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Zoomorphology

Are the funnel-canal organs the "campaniform sensilla" of the shore crab *Carcinus maenas* (Crustacea, Decapoda)?

I. Topography, external structure and basic organization*

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Summary. The topography of the funnel-canal organs of *Carcinus maenas* (Decapoda, Crustacea) and their stimulus-receiving cuticular and sensory apparatus were studied in the light and electron microscopes.

About 4000 funnel-canal organs are situated within the exoskeleton of *Carcinus*. Almost all of them are on the distal segments of the walking legs, in particular on the epicuticular cap at the tip of the dactyl. They were not found to be arranged in groups or sensilla fields, and no sex-specific differences were observed.

Characteristic features of the funnel-canal organs are as follows: (a) There is a terminal pore (0.5×0.8 µm diameter) in the cuticle, at the tip of a small projection. It is closed by a plug of electron-dense material. (b) The terminal sections of the dendrites are enclosed in a dendritic sheath up to ca. 10 µm below the pore. (c) The dendrites, 3–24 in number, end below the plug; none of the dendrites exhibits a tubular body; two of the dendrites are distinguished from the others by the greater number of microtubules in their outer segments.

The structural characteristics, in particular the "gustatory pore" and the number of dendrites, are typical of bimodal receptors in arthropods. In such receptors, as in the contact chemoreceptors of insects and arachnids, mechano- and chemosensitive sensory cells are combined.

This interpretation of the function of the funnel-canal organs is supported by electrophysiological data of other authors.

The morphological parameters we find for the funnel-canal organs, in comparison with those of insect campaniform sensilla, provide clear evidence against the reclassification of the funnel-canal organs as "crustacean campaniform organs" proposed by Shelton and Laverack (1968).

A. Introduction

The cuticular exoskeleton of arthropods (insects, crustaceans, arachnids) is continually exposed to mechanical forces, either produced by the activity of the animals themselves or externally imposed. Mechanical stress causes local deformation of the exoskeleton, which is detected by special cuticular receptors: the campaniform sensilla in insects, and the slit sense organs in arachnids (see e.g. Pringle 1955; Barth 1972; Chapman et al. 1973; Dumpert and Gnatzy 1977; see also the review by Barth 1981).

Among the crustaceans, there are reports of "campaniform sensilla" on the epicuticular caps (a region of flexible cuticle at the tips of the walking legs) of *Carcinus maenas* and *Homarus gammarus* (Shelton and Laverack 1968; Laverack 1976; Barth 1980). Campaniform sensilla have also been reported to be located on the lateral antennular flagella of *Homarus americanus, H. gammarus, Nephrops norvegicus* and *Crangon vulgaris* (Laverack 1976; Derby 1982). The "campaniform sensilla" of the shore crab *Carcinus maenas*, which we have now examined in the light and electron microscopes, were originally called funnel-canals (*Trichterkanäle*; Luther 1930). From ablation experiments and from the distribution of the sensilla, Luther concluded that the funnel-canals were chemoreceptors.

These organs, called funnel-canal organs by Laverack (1963), were classified as "crustacean campaniform organs" by Shelton and Laverack (1968) on the basis of electrophysiological and light microscopic observations (e.g., suspension of two dendrites in a delicate cap). The "crustacean campaniform organs" were characterized as touch- and vibration-sensitive mechanoreceptors. According to Shelton and Laverack (1968), the chemosensitivity of the funnel-canal organs proposed by Luther (1930) could be ruled out, inasmuch as their recordings showed no response when the "campaniform organs" were stimulated with *Mytilus* extract. On the basis of his electrophysiological and topographical findings in *Carcinus maenas*, Barth (1980) concurred with Shelton and Laverack's (1968) interpretation, that the funnel-canal organs are "campaniform sensilla" (see also Barth 1981).

The present study is concerned with the following aspects of the so-called "campaniform organs" of the shore crab *Carcinus maenas* L.: (1) the topography, (2) the external structure, (3) the main features of their fine structure and (4) a comparison with the insect campaniform sensilla.

A preliminary report has already appeared (Gnatzy and Schmidt 1982). An extensive ultrastructural analysis of the sensory apparatus and the cellular and spatial organization of the enveloping cells are presented in another paper (Schmidt and Gnatzy, in press).

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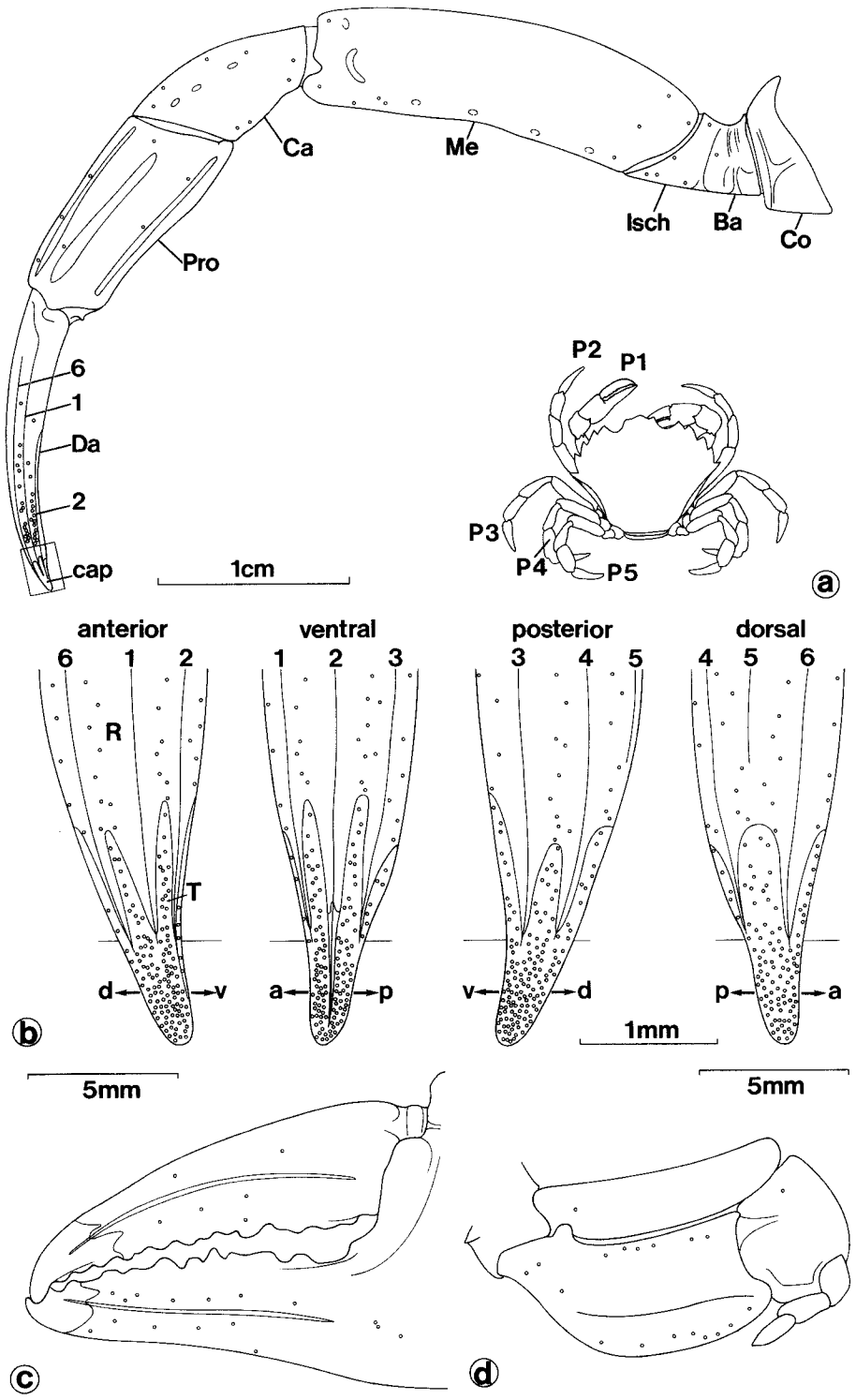

