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Volume and surface of receptor and auxiliary cells in hygro-/thermoreceptive sensilla of moths (*Bombyx mori*, *Antheraea pernyi*, and *A. polyphemus*)

R.A. Steinbrecht [1], J.-K. Lee [1] *, H. Altner [2], and B. Zimmermann [2]

[1] Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, Federal Republic of Germany;
[2] Institut für Zoologie der Universität, Regensburg, Federal Republic of Germany

Summary. The thermo-/hygroreceptive sensilla styloconica of the silkmoths *Bombyx mori*, *Antheraea pernyi*, and *A. polyphemus* were reconstructed from serial sections of cryofixed and chemically fixed specimens. The volume and surface area of the different sensillar cells were calculated from the area and circumference of consecutive section profiles. In addition, data are provided on the length and diameter of the outer and inner dendritic segments of the receptor cells. The morphometric data obtained from the three species are highly consistent and significantly different from those of olfactory sensilla trichodea of the same species. In each sensillum two type-1 receptor cells (hygroreceptors) are associated with one type-2 cell with a lamellated outer dendritic segment, a comparatively thick inner dendritic segment, and a particularly large soma (thermoreceptor). In contrast to olfactory sensilla, the thecogen cell is the largest auxiliary cell forming an extensive apical labyrinth bordering the inner sensillum-lymph space, whereas an inconspicuous trichogen cell and a medium-sized tormogen cell border a comparatively small outer sensillum-lymph cavity. Moreover, both sensillum-lymph spaces are separated from each other not only by the dendrite sheath, but also by the trichogen cell. The results are discussed with regard to recent electrophysiological observations and current hypotheses on the function of sensilla.

Key words: Thermoreceptors – Hygroreceptors – Sensillum styloconicum – Sensillum-lymph space – Morphometry – *Bombyx mori*, *Antheraea pernyi*, *A. polyphemus* (Insecta)

Insect sensilla are generally thought to consist of (1) an external modality-specific portion, viz. the sensory ending, and special external or internal stimulus-transport structures, and (2) an internal modality-unspecific cellular organization (reviews: Altner and Prillinger 1980; Keil and Steinbrecht 1984; Steinbrecht 1984). Indeed, the cellular organization of insect sensilla is basically uniform and reflects their fundamentally similar development (Henke 1953). It also indicates conformity with respect to essential mechanisms of excitation. However, the basic electrical events leading from the stimulus-mediated receptor current to the finally propagated action potential are still poorly understood. Of the various equivalent circuit models we mention only the widely known hypothesis of Thurm (1970; Thurm and Küppers 1980), which assigns an important active electrical role to the auxiliary cells in addition to that of the receptor neurons. Since such circuit models partly rely also on structural parameters, quantitative data concerning such parameters are needed for a consistent analysis. Comparison of sensilla serving different stimulus modalities so far is hampered by differences among species. For example, olfactory sensilla have been mostly studied in moths, gustatory ones in the fly, and mechanoreceptors in the cricket (for references, see the reviews cited above). Better correlation of morphological and physiological data is to be expected if different modalities are studied in the same species.

The first extensive morphometric study on the cellular components of an insect sensillum was performed with the pheromone-sensitive s. trichodea of *Bombyx mori* (Bombycidae) and *Antheraea pernyi* (Saturniidae) (Gnatzy et al. 1984). The data were remarkably consistent, not only qualitatively but also quantitatively, and good correspondence was observed between the two moth species despite their belonging to different families.

We continued this type of study with the s. styloconica. We observed striking differences between the thermo-/hygrosensitive s. styloconica and the olfactory s. trichodea in the same species. These differences are not restricted to the outer, so-called modality-specific parts, but pertain to the internal cellular organization as well, in qualitative and particularly in quantitative terms.

Materials and methods

Moth pupae were obtained from the following sources: *B. mori* L. from Istituto Sperimentale per la Bachicoltura, Padova, Italy; *A. pernyi* (Guérin-Méneville) from local breeders; *A. polyphemus* (Cramer) were kindly provided by Prof. H.J. Bestmann, Erlangen, FRG, and Prof. K.-E. Kaissling, Seewiesen, FRG.

