Cell Tissue Res (1984) 236:729–731

Cell and Tissue Research

Short Communication

'Campaniform' structures on lobster antennae are dermal glands

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Summary. The dome-shaped ('campaniform') cuticular structures found in small depressions on the lateral antennular flagella of the lobster (*Homarus gammarus*) were investigated by means of electron-microscopic methods. Each dome (diameter: 4–5 μm), which is surrounded by a 3–5 μm wide cuticular collar, is associated with a cell (soma size: long axis 90 μm, short axis 24 μm) showing fine-structural details characteristic of a dermal gland, e.g., a ductule lined by thin (cuticulin-like) cuticle and a well-developed granular endoplasmic reticulum. This ductule ends within the dome, which consists of spongious cuticle and, when seen from outside, resembles the cuticular cap of a typical campaniform sensillum of insects (Fig. 1b). The fine-structural findings, especially the lack of any sensory element, are clear evidence against previous descriptions of these structures as representing 'campaniform sensilla of crustaceans'.

Key words: Dermal glands – Campaniform structure – Antennae – Lobster, *Homarus gammarus*

The cuticular exoskeleton of arthropods (insects, crustaceans, arachnids) is continually exposed to mechanical forces that are either produced by the activity of the animals themselves or by external factors. Mechanical stress causes local deformations of the exoskeleton, which are perceived by special cuticular receptors such as the campaniform sensilla in insects and the slit sense organs in arachnids (reviewed by Barth 1981).

There are reports of two types of campaniform sensilla among crustaceans: *Type I* is found on the epicuticular cap (a region of flexible cuticle) at the tips of the walking legs of *Carcinus maenas, Palinurus elephas, P. argus,* and *Homarus gammarus* (Shelton and Laverack 1968; Laverack 1976; Barth 1980; Bush and Laverack 1982; Derby 1982). *Type II* was reported to occur at the antennules of *Nephrops norvegicus, Homarus gammarus,* and *Crangon crangon.* In *Crangon,* a single sensillum was described for each annulation of the antennular flagellum, and in the two former species up to six sensilla were reported lying at the base of large hairs (Laverack 1976; Bush and Laverack 1982; Derby 1982). Based only on SEM-observations, these 'crustacean campaniform structures' were described as small domes located in a shallow depression very similar to insect campaniform sensilla.

We have recently clarified the fine structure of *type-I* campaniform sensilla in the dactyls of *Carcinus maenas* (Gnatzy and Schmidt 1982; Gnatzy et al. 1984). Rather than being pure mechanoreceptors of the 'campaniform' type (Shelton and Laverack 1968) these sensilla, originally called 'funnel canals' (*'Trichterkanäle'*) by Luther (1930) are probably bimodal sense organs, similar to the contact chemoreceptors of insects and arachnids, which combine mechano- and chemosensitive elements (Schmidt and Gnatzy, in press). The present study examines the fine structure of so-called *type-II* 'campaniform sensilla' on the antennules of the lobster.

Materials and methods

Adult lobsters (*Homarus gammarus*) from St. Andrews, Scotland, were used immediately or 4 days after their latest ecdysis. Pieces of antennules, 0.5–1 mm long, were prepared for fine-structural examination as described in Gnatzy et al. (1984). For SEM-investigation the specimens were fixed as for TEM, dehydrated, and then either air-dried from 100% ethanol or critical-point dried with CO_2 via amylacetate. The dried preparations were gold-coated.

Results and discussion

Dome-shaped cuticular structures lying in shallow depressions are found near the bases of all large setae of the antennal flagellum (Fig. 1a, b; cf. Fig. 1. 19 in Laverack 1976; and Fig. 6A, F in Derby 1982). The domes are 4–5 μm in diameter and are surrounded by a cuticular 'collar' ca. 3–5 μm wide. Externally these structures resemble the cuticular cap and collar of a typical campaniform sensillum in insects (Gnatzy et al. 1984). Compared with the smooth cap of the campaniform sensillum of insects the surface of the lobster dome is wrinkled (Fig. 1b, c). It consists of spongious cuticle (Fig. 1e) and possesses a up to 3 μm long slit-shaped opening (Fig. 1c) and not a molting pore as is characteristic for cuticular insect mechanoreceptors (Schmidt and Gnatzy 1971).

