

The fine structure of scorpion sensory organs. II. Pecten sensilla

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Summary

The peg sensilla on the pectines of scorpions (*Euscorpium italicus*, *Androctonus australis*) were studied using transmission and scanning electron microscopy. Their morphological characteristics are: (1) a pore opening at the tip, (2) a double lumen of the peg shaft, and (3) a multiple innervation of typically 12 neurons per sensillum; one mechanoreceptive dendrite terminates with a tubular body at the base of the peg, while the other dendrites enter the peg lumen. Such structural properties are well-known from contact chemoreceptors in other arthropods. The axons of the peg sensilla form numerous synaptic connections with each other, thus giving rise to a ganglionic structure located within the pectine.

Introduction

The pectines of scorpions are conspicuous comb-like appendages on the ventral side of the ninth body segment. They have stirred a scientific interest for almost two centuries (for references see Cloudsley-Thompson, 1955). Nevertheless, their structure and especially their function has remained enigmatic. Although most recent workers have agreed that the pectines represent some kind of sense organ, the presumed modalities have ranged from merely tactile receptors to organs of hearing, equilibrium, ground vibrations and chemoreception.

The histological structure of the pectines, particularly of their small sensory hairs (pegs), was described quite early with the light microscope (Gaskell, 1902; Schröder, 1908), and more recently after investigations with the electron microscope (Carthy, 1966, 1968). The most recent fine structural work by Ivanov & Balashov (1979) appeared after we had completed our own studies on some different species of scorpions. Although our results largely confirm their observations, we also obtained some

interesting additional information which we present here.

Materials and Methods

Pectines of adult scorpions (*Euscorpium italicus* (Herbst) and *Androctonus australis* (L.)) were severed from CO₂-anaesthetised animals, cut into small pieces and fixed in cacodylate-buffered 5% glutaraldehyde for 6-12 hours. After post-fixation in 1% OsO₄ for 2-3 hours and dehydration in an ethanol series, the teeth of the pectines were embedded in Epoxy resin (Epon 812). For the light microscope 1-2 µm sections were stained with Methylene Blue/Basic Fuchsin; ultra-thin sections were treated with uranyl acetate and lead citrate before examination in a Siemens 101 electron microscope. The surface structures of pectines were examined on fixed material using scanning electron microscopes (Jeol JSM 2U and ISI Super 3A).

Results

Each pectine of *E. italicus* consists of eight teeth which articulate via small triangular *fulcra* with two rows of basal segments (Fig. 1). The ventral surface of each tooth is distally studded with small peg sensilla. These fields of sensilla measure about 70 x 300 µm and contain between 150 and 200 sensilla each (Fig. 2). On the proximal half of each tooth stand short hairs which are slightly curved and blunt-tipped (Fig. 2). Cross-sections of their hair shafts reveal a double lumen with several dendrites inside, a picture which is typical for contact chemoreceptors of arthropods (Slifer, 1970; Zacharuk, 1980).

Fine structure of the peg sensilla

The peg sensilla are relatively short, i.e. 8 µm long in *Euscorpium italicus* and only 2 µm in *Androctonus australis*. The shaft is paddle-shaped and squared off at the top (Fig. 3). A cross-section of the shaft measures about 1.5 x 3 µm; its circular base is only 2 µm in diameter. This stalk attaches to a bulbous base which is largely hidden in a deep socket (Fig. 4). This is very pronounced in *Androctonus australis* where the peg sensilla extend very little above their sockets. The rims of neighbouring sockets almost touch each other, thus giving rise to the high

more apparent when examining thin sections in the electron microscope (Figs. 5-7). A series of cross-sections (Figs. 6-10) through the peg shaft demonstrates that the narrow slit is restricted to one side of the peg tip. The slit leads into a fluid-filled chamber (Fig. 6) which is separated from the lower part of the peg shaft by a cuticular platelet (Fig. 5). This platelet sits like a lid on the central cuticular tube that contains the dendrites. However, as can be seen from Figs. 5 and 7, the cuticular platelet is not entirely fused with the wall of the peg shaft but leaves an open connection between the lumen of the cuticular tube and the fluid-filled chamber. Thus the dendrites inside the cuticular tube can communicate with the outside.