Antennae of *B. mori* were cryofixed by rapid immersion in liquid propane (−180° C), freeze-substituted in acetone (+2% OsO_4) at −79° C as described by Steinbrecht (1980, 1985), and embedded in Epon 812. Antennae of *A. pernyi* and *A. polyphemus* were chemically fixed by immersion in a mixture of glutaraldehyde (5%) and formaldehyde (4%)

* *Present address:* ARL Division of Neurobiology, University of Arizona, Tucson, AZ 85721, USA

Send offprint requests to: Prof. Dr. R.A. Steinbrecht, MPIV, D-8130 Seewiesen, FRG

in 0.1 M sodium cacodylate buffer, pH 7.2 (Karnovsky 1965). After 4 washes with buffer, postfixation in 1.5% OsO_4 in the same buffer, dehydration in an ethanol series, the specimens were embedded in Durcupan ACM. Cross section series were cut with diamond knives on Reichert OMU2 or Ultracut E microtomes, stained with uranyl acetate and lead citrate and studied in Zeiss EM 10A and 10CR electron microscopes, calibrated by cross grating replicas.

The morphometric procedure used in *B. mori* was described in detail by Gnatzy et al. (1984). Micrographs were taken at intervals of 2.5 µm from the complete section series, and the contours of cell profiles traced on a digitizer tablet (Summagraphics) connected to a PDP 11 computer programmed to give the outline and area of each profile. Cell volume was calculated by summing the area of consecutive section profiles multiplied by the interval thickness. Cell surface was calculated in a step approximation using the circumference, thickness, and differences in area of consecutive section profiles ("extended cylinder approximation" as defined by Gnatzy et al. 1984, appendix). In *A. pernyi*, cell profiles were traced by a mechanical curvimeter. The perimeters obtained were summated and multiplied with the interval thickness ("cylinder approximation", Gnatzy et al. 1984).

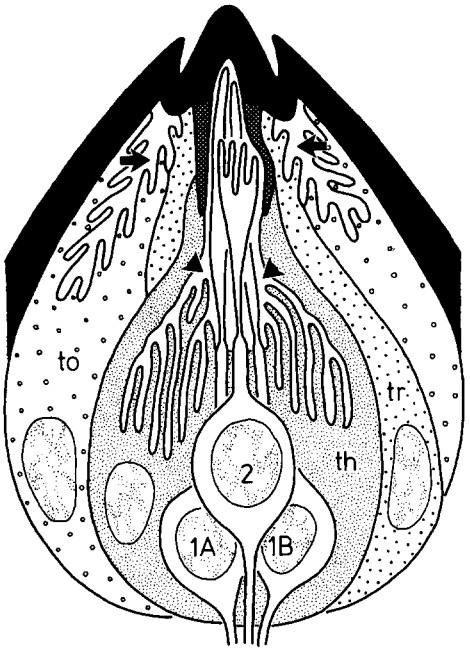

Fig. 1. Schematic representation of the cellular organization of s. styloconica in *Bombyx* and *Antheraea*. One type-2 receptor cell (*2*) and two type-1 receptor cells (*1A, 1B*) are associated with three auxiliary cells, the thecogen (*th*), trichogen (*tr*), and tormogen (*to*) cell. The apical cell membranes of the auxiliary cells are highly folded and border the inner (*arrowheads*) and outer (*arrows*) sensillum-lymph spaces, respectively. The cuticle is drawn in black, the dendrite sheath in dark cross-hatching

Results

The styloconic sensilla of *Antheraea pernyi* and *A. polyphemus* are extremely similar in fine structure, so that data can be pooled for both species. There were also remarkable similarities in the cellular organization of styloconic sensilla when we compared the two *Antheraea* species with *Bombyx mori*, although the external appearance is highly different in the two genera: In *Antheraea* we find typical cones on prominent styli (Haug 1985), whereas in *Bombyx* the stylus is usually reduced and the cuticular apparatus consists of a slender peg partly hidden in a groove (Steinbrecht 1988). The present report is based mainly on the study of *B. mori*, because in this species cryofixation gave better preservation. However, unless stated otherwise, the description is valid for *A. pernyi* and *A. polyphemus* as well.