Fig. 1 a–d. Topography of the funnel-canal organs (*circles*); *Carcinus maenas* (carapace width ca. 5 cm).
a Anterior view of entire 2nd pereiopod. Coxa (*Co*), basis (*Ba*), ischium (*Isch*), merus (*Me*), carpus (*Ca*), propodus (*Po*) dactyl (*Da*); epicuticular cap (*cap*); on the dactyl the furrows 1, 2, 6 are visible; Inset: *Carcinus* with pereiopods (P1–P5); 1st pereiopod (*chela*), 5th pereiopod (=swimming leg). The dactyl tip, in rectangle, enlarged in Fig. 1b.
b Anterior (*a*), dorsal (*d*), posterior (*p*) and ventral (*v*) view of the dactyl tip of 2nd pereiopod. Furrows (1–6); tongues of epicuticle (*T*), ribs (*R*); region of epicuticular cap below the line.
c chela region of the 1st pereiopod; anterior.
d 3rd maxilliped; posterior

B. Materials and methods

1. Animals: Male and female *Carcinus maenas* L. of various sizes (carapace width 1.5–7.6 cm). Origin: St. Andrews, Scotland, and the Meeresbiologische Anstalt Helgoland.
2. Light microscopy (LM): For whole-mount preparations dactyl tips were partially opened after dehydration, as for transmission electron microscopy (see below), and then covered with Epon.

Semi-thin (1 μm) sections (of TEM preparations) were stained with methylene blue. For azan and Mallory staining, dactyl tips of newly molted animals were fixed with 5% glutaraldehyde in phosphate buffer (according to Sörensen) to which 15% sucrose had been added, dehydrated in an alcohol series and embedded in glycol methacrylate by the method of Leduc and Bernhard (1967). Polymerization occurred under UV light (12 h at 4° C). The sections, 2–3 μm thick, were stained by a modified method (without

differentiation in 96% alcohol) with azan (Romeis 1968) or Mallory's stain (Burck 1973) and covered with "Entellan".
3. Transmission electron microscopy (TEM): Pieces of dactyl tips 0.5–1 mm long were treated as follows (cf. Weatherby 1981):
– Prefixing with 5% glutaraldehyde in 0.1 *M* phosphate buffer (P-buffer) according to Sörensen, pH 7.4, with 15% sucrose added, 4 h at room temperature
– Washing in P-buffer plus 15% sucrose, 4 × 15 min.
– Postfixing in 2% OsO_4 in P-buffer plus 15% sucrose, 2 h
– Washing in P-buffer plus 15% sucrose, 4 × 15 min. Subsequently the preparations were treated by the customary method:
– Dehydration in an alcohol series
– Embedding in Epon 812
– Preparation of ultrathin sections with a diamond knife
– Section contrasting with lead citrate by the method of Reynolds (1963), 20 min; some sections were double stained with lead citrate and uranyl acetate
– Examination of the sections in the TEM (Zeiss EM9).
4. Scanning electron microscopy (SEM): The preparations were fixed as for TEM (see 3), dehydrated and then either air-dried from 100% ethanol or "critical-point" dried from CO_2 by way of amyl acetate (2 × 15 min.). Structure was well preserved by both methods. The dried preparations were fixed to aluminum holders (in some cases attached to a rotatable tungsten wire) and gold-coated.

C Results

I. The walking legs of the crab, with special reference to the dactyl

Like all decapods, *Carcinus maenas* has five pairs of segmented walking legs (pereiopods), the first pair of which are modified to form chelae and the last pair to form swimming legs. The single leg segments are flexibly joined to one another by membraneous cuticle (Fig. 1a). The most distal segment, the dactyl (dactylopodite), tapers toward the tip and is slightly curved toward the ventral surface over its whole length (Figs. 1b, 2a, 3a).

In the proximal part of the dactyl the cuticle is three-layered, with epi-, exo- and endocuticle (see Table 1; terminology of Richards, 1951), and is subdivided into ribs and deep furrows (Figs. 1a, b, 2a, b, 3b)

Toward the tip the furrows become progressively more shallow, eventually disappearing altogether, so that the extreme tip is a smooth, conical cap (Fig. 2a). This cap consists entirely of epicuticular material, which in vivo is colored amber yellow and is more elastic than the remaining, extremely calcified cuticle, yellowish-white to brown in color. Tongues of epicuticular material, conically tapering toward the interior, project proximally from the cap, forming a continuous transition to the ribs (Fig. 3b; see also Shelton and Laverack, 1968). These tongues interrupt the cylinder of exo- and endocuticle (Fig. 3b).