Cross-sections through the mid portion of the peg show a typical double lumen (Fig. 8); both lumina are fluid-filled but only the inner lumen (i.e. of the cuticular tube) contains the dendrites. The dendrites appear more or less round in cross-section but apparently flatten out at their tips (Fig. 5). Typically,

eleven dendrites are seen within the lumen of the peg shaft. An additional dendrite ends near the base. Its terminal is relatively large and exhibits a dense array of microtubules (Fig. 10, inset). Such a 'tubular body' is characteristic for mechanoreceptors of arthropods (McIver, 1975) and hence this twelfth dendrite may be referred to as an accessory mechanoreceptor. The dendrites belong to bipolar neurons and show a typical constriction with a ciliary region (Fig. 11). These regions exhibit microtubules in a $9 \times 2 + 0$ configuration, i.e. central tubules are lacking. The peripheral doublets of microtubules arise directly from a basal body, which consists of the typical nine triplets of microtubules (Fig. 11, inset). A second basal body lies in tandem, at the very beginning of the inner dendritic segment. Distal of the ciliary regions there begin the outer dendritic segments, which are encased by a dendritic sheath. The ciliary regions are embedded in the microvilli of a sheath cell, the inner enveloping cell. This large cell contains many electron-dense inclusions which

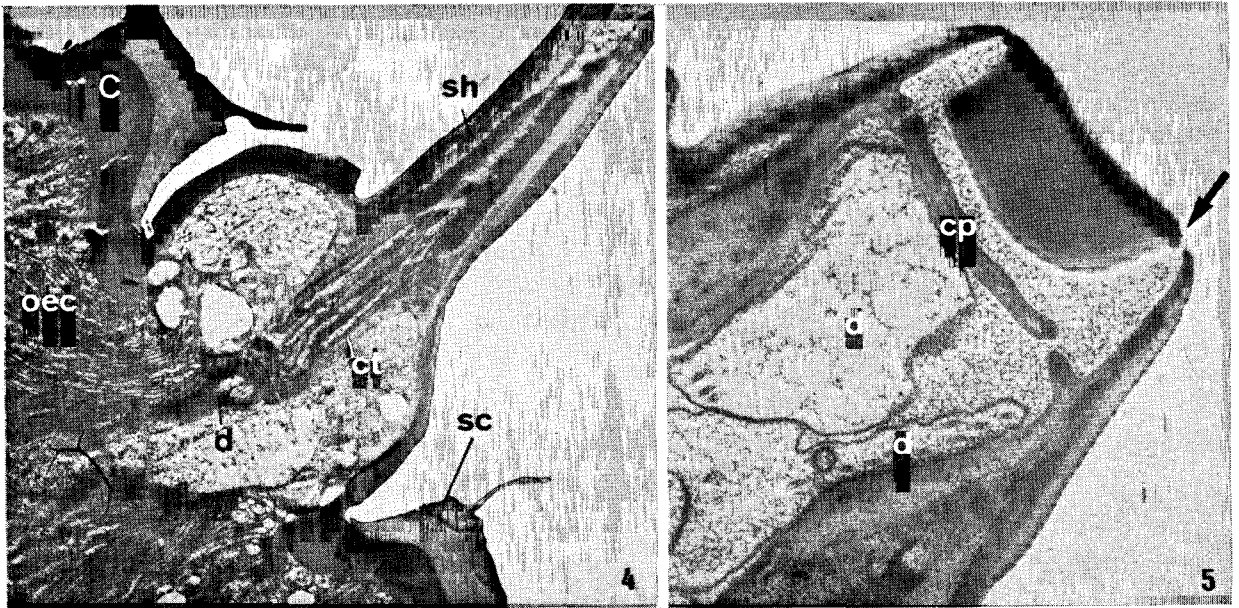
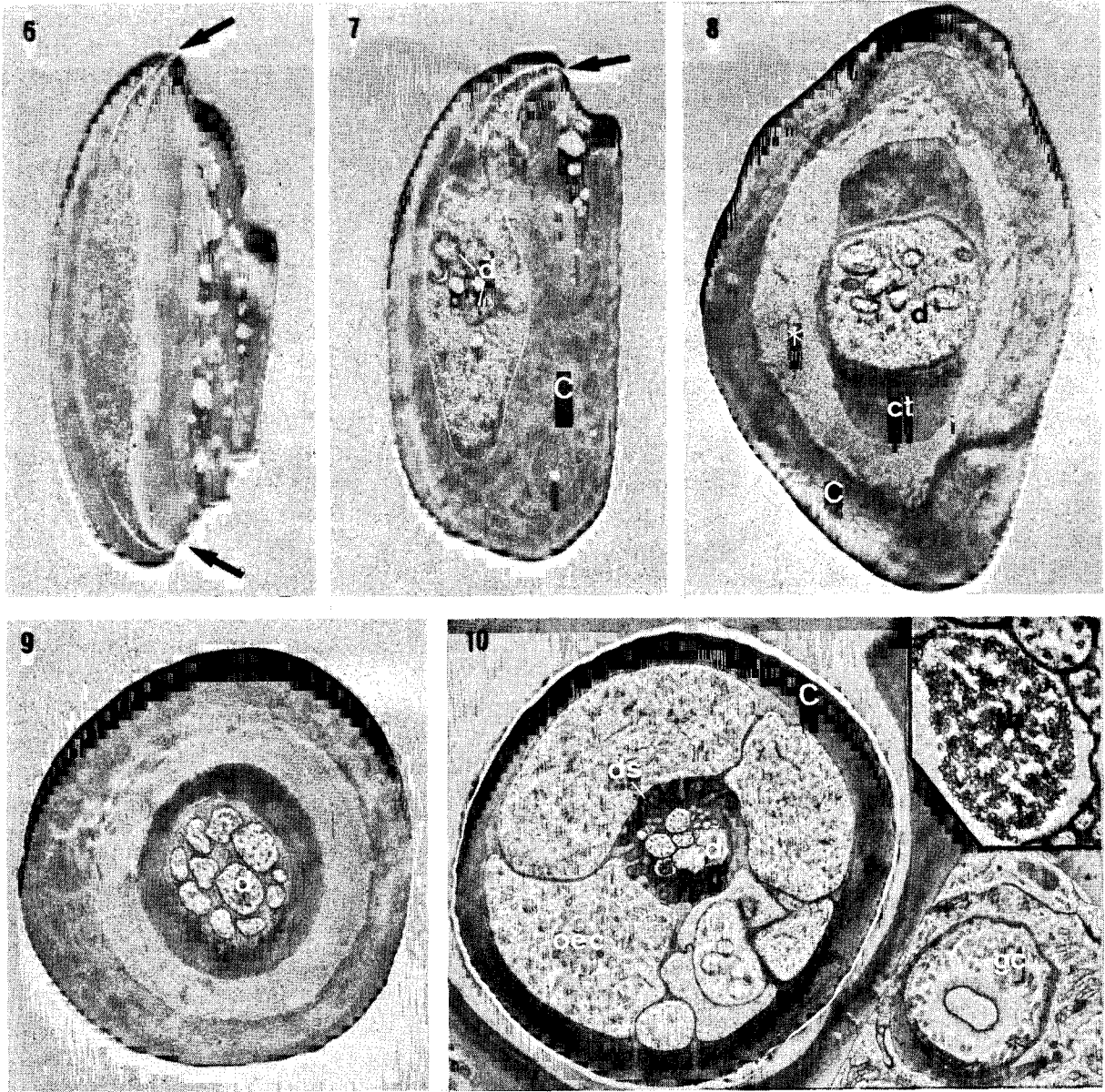
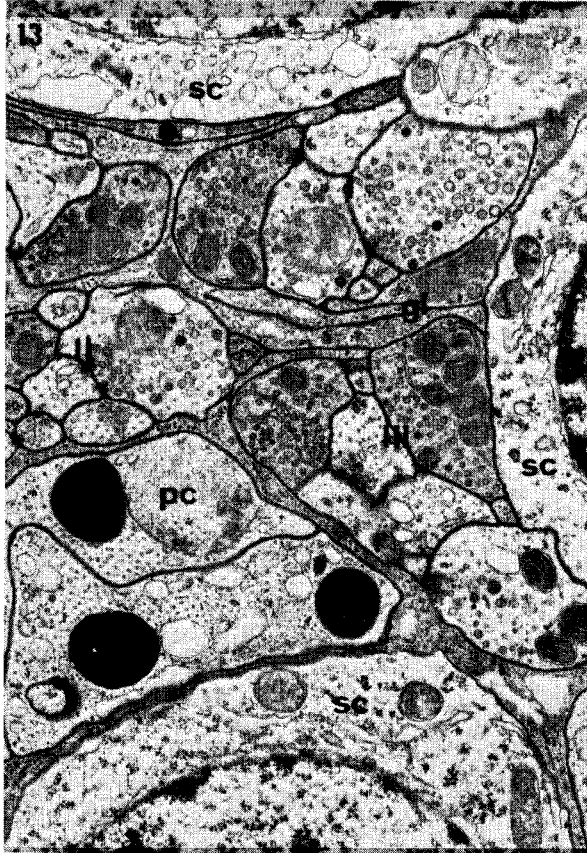
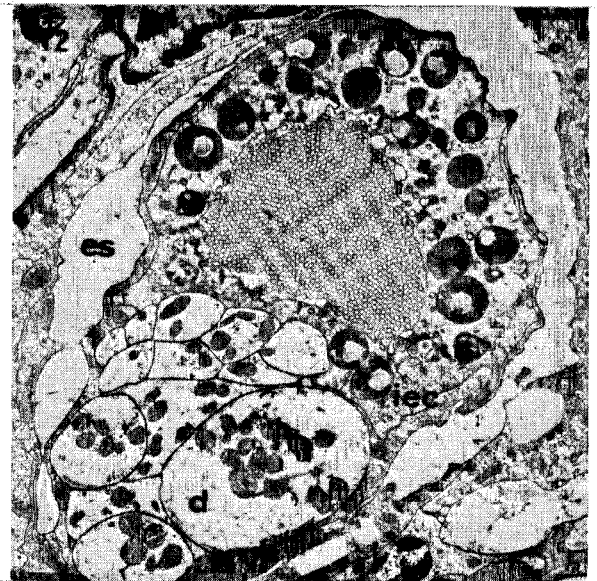
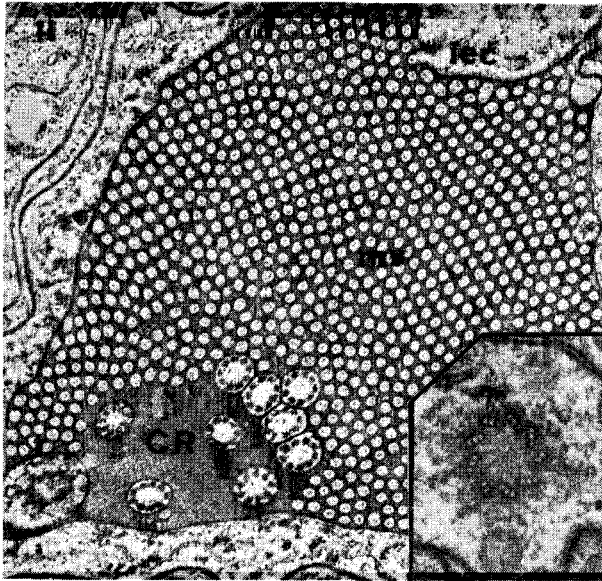