I. Receptor cells

Typically, the styloconic sensilla belong to the aporous np-sensilla (Altner and Prillinger 1980) and are innervated by a triad (Loftus 1976) consisting of one thermoreceptive and two hygroreceptive cells (Fig. 1). Morphologically, we distinguish two type-1 receptors, which invade the peg lumen with their outer dendritic segments, and one type-2 receptor terminating at the base of the peg with extensive lamellation of the dendrite (terminology: Altner et al. 1983; *A. pernyi*: Haug 1985; *B. mori*: Steinbrecht 1988).

In 7 sensilla from *Bombyx*, sectioned longitudinally, the mean *length* of the cuticular peg was 4.2 ± 0.8 (SD) µm, that of the dendrite sheath 5.8 ± 0.4 µm. The ciliary constrictions were found 12 ± 0.8 µm below the peg bases. Thus, the length of the outer segments of the type-1 receptors (D1A and D1B) was 13–14 µm (only the proximal half of the peg is innervated), that of the type-2 receptor was 12 µm on average. The inner dendritic segments of type-1 receptors measured 30.4 ± 3.4 µm in length; those of the type-2 receptors were always significantly shorter (18–22 µm). For comparison, the inner segments of the s. trichodea in this species are on average only 13 µm long.

In *Antheraea pernyi* the cones are about 12 µm long, but the length of the styli varies between 5 and 60 µm (Haug 1985). Correspondingly, the outer and in particular the inner dendritic segments vary considerably in length. The outer segments of type-2 receptor cells were between 15 and 30 µm long, those of the two type-1 receptors were always 2 and 3 µm longer. The length of inner segments varied between 18 and 42 µm, but in each triad that of the type-2 receptor was shortest (data from 20 sensilla of 13 individuals).

The *diameter* of the *outer dendritic segments* is quite variable in *Bombyx*. Moreover, due to a sharp bend at the peg base, D1A and D1B often cannot be traced with certainty. In the region of the lamellae D2 is largest, but proximal to the dendrite sheath D1A (which terminates most distally in the peg) is largest in cross section, followed by D2 and D1B (Fig. 2a). There are no striking differences in the volume of the dendritic outer segments. However, due to the lamellation, the surface area of the outer dendritic segment of D2 is by far the largest (Tables 1, 2).

The *diameter* of the *inner dendritic segments* consistently showed a significant difference between type-1 and type-2 receptors in both genera. In *Bombyx* the inner segments of type-1 cells are 0.5–1.4 µm (mean 1.0 µm) thick as compared to 1.6–2.7 µm (mean 2.0 µm) in type-2 cells ($n = 11$). In *Antheraea* the corresponding values are 0.6–2.1 µm (mean 1.4 µm) for type-1 and 1.6–5.5 µm (mean 3.7 µm) for type-2 cells ($n = 25$).

The larger diameter of type-2 inner segments is partly compensated by their shorter length. Thus, there is no strik-