The epicuticle of the cap and the tongues differs from that in the proximal section, in that (a) it has a chromophobic (not stained by azan and Mallory) outer layer (Figs. 3a, b) and (b) it is penetrated by pore canals. In a newly molted animal with a dactyl 10 mm in length, the cap is about 1.5 mm long and the tongue region extends over about 1 mm proximal to it. The cap gradually becomes shorter as it wears down.

Table 1. Cuticular structure in the proximal dactyl

Layer	Thickness in % of total	Structure	Pore canals	Mallory staining
Epicuticle	5–10%	homogenous	–	red
Exocuticle	10–15%	lamellated	+	deep blue
Endocuticle	80%	lamellated	+	light blue

II. External morphology of the funnel-canal organs (SEM observations)

In newly molted animals the funnel-canal organs appear as shallow (about 1–2 µm deep) oval depressions in the cuticle surface (Figs. 2b, c), with a long diameter of about 8–10 µm. From this depression arises a small projection, 1–1.5 µm high, shaped like a truncated cone. It is located somewhat off-center and is inclined toward the nearest edge of the depression. At its tip is an elongated pore (ca. 0.8 × 0.5 µm). It was evident in some sensilla that this pore is filled with loose material (Fig. 2c). The floor of the depression is not as smooth as the surrounding cuticle surface, but appears to undulate slightly. As the next ecdysis approaches, the funnel-canal organs become less distinct, and eventually are only vaguely delimited indentations in the cuticle surface with a somewhat eccentric pore (Fig. 2c, inset).

III. Topography of the funnel-canal organs

For the barely 4000 funnel-canal organs in the exoskeleton of an adult crab (carapace width ca. 5 cm), the following distribution pattern was found (see Figs. 1a–d and Table 2):

1st pereiopods (chelae): The claw-bearing legs have a total of only ca. 50 funnel-canal organs. The epicuticular cap of the dactyl is entirely free of funnel-canal organs (Fig. 1c).

2nd–4th pereiopods: Funnel-canal organs can be found on nearly all segments of the walking legs, but in each leg more than 50% of the total are located on the epicuticular cap of the dactyl. Moreover, in the dactyl the funnel-canal organs are relatively numerous on the ribs, as compared with the other segments of the legs. Their number decreases sharply from distal to proximal. Near the propodite joint only a few organs can be found. On the epicuticular cap the density of the funnel-canal organs is greater by a factor of 10 than on the ribs (Figs. 1a, b).

5th pereiopods (swimming legs): The distribution of the funnel-canal organs here is basically the same as on the 2nd–4th walking legs, although the number of organs on the swimming legs is over 60% lower.

As far as the rest of the body is concerned, funnel-canal organs were found only on the two 3rd *maxillipeds* (20; Fig. 2d), and not on the other appendages (1st and 2nd maxillipeds, 1st and 2nd antennae) or the carapace, abdo-