Examination of the internal morphology of these crusta-

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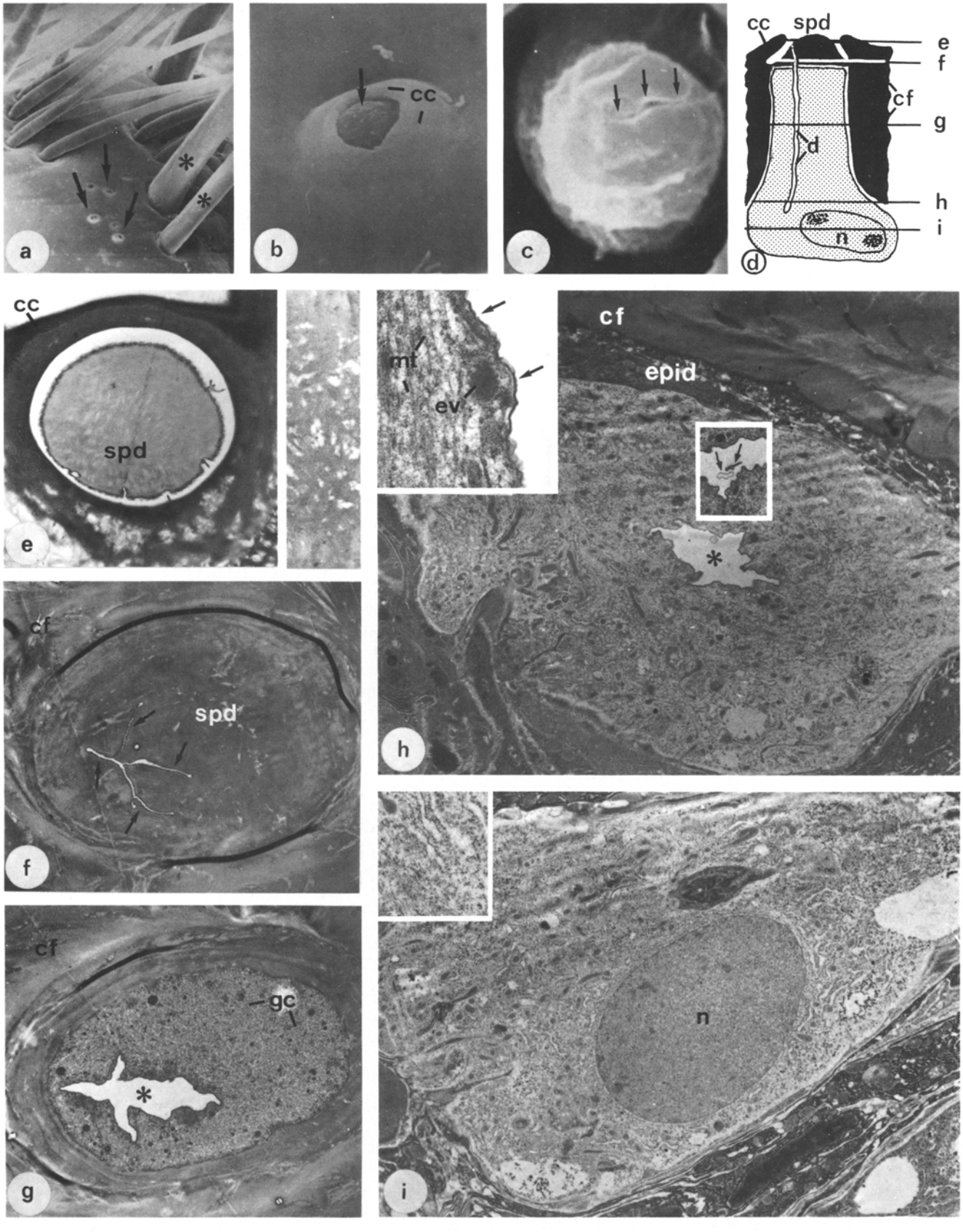
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Fig. 1. a–c SEM micrographs of various external cuticular structures on the lateral antennular flagellum of the lobster *Homarus gammarus*: **a** Campaniform structures (*arrows*) arranged around the base of large hairs (*asterisks*). ×100. **b** External view of a single campaniform structure at higher magnification showing a cuticular collar (*cc*) and a dome-shaped cap (*arrow*). ×2000. **c** The dome has a slit-like opening (*arrows*). ×5500. **d** Schematic diagram (not drawn in scale) of a longitudinal section through a gland unit (cell soma: lightly dotted) lying under each of the external cuticular structures shown in **a–c**. Cuticular collar (*cc*); cuticle of flagellum (*cf*); ductule (*d*); nucleus (*n*); dome of spongious cuticle (*spd*). **e–i** Cross-sections through a gland unit from the base of a large hair of *Homarus* (the levels corresponding to **e–i** are indicated in Fig. 1d): **e** Cross section of dome tip through spongious cuticle (*spd*); cuticular collar (*cc*). ×3600. *Inset:* Spongious cuticle from the dome. ×5400. **f** Section through dome base (*spd*); note the branched ductule passing through the dome (*arrows*); cuticle of antennular flagellum (*cf*). ×3600. **g** Section through the gland cell (*gc*), which remains at this level completely surrounded by flagellar cuticle (*cf*); lumen of the ductule (*asterisks*). ×3600. **h** Section through the middle region of the soma of the gland. Cuticle of flagellum (*cf*); epidermis (*epid*); enlargement showing myeloid bodies (*arrows*) within the ductule lumen (*asterisk*). ×3600. *Inset:* Longitudinal section showing the cuticulin layer (*arrows*) that lines the ductule. Electron-dense vesicles (*ev*); longitudinally oriented microtubules (*mt*). ×16000. **i** Basal region of the gland at the level of the nucleus (*n*). ×3600. *Inset:* The cytoplasm of the gland is characterized by extensive rough endoplasmic reticulum. ×9400