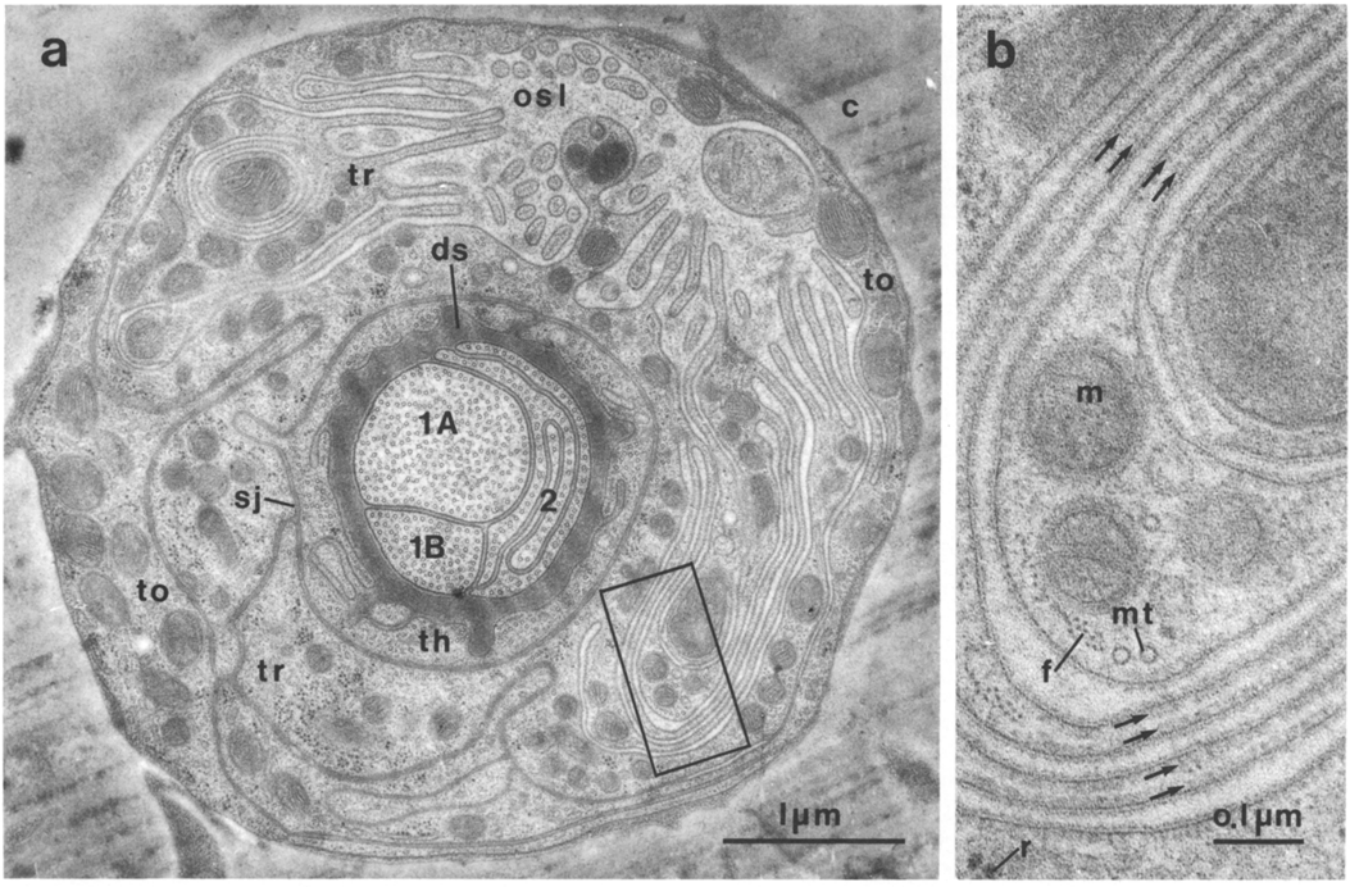

Fig. 2. **a** *Bombyx mori*, s. styloconicum, cross-sectioned about 5 µm below the base of the cuticular peg. The dendrite sheath (*ds*) tightly envelopes the outer dendritic segments of 2 type-1 receptor cells (*1A, 1B*) and 1 type-2 receptor cell (*2*). The latter is forming dendritic lamellae, which are most numerous at more distal levels. The dendrite sheath is surrounded by the thecogen cell (*th*), and this in turn by the trichogen cell (*tr*). The outermost envelope is formed by the tormogen cell (*to*). Both trichogen and tormogen cells border with lamellae and microvilli a small outer sensillum-lymph cavity (*osl*). **b** *Boxed area* of Fig. 2a at higher magnification showing portasomes (*arrows*) on the membranes of the lamellae of the trichogen cell. *c* Cuticle of branch tip; *f* filaments (actin?); *m* mitochondrion; *mt* microtubule; *r* ribosome; sj septate junction. a ×24000; b ×120000

ing difference in surface area, whereas the volume ratios between type-1 and type-2 inner segments as calculated from the above data are 1:1.8 and 1:2.6 in *Bombyx* and *Antheraea*, respectively. Nevertheless, in the two reconstructed sensilla of *Bombyx* not only the surface areas, but also the volumes of all three inner dendritic segments did not differ significantly. Larger differences were found with respect to the volume and surface of the *somata* of the type-2 receptor cells compared to those of type-1 cells (Tables 1, 2). Among the *axons* pronounced differences in diameter were only observed close to the somata.