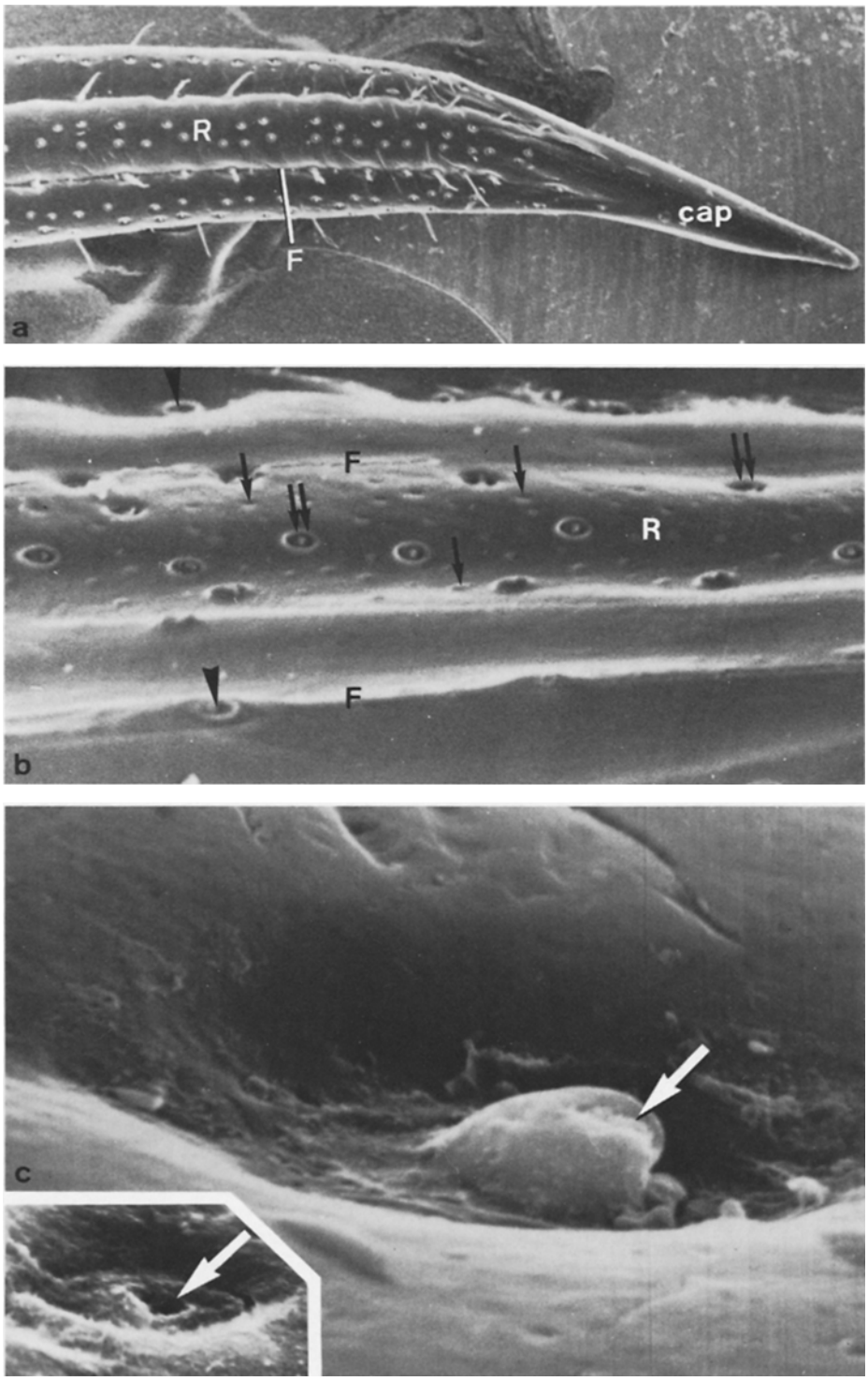

Fig. 2a–c. Dactyl of *Carcinus maenas* as seen in SEM.
a Dactyl tip of a newly molted (small) animal; epicuticular cap (*cap*), rib (*R*), furrow (*F*). ×26.
b Proximal region of dactylus; on the rib (*R*) are hair peg organs (double arrows) and funnel-canal organs (*arrows*), and the furrows (*F*) contain some sockets of (*broken-off*) hair sensilla (*arrowheads*). ×140.
c Single funnel-canal organ (of a newly molted animal): an oval depression within which is a projection like a truncated cone with a pore at its tip. The pore is closed by a plug (*arrow*). ×9400. Inset: funnel-canal organ of an animal long after the molt; a large pore is now discernible where normally the truncated cone is located (arrow). ×2000

Table 2a. Number of funnel-canal organs on the dactyls of the pereiopods (P 2–P 5) of *Carcinus maenas*

	P 2	P 3	P 4	P 5
Cap	270	240	260	110
Ribs	200	170	210	60
Total dactyl	470	410	470	170

Table 2b. Number of funnel-canal organs on the different segments of the 2nd pereiopod of *Carcinus maenas*

Dactyl	Propodus	Carpus	Merus	Basis-Ischium	Coxa
470	20	20	20	10	0

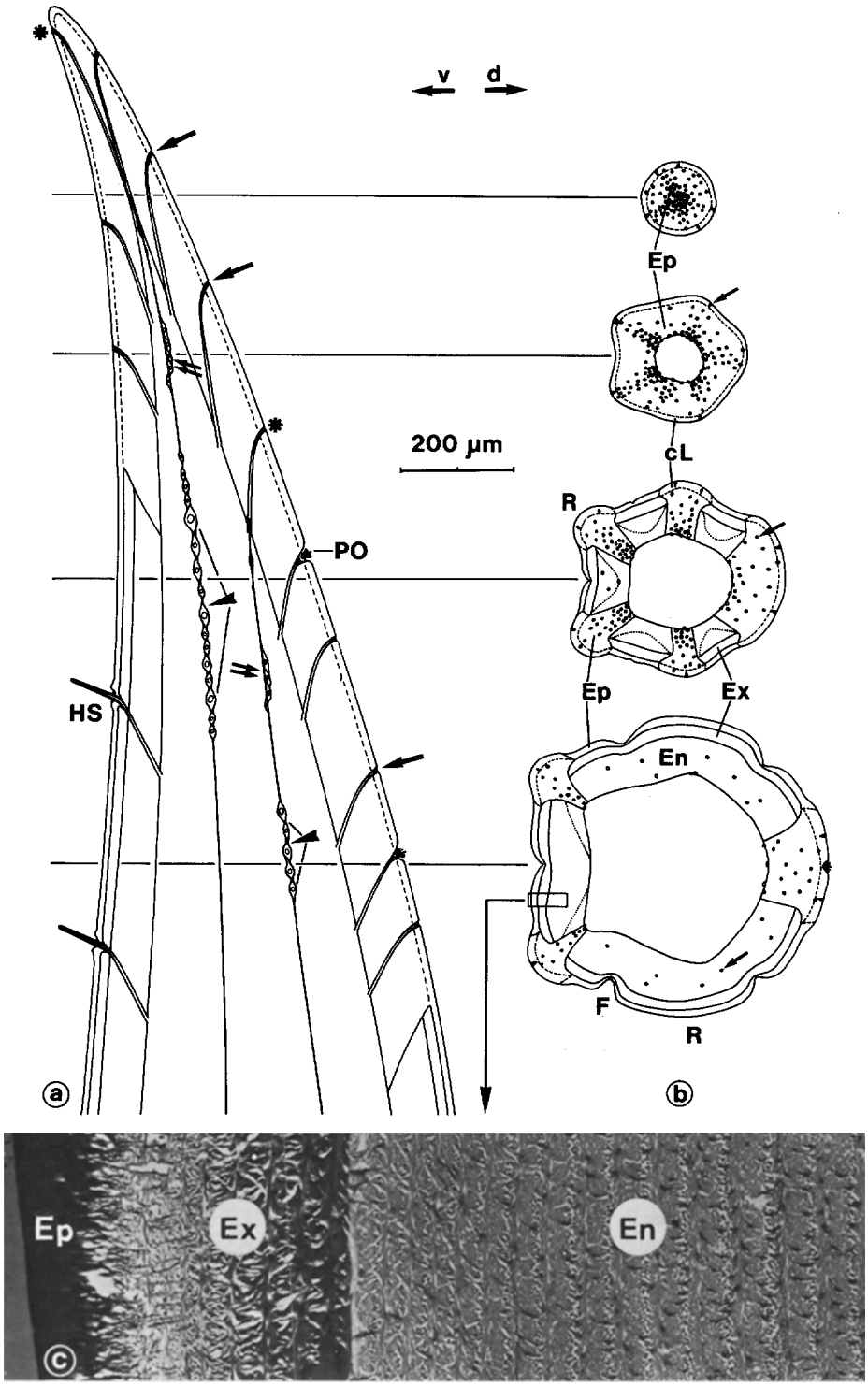

Fig. 3a–c. Dactylus tip, *Carcinus maenas*.
a Schematic longitudinal section showing funnel-canal organs (*arrows*); for two funnel-canal organs (*asterisks*) the course of the dendrites, the position of the enveloping cells (*double arrows*) and that of the sensory cells (*arrowheads*) are shown. Hair peg organs (*PO*), hair sensilla (*HS*). ×80.
b Schematic cross sections through the dactylus tip at different levels (planes of section shown in Fig. 3a). Differently structured regions of the endocuticle are demarcated by dotted lines. Chromophobic outer layer of the epicuticle (*cL*) is demarcated by dashed lines; for clarity profiles of sensilla have been omitted from the lumen of the dactyl. Endocuticle (*En*), epicuticle (*Ep*), exocuticle (*Ex*), furrows (*F*), ribs (*R*), canals (*arrows*), dorsal (*d*), ventral (*v*). ×80.
c Cross section through the cuticle (TEM picture; orientation of section is indicated in Fig. 3b). The epicuticle (*Ep*) is homogenous, electron-dense and without pore canals. It sends pierlike processes into the exocuticle (*Ex*). The electron density of the exocuticular lamellae increases with proximity to the endocuticle (*En*). Pore canals (*arrows*) penetrate the exocuticle and the lamellated endocuticle, ×1800

men, or abdominal legs. No arrangement of the organs in groups or sensilly fields was observed, nor were any sex-specific differences detected ($n = 12$).