Fig. 4: Longitudinal section of a peg sensillum (*Euscorpilus*). The hair shaft (sh) is suspended in a cuticular socket (sc). Several dendrites (d), encased by a dendritic sheath, enter a cuticular tube (ct) inside the hair shaft. C = cuticle, oec = outer enveloping cells. x 7,700.

Fig. 5: Longitudinal section of the blunt tip of a peg (*Androctonus*). The slit pore is indicated by an arrow. d = dendrites, cp = cuticular platelet. x 47,000.



Figs. 6-10: Consecutive cross-sections of the peg sensillum in *Euscorpis* (from distal to proximal). **6** Tangential section of the top with the slit opening indicated by arrows. x 30,000. **7** Only a few μm proximad, dendrites (d) appear, surrounded by a dense fluid and the thick cuticle (c) of the hair shaft. One opening is still visible (arrow). x 26,000. **8** The flat peg gradually changes to a cylindrical shape toward its base. The dendrites (d) lie within the lumen of the cuticular tube (ct), which is surrounded by a fluid-filled space (asterisk) and the wall of the hair shaft (c). x 32,000. **9** The peg becomes circular near the base and still shows two distinct lumina. Only the inner lumen contains the dendrites (d). x 22,000. **10** At the level of the hair socket a dendritic sheath (ds) and extensions of outer enveloping cells (oec) surround the dendrites (d). gc = duct of a glandular cell. x 9,000. *Inset*: One of the dendrites is characterised by a tubular body (tb). x 41,000.



are presumably secreted into the receptor lymph cavity above the microvilli. Two outer enveloping cells enclose the dendritic inner segments and the inner enveloping cell.

The somata of the sensory cells have a large, round nucleus and an electron-lucent cytoplasm with the typical inclusions of mitochondria, Golgi apparatus and rough endoplasmic reticulum. Each soma is surrounded by a thin glial cell layer. The area between and immediately below the somata of the sensory cells is filled by numerous sensory axons. About six fibres are usually grouped together to form one small axon bundle which is wrapped by a glial extension (Fig. 13). Most interesting is the fact that these axons make many synaptic connections with each other. The most common interaction is the *dyad* synapse, where one presynaptic fibre contacts two postsynaptic fibres (Fig. 14). The postsynaptic fibre often also contains synaptic vesicles and may be presynaptic with respect to another neighbouring fibre. Even reciprocal synaptic contacts between two adjacent axons have been observed. The synaptology within these axon bundles is very complex and has not yet been analysed in detail. Occasionally, synaptic contacts also occur on the somata of the sensory cells and on the glial cell extensions.

Discussion

The first electron-microscopical studies of scorpion pectines (Carthy, 1966, 1968) described a

Figs. 11-14: Consecutive cross-sections of a peg sensillum below the socket (11, 12: *Euscorpium*; 13, 14: *Androctonus*). 11 Cross-section through the ciliary region (CR) of the dendrites surrounded by microvilli (mv) of the inner enveloping cell (iec). x 26,000. *Inset*: Cross-section of a basal body that gives rise to the ciliary structure. x 50,000. 12 Below the ciliary region the inner segments of the dendrites (d) contain many mitochondria. Numerous dark granules characterise the inner enveloping cell (iec). es = extracellular space (fixation artifact). x 5,800. 13 Bundles of axons (I, II, III) are surrounded by glial cells (gl). Numerous synapses occur between axons. pc = pigment cell, sc = sensory cells. x 17,000. 14 Synaptic interactions among axons (1-6) are mostly of the dyad type, i.e. one presynaptic fibre (1) contacts two postsynaptic fibres (2, 4). gl = glial cell extension. x 37,000.