The *diffusion barrier* formed by the belt of septate junctions (cf. Keil and Steinbrecht 1987) is located about 2 µm proximal to the ciliary constriction (Fig. 3, 4a). Therefore, in equivalent circuit models this part of the inner dendritic membrane area has to be added to the outer dendritic segments; in *B. mori* this amounts to about 8 µm² in D1A and D1B and to about 12 µm² in D2.

Table 1. Volume of receptor cells (µm³) (*Bombyx mori*, s. styloconicum)

	Sensillum No		
	1	2	Mean
Type-1 receptor A			
soma	201	270	235
inner dendritic segment	39	20	29
outer dendritic segment	3.7	3.7	3.7
Type-1 receptor B			
soma	133	159	146
inner dendritic segment	34	32	33
outer dendritic segment	3.5	5.7	4.6
Type-2 receptor			
soma	344	333	339
inner dendritic segment	41	43	42
outer dendritic segment	6.7	4.3	5.5

II. Auxiliary cells

Although the three typical auxiliary cells are present in styloconic sensilla, similar to other sensilla (Fig. 1), there are striking differences in fine-structural details, and also in cell volume and surface area, when we compare s. styloconica with s. trichodea in the same species. Moreover, these differences are consistent in *Bombyx* and in *Antheraea*.

The *tormogen cells* of the s. styloconica have more than double the volume of those of s. trichodea in *Bombyx*. As

Table 2. Surface area of receptor cells (μm^2) (*Bombyx mori*, s. styloconicum)

	Sensillum No		
	1	2	Mean
Type-1 receptor A			
soma	264	283	273
inner dendritic segment	111	91	101
outer dendritic segment	32	26	29
Type-2 receptor B			
soma	208	208	208
inner dendritic segment	115	113	114
outer dendritic segment	28	39	34
Type-2 receptor			
soma	350	321	336
inner dendritic segment	93	99	95
outer dendritic segment	80	129	104

far as the apical cell membrane, which borders the outer sensillum-lymph space, is concerned, we find that of the s. styloconica almost three times as large as that of s. trichodea. In *Antheraea*, this difference is even more pronounced (Tables 3, 4).

The *trichogen cells*, which are the largest of the auxiliary cells in s. trichodea, are the smallest in s. styloconica. In *Bombyx*, the volume ratio is 1:3 (styl:trich).

By far the most striking differences are observed when the *thecogen cells* are compared in the two types of sensilla. In *Bombyx*, the volume ratio is almost 10:1 (styl:trich). The thecogen cell borders the inner sensillum-lymph space and shows no marked surface differentiation or enlargement of the apical cell membrane in s. trichodea. In s. styloconica, however, the apical cell membrane of the thecogen cell is invaginated and folded to form a complex labyrinth, which extends almost down to the level of the sensory cell somata (Figs. 4a, 5a). It is, therefore, not surprising that the surface area of this membrane in s. styloconica is far more than 100 times larger than that in s. trichodea (Table 4). It is striking, however, how similar this ratio is in both species (styl:trich = 143:1 in *Bombyx*; 140:1 in *Antheraea*).