IV. Cuticular apparatus of the funnel-canal organs (LM and EM observations)

The dendrites of the funnel-canal organs pass through the cuticle within canals (see also Luther, 1930; Shelton and Laverack 1968). For the first few µm they are almost perpendicular to the cuticle surface; then they bend toward the long axis of the dactyl (Fig. 3a). The canals associated with the organs on the cap are nearly parallel to the cuticle surface in their proximal sections, attaining an overall length of 300–400 µm. The funnel-canal organs proximal to these have canals with their proximal sections at a greater angle to the long axis of the dactyl, as a result of which their overall length is less (ca. 100 µm). The canals end

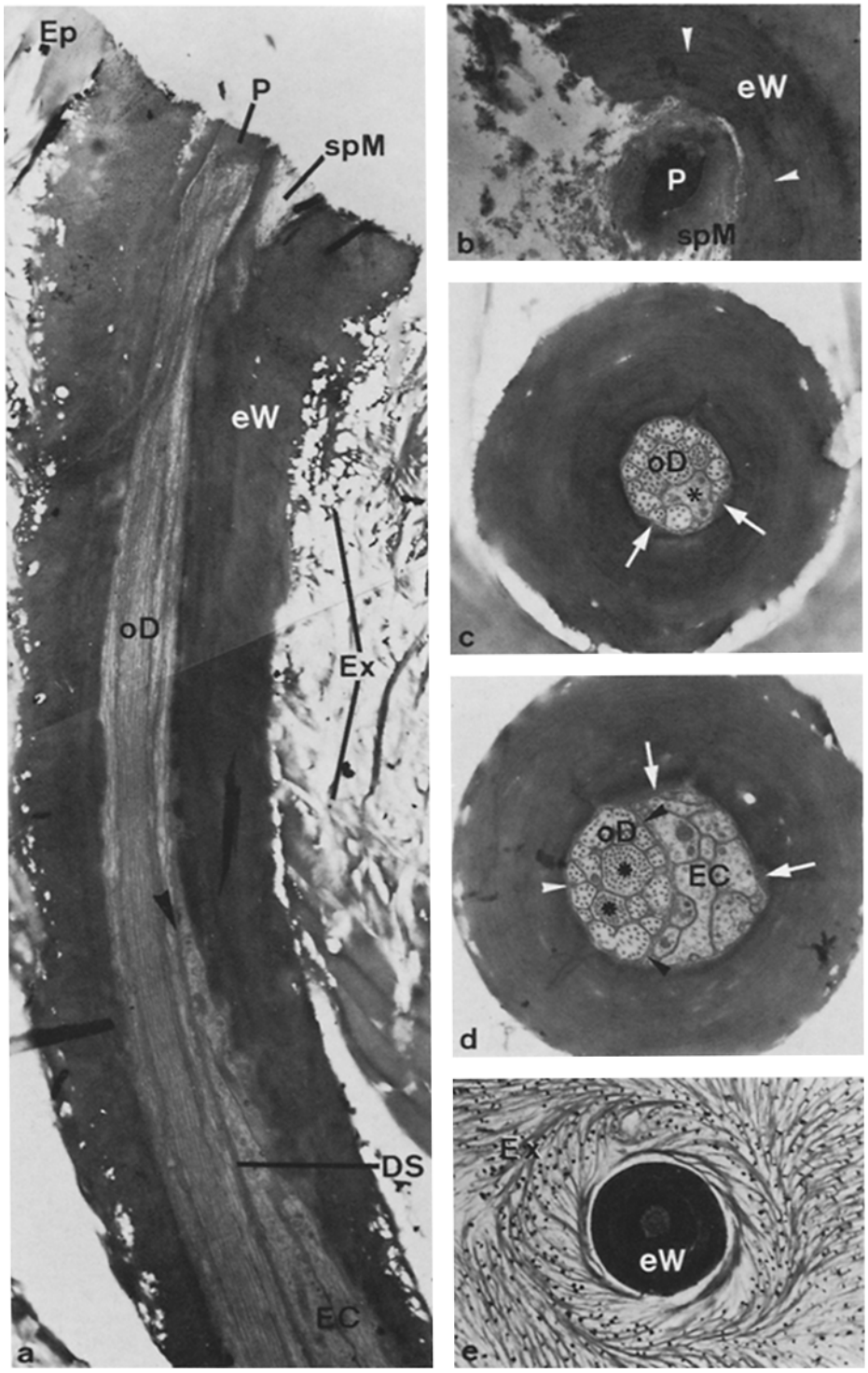

Fig. 4a–e. Terminal region of a funnel-canal organ in the proximal region of a dactylus of *Carcinus*.
a Longitudinal section; the epicuticular wall (*eW*) of the canal becomes thicker toward the end and forms a depression in the surface of the cuticle. The outer dendritic segments (*oD*) end below an electron-dense plug (*P*) which closes the terminal pore. Epicuticle (*Ep*), exocuticle (*Ex*), spongy material (*spM*), processes of enveloping cells (*EC*), dendritic sheath (*DS*), end of dendritic sheath (*arrowhead*). × 9000.
b Cross section at the level of the cuticle surface. Terminal pore with electron-dense plug (*P*). Epicuticular wall of the canal (*eW*) with electron-dense fibers (*arrowheads*), spongy material (*spM*). × 15000.
c Cross section ca. 5–6 µm below the surface. Outer dendritic segments (*oD*) and enveloping cell processes (*asterisks*) fill up the lumen of the canal. Amorphous material (*arrows*) is lining the canal wall. × 15000.
d Cross section ca. 20–25 µm below the surface. Outer dendritic segments (*oD*) and enveloping cell processes (*EC*) are separated from one another by the dendritic sheath (*arrowheads*). Two dendrites (*asterisks*) contain more microtubules than the others. Material lining the canal wall (*arrows*). × 15000.
e Cross section at the level of the outer layer of the exocuticle, showing the changed course of the exocuticular fibers in the vicinity of the canal. Epicuticular canal wall (*eW*), exocuticle (*Ex*). × 4000

at the cuticle surface in a pore measuring 0.5 × 0.8 µm. This pore is closed by a plug of extracellular, electron-dense, homogeneous material (Figs. 4a, b), 0.3–0.4 µm thick, that sends small processes proximally.