multiple innervation of the peg sensilla but the dendrites were not found to enter the lumen of the peg. After examining the original publications, however, it becomes evident that incomplete series of sections and inadequate fixation had led to this interpretation. The recent electron micrographs by Ivanov & Balashov (1979), as well as our own pictures, show clearly that the peg lumen is filled with the dendrites of about ten sensory cells. Furthermore, a long slit, apparent at the tip of the peg, provides for communication between the dendrites and the outside. Thus, the pecten sensilla are quite similar to the typical chemoreceptive hairs (contact chemoreceptors) which we described on the walking legs of scorpions (Foelix & Schabronath, 1983). In contrast to four mechanoreceptive dendrites ending at the base of the chemoreceptive hair sensillum, we found only one accessory mechanoreceptive dendrite at the peg base. The presence of such a mechanoreceptive dendrite is also implied in the description given by Ivanov & Balashov (1979), yet neither their electron micrographs nor their diagrams show such a terminal. It seems quite important, though, to demonstrate a mechanoreceptive innervation,

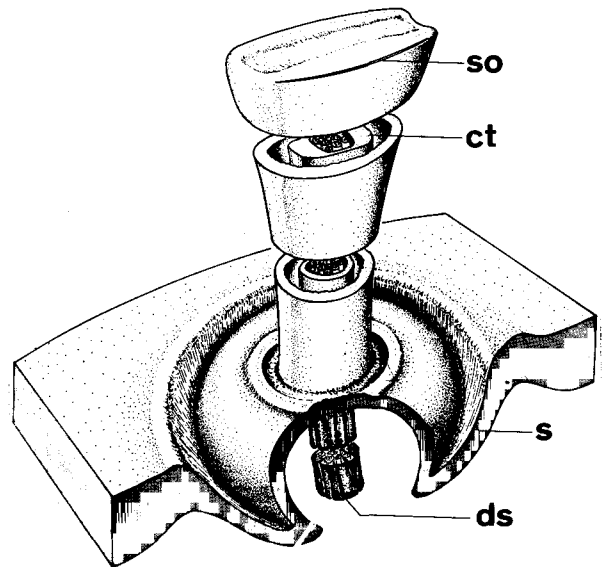


Fig. 15: Diagram of a pecten sensillum of *Euscorpium italicus*. The hair shaft is deeply socketed and flattened at the top. A fine slit opening (so) connects to the outside. Note the double lumen of the hair shaft and the (chemoreceptive?) dendrites within the cuticular tube (ct). ds = dendritic sheath, s = socket.

especially since the electrophysiological recordings of Hoffmann (1964) had proved a mechanoreceptivity of the peg sensilla. In fact, Hoffmann even noted that deflection of a single peg sensillum sufficed to elicit twitching of the entire pectine.

Proof of a dual innervation of the peg sensilla on the scorpion's pectines is the main result of this work. Chemoreceptivity was formerly excluded as a possible sensory modality of the peg sensilla (Hoffmann, 1964), but now seems a very likely candidate again. New electrophysiological and behavioural experiments need to be done before we can understand how these receptors function and how they are put to use in the scorpion's behaviour.