cean 'campaniform' structures reveals the following (cf. with Fig. 1d): (i) Neither sensory elements such as a dendrite (Gnatzy and Romer 1980) nor stimulus-transmitting structures such as a chorda (Kouyama and Shimozawa 1982) are found in association with the domes. (ii) Rather, each dome lies above the apex of a large, ovoid cell (more than 90 μm long and up to 24 μm wide). This cell contains a ductule of irregular shape, which originates near the nucleus, passes through the cell parallel to its long axis, and ends in the dome cuticle (cf. Fig. 1f–h; see also Fig. 1d). (iii) The ductule diameter increases in the central and distal regions, thus forming an extracellular compartment (Fig. 1g, h). The wall of the ductule consists of a thin (20 nm) cuticulin-like layer (Fig. 1h, inset). No secretory products were found in the reservoir except for a few very small myeloid bodies in specimens examined up to 4 days after ecdysis (Fig. 1h). (iv) The nucleus in the basal region of the cell is oval shaped (diameter: long axis 13 μm; short axis 9 μm) (Fig. 1i). Four days after ecdysis the cytoplasm is characterized by extensive rough endoplasmic reticulum (Fig. 1i, inset) and numerous mitochondria. The cytoplasm also exhibits minute vesicles of small diameter and many microtubules oriented longitudinally (Fig. 1h, inset).

These ultrastructural findings clearly indicate that the *type-II* 'campaniform structures' of *Homarus* are unicellular glands and not sensilla. Presently the nature of the secretion of this gland remains unknown.

Further morphological and physiological studies are required to show whether crustaceans do in fact possess true campaniform mechanoreceptors, comparable to the typical campaniform sensilla of insects and the slit sense organs of arachnids.

Acknowledgements. Many thanks are due to Dr. E.A. Seyfarth for helpful discussions and to Mrs. H. Henkel and Mr. M. Schmidt, Dipl. Biol., for their technical assistance. Portions of this study were supported by the Deutsche Forschungsgemeinschaft (SFB 45/A1).

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Accepted February 22, 1984