As they proceed inward the canals expand, their final diameter (4–10 µm) being correlated with the number of dendrites in the sensillum. The canals are lined with epicuticular material, which is stained an intense red by azan and Mallory. The thickness of this epicuticular lining diminishes from 1.5 µm in the distal section of the canal to ca. 0.2–0.3 µm proximally. At the cuticle surface the epicuticular canal wall fuses with the surrounding epicuticle. It is distinguished from the latter by its more compact structure, its greater electron density and the presence of fine, electron-dense fibers arranged concentrically with the lumen of the canal (Fig. 4b).

In the region of the pore a ring of spongy cuticle is inserted into the epicuticular material of the wall. This spongy material tapers conically toward the interior (Figs. 4a, 6a), and in the funnel-canal organs of animals

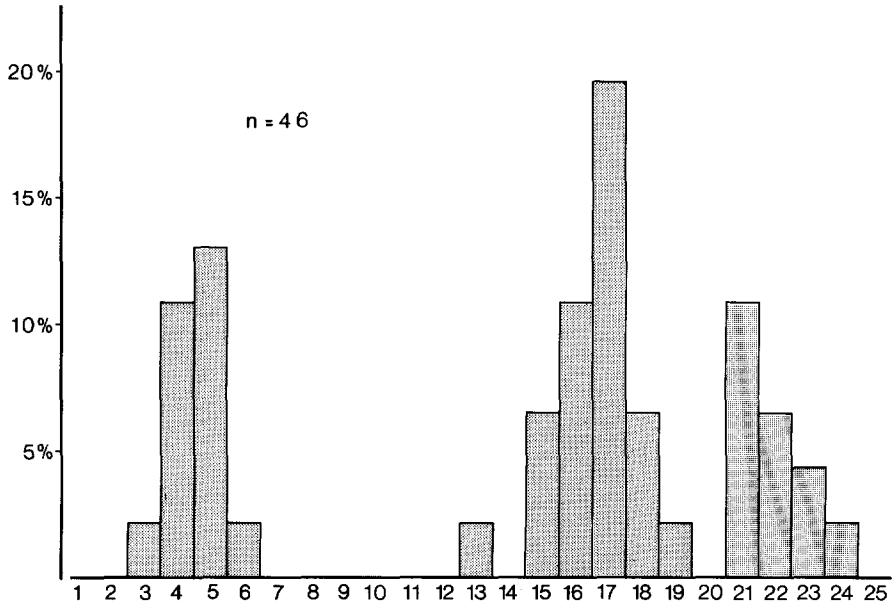

Fig. 5. Histogram of the dendrite counts in funnel-canal organs of *Carcinus maenas*. Abscissa: number of dendrites; ordinate: percentage of the total number of funnel-canal organs examined that had the indicated number of dendrites

that have not recently molted it extends as much as 2 µm into the cuticle, with a width of ca. 1 µm at the cuticle surface. In newly molted animals this differentiated region is considerably larger.

The floor of the depression discernible in the SEM (cf. Fig. 2c) is formed by the epicuticular canal wall; the projection consists mainly of the spongy cuticular material. In the vicinity of the canals the orientation of the lamellae of the exo- and endocuticle is altered. In longitudinal sections the lamellae appear bent so as to parallel the long axis of the canal (Fig. 6a), and in cross sections they take the form of fibers spiralling outward from the canal (Fig. 4e).

V. Sensory apparatus, dendritic sheath and enveloping-cell processes; fine structure

The outer segments of the dendrites pass through the interior of the canal, tapering toward their ends and terminating beneath the plug that closes the pore (Fig. 4a). No bridge structures between the outer dendritic segments and the canal wall or the plug material could be seen. In none of the dendrites was a tubular body found.

Counts of the outer dendritic segments of a number of funnel-canal organs ($n=46$) in a proximal section through the canals gave a trimodal distribution, with maxima at 4–5, 16–17 and 21–22 dendrites per funnel-canal organ (Fig. 5). In each case two of the outer dendritic segments of the organ had a greater number of microtubules (MT) than the rest (Fig. 4c, d). The outer segments (0.1–0.7 µm in diameter, with 2–100 MT) are closely surrounded by a dendritic sheath (Figs. 4a, d, 6a) consisting of homogeneous electron-dense material stained blue by azan. The thickness of the dendritic sheath (DS) is 40–60 nm in the proximal section of the canal and becomes distinctly less distally. About 10–15 µm below the terminal pore the dendritic sheath ends (Fig. 6a). Its distal section makes connection with a material that lines the canal wall here and is very similar to the dendritic sheath material (Figs. 4c, d). This lining material in some places is as much as 0.3 µm thick. The dendritic sheath is surrounded by the processes of enveloping cells, which entirely fill the remaining lumen of the canal (Figs. 4c, d). The enveloping-cell processes taper distally; the longest end ca. 3–5 µm below the terminal pore (Fig. 4a; cf. Fig. 6a).

D. Discussion

1. Topography

The "crustacean campaniform organs" of *Carcinus maenas* have been said to be mechanically stimulated by deformation of the exoskeleton owing, for example, to touching objects or to substrate vibration (Shelton and Laverack 1968; Barth 1980), like the campaniform sensilla of insects and the slit sense organs of arachnids.

