}, SO_4 and Cl^- but nitrogen excretion through them is small (Phillips et al., 1982). The dorsal organ gland cell is located anterior to the the dorsal portion of the cardiac stomach and opens through a duct or canal in a dorsal dome of the head region. Thus, the two glands are placed more or less in parallel, one dorsally (Dorsal organ gland cell), and the other ventrally (antennal gland). Consequently the duct of the gland cell unit may

be an analogous structure to the duct that empties (the bladder of the antennal gland) to the exterior.

Needham (1942), while describing the embryonic excretory organs of Asellus, referred to the ectodermal duct of the maxillary organ as being homologous to the nephridia of other groups of animals. The antennal organ (Nemec'gland) originates close to the epidermis at the antennal mandibulary intersegment and, having no external opening, it has a potential role as an internal secretory organ in the adult.

Secretion digestion systems such as those found in the crayfish (Riegel, 1966) have been proposed to be important in the elimination of complex waste products. It may thus be suggested that the cell gland unit component of this dorsal organ is a new excretory/secretory compartment to be included in the excretory system of decapod larvae.

Dorsal Organ: Cell Gland Unit: Sensory Innnervation

Ultrastructural studies reporting sensory gland innervations are few and most of them limited due to the apparent lack of nerve innervation in the epidermal cells. Noirot and Quennedey (1974) pointed out that, in

this sense, campaniform sensilla have always been found in sternal glands of termites. According to these authors the presence of an efferent innervation indicates the possibility of an additional regulation for secretion.

In the present study it was found that the gland cell is surrounded by four sensory plate-pits whose ultrastructural features permit their characterization as one of the more uncommon types of sensilla in Crustacea. The presence of two bicilliary sensory cells per plate-pit, as found in aesthetasc neurons (Ghiradella et al., 1968c; Snow, 1973; Guse, 1979), as well as the presence of a thin and compartmentalized dendritic sheath, and the absence of scolopale, are sufficient anatomical features to allow a potential chemosensory function to be ascribed to these plate-pits. A more unusual feature is found in the area where the four dendritic endings join the electron dense and spongy matrix which form the outer region of the plate-pit. A number of possible "dendritic branches" were found to be arranged in a circular fashion (Fig. 32 a, arrow) within the amorphous-like electron dense matrix containig microtubules. They are absent from the regions where the dendrites enter the intercuticular space. Slifer and Sekhon (1969) found similar branching in insect sensory

dendrites and suggested that the microtubules may form a link between the ciliary regions of the dendrites and the microtubules in the dendritic branches. In the present study, however, the distinct connections between them were not observed, but the coil-like arrangement was evident.

The sensory structures reported in the literature as the funnel-canal organs, present in the dactyl of the walking legs of C. maenas, resemble, to a certain extent, some of the main morphological components of the plate-pits reported here (especially at their distal end, TEM and SEM information). In this case, however, the sensory plate-pits lack the anatomical element suggesting any mechanosensitivity (mechanoreceptor sensory cells). The nature of the central cone or pimple shows this is probably the most important feature to be regarded as the end apparatus of this type of sensillum, an analogous end organ being found by Gnatzy et al., (1984) in the funnel-canal organs. Another example of an analogous functional external chemoreceptor structure may be the sensory pore in the eye-stalk of Malacostraca (Altner and Prillinger, 1980).

The vicinity of these four sensory plate-pits around the gland cell specifically in the arborescent basal invaginations may suggest a sensory control of the gland cell through them, via the CNS. It is unknown which chemicals they detect or whether they have any other function.

In conclusion, this dorsal organ present in the decapod larvae represents a new component to add to the exocrine system of the animal, in addition to the previously known antennal and mandibular glands. It is a very intriguing organ because it becomes vestigial (SEM) or may be internal once the juvenile instar is reached.

No particular function can be attributed to it at present. The preliminary physiological experiments, however, after glue-blocking the organ, seem to indicate some influence on body and eye-stalk chromatophore behaviour. The close position of this organ to the post-commissural organs may be responsible for this reaction. More research will have to be carried out in order to find out more about the role of this organ in the physiology and behaviour of the crustacean larvae.

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Subclass Malacostraca
Superorder Eucarida
Order Decapoda
Suborder Reptantia
Section Astacura
Superfamily Nephropoidea
Family Nephropoidae
Homarus gammarus
Nephrops norvegicus

Section Anomura
Superfamily Galatheoidea
Family Galatheidae
Galathea strigosa

Porcellanidae
Porcellana longicornis
Porcellana platicheles

Section Brachyura
Subsection Oxystomata
Family Dorippidae
Dorippe lanata

Leucosiidae
Ebalia tuberosa

Subsection Brachygmata
Infrasubsection Oxyrhyncha
Family Maiidae
Pisinae
Hyas cornutatus

Family Portunidae
Carcinus maenas
Portunus puber

Subsection Atelecyclidae
Family Cancrinae
Cancer pagurus

Subclass	Malacostraca	
Superorder	Peracarida	
Order	Cumacea	
Family	Diastylidae	
	Diastylis cornuta	
Order	Isopoda	
Family	Cirolanidae	Idotheidae
	Eurydice pulchra	*Idothea pelagica*
Order	Amphipoda	
Family	Ampeliscidae	
	Ampelisca typica	
Family	Pontoporeiidae	
	Haustorius spp	
Family	Hyperiidae	
	Hyperia galba	

Subclass	Malacostraca
Order	Isopoda
Infraorder	Bopyrina
Family	Bopyridae
	Pseudione hyndmani