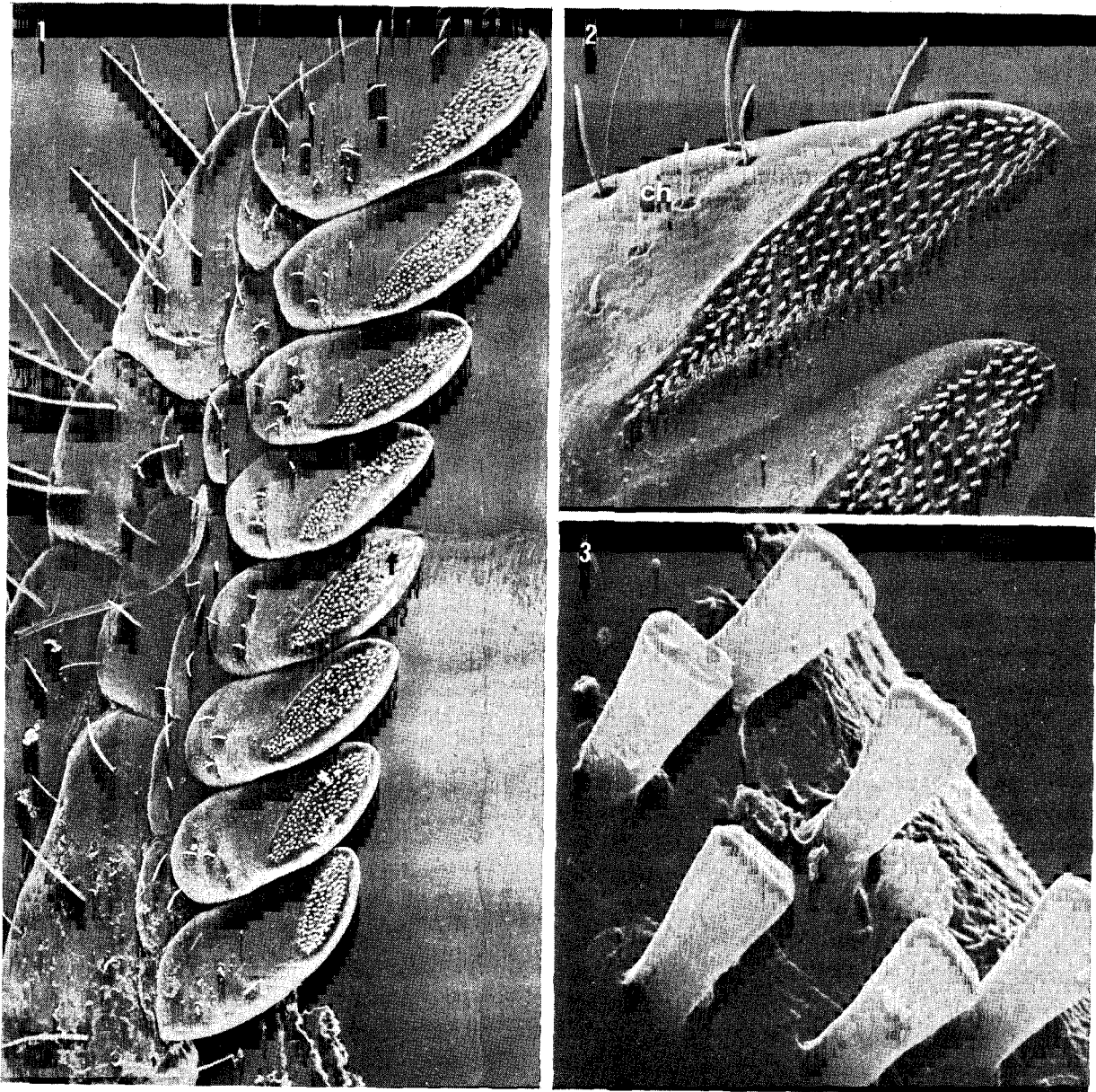
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density of peg sensilla within a field of sensilla.

Although the shaft of a peg sensillum is relatively thick-walled ($> 0.5 \mu\text{m}$) and does not exhibit any conspicuous pore openings, there seems to be a com-

munication between the interior of the peg and the outside. In high-power scanning electron micrographs a slight furrow is visible along the edge of the squared-off tip (Fig. 3). This slit opening becomes



Figs. 1-3: Scanning electron micrographs of a pectine of *Euscorprius italicus*. **1** Whole pectine, showing eight teeth with fields (f) of sensory pegs. Long and short hair sensilla are distributed at the base of the pectine. $\times 85$. **2** Detail of a single tooth showing a field of sensilla with 188 pegs and several chemoreceptive sensilla (ch). $\times 250$. **3** Lateral view of several pegs. Note the flattened top and the wide socket. $\times 2,800$.