In the cases of insect campaniform sensilla and slit sense organs, there is evidence that their position and orientation depend on the magnitude and direction of the tensions induced in the cuticle by the normal stimuli (see review by Barth 1981; Zill and Moran 1981). Accordingly, there are points of agreement in the topography of the two organs (see review by Barth 1981). Campaniform sensilla of insects and slit sense organs are located mainly on the proximal segments of the legs, the trochanter in particular. They are also commonly found in the vicinity of the leg joints. By contrast, the "crustacean campaniform organs" are mainly concentrated on the distal parts of the legs, and here in turn on the epicuticular cap of the dactyl tip. Unlike the insect campaniform sensilla and the arachnid slit sense organs, they had no observable tendency to be arranged in groups or composite organs (cf., e.g., the arrangement of campaniform sensilla on the cockroach trochanter: Krämer and Markl 1978; the sensilla fields on the halteres of Diptera: Pflugstaedt 1912; and the lyriform organs of arachnids: Barth and Libera 1970). Moreover, no sex-specific variation in the number or distribution of the sensilla was found. The only respect in which there was not much difference was the total number of such receptors (ca. 1100 campaniform sensilla in the fly *Calliphora:* Gnatzy et al., in

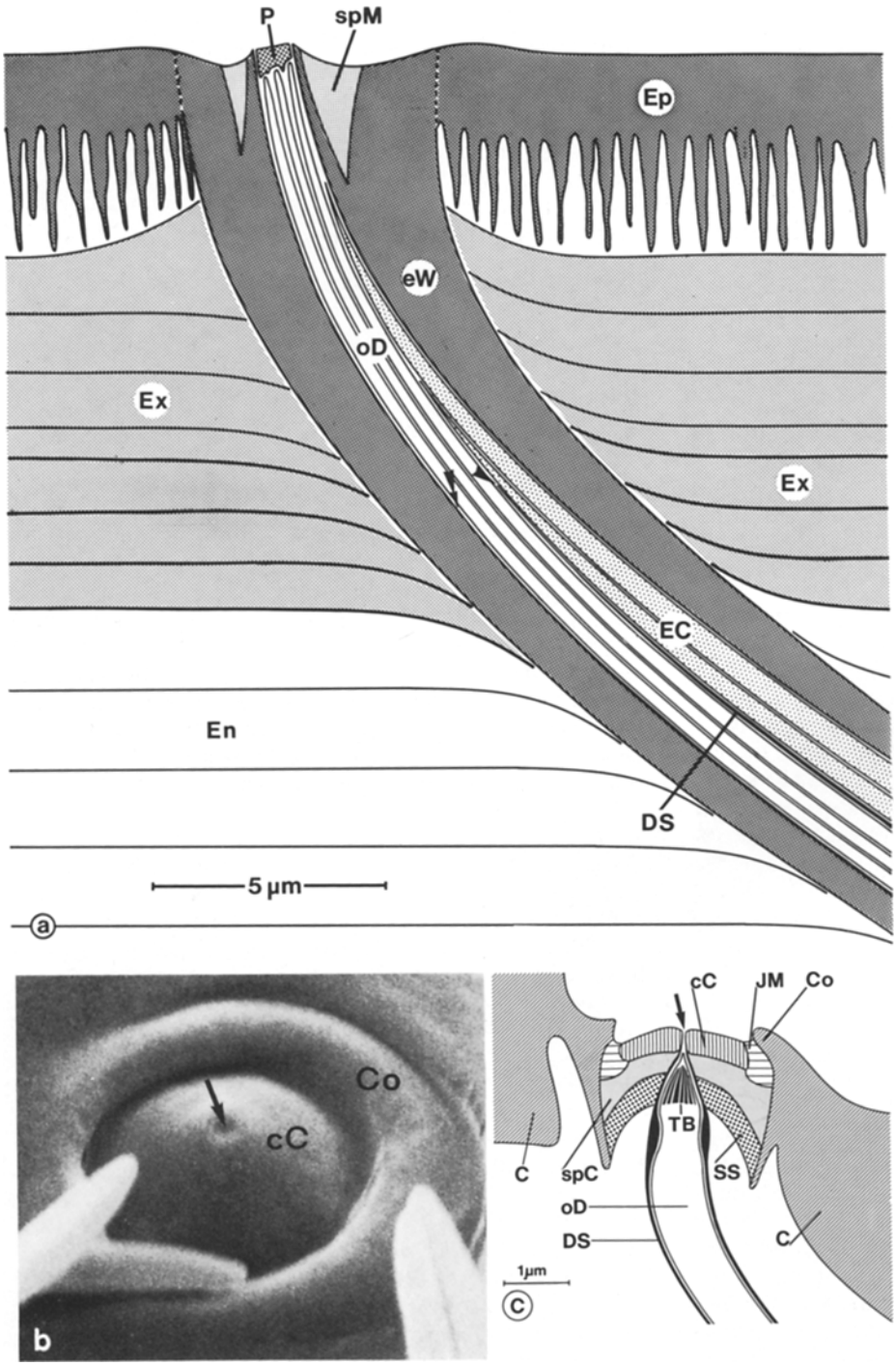

Fig. 6. a Funnel-canal organ; *Carcinus maenas*; schematic longitudinal section through the terminal region. Process of enveloping cells (*EC*), outer dendritic segments (*oD*), dendritic sheath (*DS*), endocuticle (*En*), epicuticle (*Ep*), exocuticle (*Ex*), epicuticular wall of the canal (*eW*), electron-dense plug (*P*), spongy material (*spM*), end of dendritic sheath (*arrowheads*). × 6400.
b Campaniform sensillum; *Gryllus bimaculatus* (Insecta); SEM picture. Cuticular cap (*cC*), cuticular collar (*Co*), molting canal (*arrow*). × 10000.
c Campaniform sensillum; *Gryllus* (Insecta); schematic longitudinal section. Cuticular cap (*cC*), cuticular collar (*Co*), cap and collar are connected by a joint membrane (*JM*); between the socket septum (*SS*) and the cap is spongy cuticle (*spC*). The dendrite contains a tubular body (*TB*) in its terminal section, and is completely enclosed in the dendritic sheath (*DS*). Molting canal (*arrow*)

prep.; ca. 3300 slit sense organs in the wandering spider *Cupiennius*: Barth and Libera 1970; ca. 4000 "campaniform organs" in the shore crab *Carcinus:* this paper), especially when the considerable differences in size of the animals are taken into account.

2. Cuticular and sensory apparatus

When the stimulus-receiving cuticular and sensory apparatus of the "crustacean campaniform organs" is compared with that of the insect campaniform sensilla, it becomes apparent that the two types of sensilla differ fundamentally in a number of structural features (cf. Figs. 2d and 6a with 6b).

It is typical of the insect campaniform sensilla that a cuticular cap, usually elliptical in shape, rises above a hollow in the surrounding cuticle that is ca. 5–15 µm in diameter. As a rule there is also an encircling cuticular collar, from which the cap is suspended by a joint membrane (Figs. 6b, c).

The light-microscopic studies of Shelton and Laverack (1968) indicated that the "crustacean campaniform organs" have a cupola structure. Our observations in the electron microscope, however, revealed no external cuticu-

lar differentiation comparable to the campaniform sensilla of insects.

Whereas insect campaniform sensilla are innervated by only one dendrite, there are 3–24 dendrites in the "crustacean campaniform organs". Moreover, the dendrite of a campaniform sensillum always contains a tubular body. Tubular bodies are considered to be modality-specific structures of the cuticular mechanoreceptors of insects (see, e.g., Thurm et al. 1975; Gnatzy and Tautz 1980) and arachnids (see, e.g., Barth 1971; Foelix and Chu-Wang 1973a). None of the dendrites of the "crustacean campaniform organs" we examined exhibited such a tubular body. In each of these organs, however, two of the outer dendritic segments had a larger number of microtubules than the remaining 1–22 outer segments.

The conspicuous terminal pore of the "crustacean campaniform organs" is identifiable as a "gustatory" pore by its size (cf. Blaney and Chapman 1969; Foelix and Chu-Wang 1973b; Altner et al. 1983) and even more by the electron-dense plug. A "gustatory" pore of this kind (see, e.g., Stürckow 1967; Hansen and Heumann 1971; Foelix and Chu-Wang 1973b) is present in all arthropod contact chemoreceptors and is therefore regarded as a modality-specific structure of this type of sensillum (see also reviews by Altner 1977; Altner and Prillinger 1980; Zacharuk 1980; for opposite opinion, see Gaffal 1979;).

To sum up: The data on topography and the morphological findings presented here contradict the views of Shelton and Laverack (1968) and Barth (1980, 1981), that the funnel-canal organs correspond to the campaniform sensilla of insects. It therefore seems unjustified to give the funnel-canal organs the new name "crustacean campaniform organs". The funnel-canal organs are probably *bimodal* sensilla in which – in analogy to the contact chemoreceptors of insects and spiders – mechano- and chemosensitive sensory cells could be combined.

Electrophysiological data corroborating this view are already available, as follows.

a) Mechanoreception: Recordings from axons in the dactyl and propodite have shown that the funnel-canal organs of *Carcinus* are mechanosensitive (Shelton and Laverack 1968; Barth 1980). Our description of the fine structure (see also Schmidt and Gnatzy, in press) support this inference. However our findings regarding the structural features of the sensory apparatus provide no explanation of the differences in response characteristics of the two sensory cells (one discharged large spikes at the onset of the stimulus and the other small spikes at its end) found by Shelton and Laverack (1968).

Various mechanisms could mediate the stimulating action of mechanical stress. (1) Bending of the cuticular cylinder of a leg segment causes changes in length of the canals. The tension thereby imposed on the outer dendritic segments could be the adequate stimulus. This model would also explain why most of the funnel-canal organs are located on the relatively flexible cap of the dactyl. (2) The high sensitivity of the funnel-canal organs to even the lightest touch (Shelton and Laverack 1968; Barth 1980), on the other hand, is an indication that local mechanical changes can be effective stimuli. It is conceivable that when something touches the cuticle it causes displacement of the small projection embedded in the ring of spongy (soft?) cuticular material. In this way both pressures and tensile forces could be transmitted to the outer dentritic segments. It should be noted, however, that – unlike the campaniform sensilla of insects in this region – the funnel-canal organs exhibit no differentiation within the outer dendritic segments, in form of a tubular body, for instance, and/or of bridge structures between peripheral microtubules and the dendrite membrane (cf. the findings in insects of Gnatzy and Tautz 1980)

b) Chemoreception: In an electrophysiological study of chemoreceptors on the dactyl of *Carcinus maenas* Case and Gwilliam (1961) found that glutamic acid and *Mytilus* extract were the most effective stimuli (threshold as low as 5×10^{-5} *M*), whereas in Laverack's (1963) experiments these substances were almost ineffective, and responses were obtained only to trimethylamin oxide (TMO), betaine, and fish extract (threshold at 0.1–0.01 *M*). This discrepancy is very probably due to the different means of applying the stimuli in the two studies. Case and Gwilliam (1961) state only that they dripped the substances onto the dactyl, whereas Laverack (1963) very probably stimulated the tip of the dactyl selectively (see Fig. 1 of Laverack 1963). Therefore two different receptor types could have been stimulated. Laverack (1963) recorded from receptors on the dactyl tip (probably the funnel-cannal organs) sensitive only to TMO, betaine, and fish extract and not to glutamic acid or *Mytilus* extract. The other, occupying a more proximal location on the dactyl, would not have been stimulated in Laverack's (1963) experiment and would respond, as found by Case and Gwilliam (1961), especially well to glutamic acid and *Mytilus* extract (see also Shelton and Laverack 1968).

In this light, the statement by Shelton and Laverack (1968) that the funnel-canal organs are not chemosensitive seems not at all compelling. In their experiments the funnel-cannal organs on the cap were stimulated selectively only by *Mytilus* extract, which according to Laverack's (1963) findings ought to be ineffective here in any case.

In conclusion, then, the publication by Laverack (1963) offers strong indications that the funnel-canal organs are chemosensitive. Our view that the funnel-canal organs could be "contact chemoreceptors" is supported by their distribution. Equally, the concentration of the funnel-canal organs on the tips of the dactyls, shows some parallels with the distribution of contact chemoreceptors in insects. The latter are also as a rule found on the tips of appendages – maxillary palps, antennae, tarsi, labella, and cerci (see, e.g. Hansen and Heumann 1971; Schmidt and Gnatzy 1972; review by Hansen 1978). Studies are now underway to clarify the chemosensitivity of the funnel-canal organs and their role in behavior.

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