Concomitantly, the volume of inner sensillum lymph in s. styloconica exceeds by far that in s. trichodea (in *Bombyx*: styl:trich = 33:1). The volume of the outer sensillum-lymph cavities below the peg/hair bases is not much different (in *Bombyx*, styl:trich = 1:1.2) (Table 5). However, the difference is enormous when we compare the volume of sensillum lymph within the lumen of the cuticular apparatus; in s. trichodea this amounts to 50 μm^3 and 600 μm^3 in *Bombyx* and *Antheraea*, respectively, whereas in the pegs of the s. styloconica of both species sensillum lymph is practically absent. These type-specific differences are easily observable on the same antenna and, therefore, cannot be due to differences among the experimental animals (e.g., age, water content).

In contrast to the s. trichodea, where the inner and outer sensillum-lymph spaces are confluent at the distal end of the dendrite sheath, these two spaces are well separated from each other, not only by the thick dendrite sheath which is contiguous with the cuticular peg, but also by a cellular sheath formed by the thecogen and trichogen cells, more distally by the trichogen cell alone (Figs. 2a, 3, 4a).

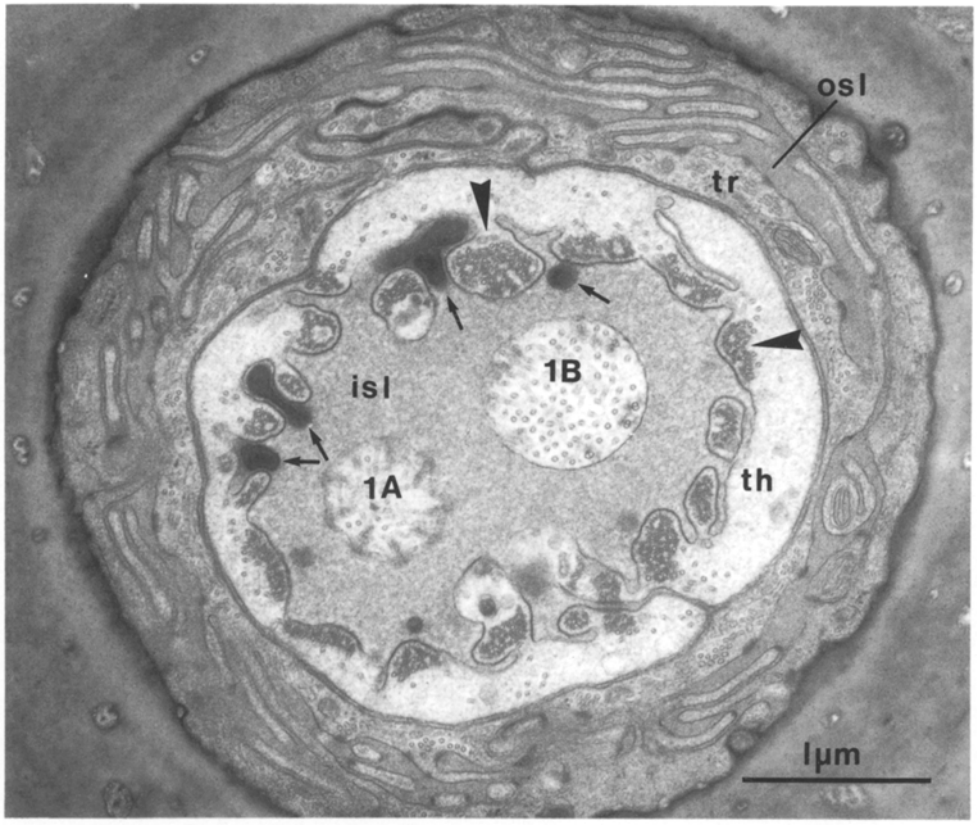

Fig. 3. *Antheraea pernyi*, exceptional s. styloconicum with only 2 type-1 receptor cells (*1A, 1B*) sectioned at ciliary level. Except for the missing type-2 receptor all other features are typical. The thecogen cell (*th*) surrounds a small inner sensillum-lymph space (*isl*). *Arrows* point to the innermost ends of the dendrite sheath. Longitudinal ribs of the thecogen cell contain microtubules and dense material (*arrowheads*) forming a scolopale-like structure (seen also in Fig. 4a). The trichogen cell (*tr*) borders with lamellae a very narrow outer sensillum-lymph space (*osl*). ×24800

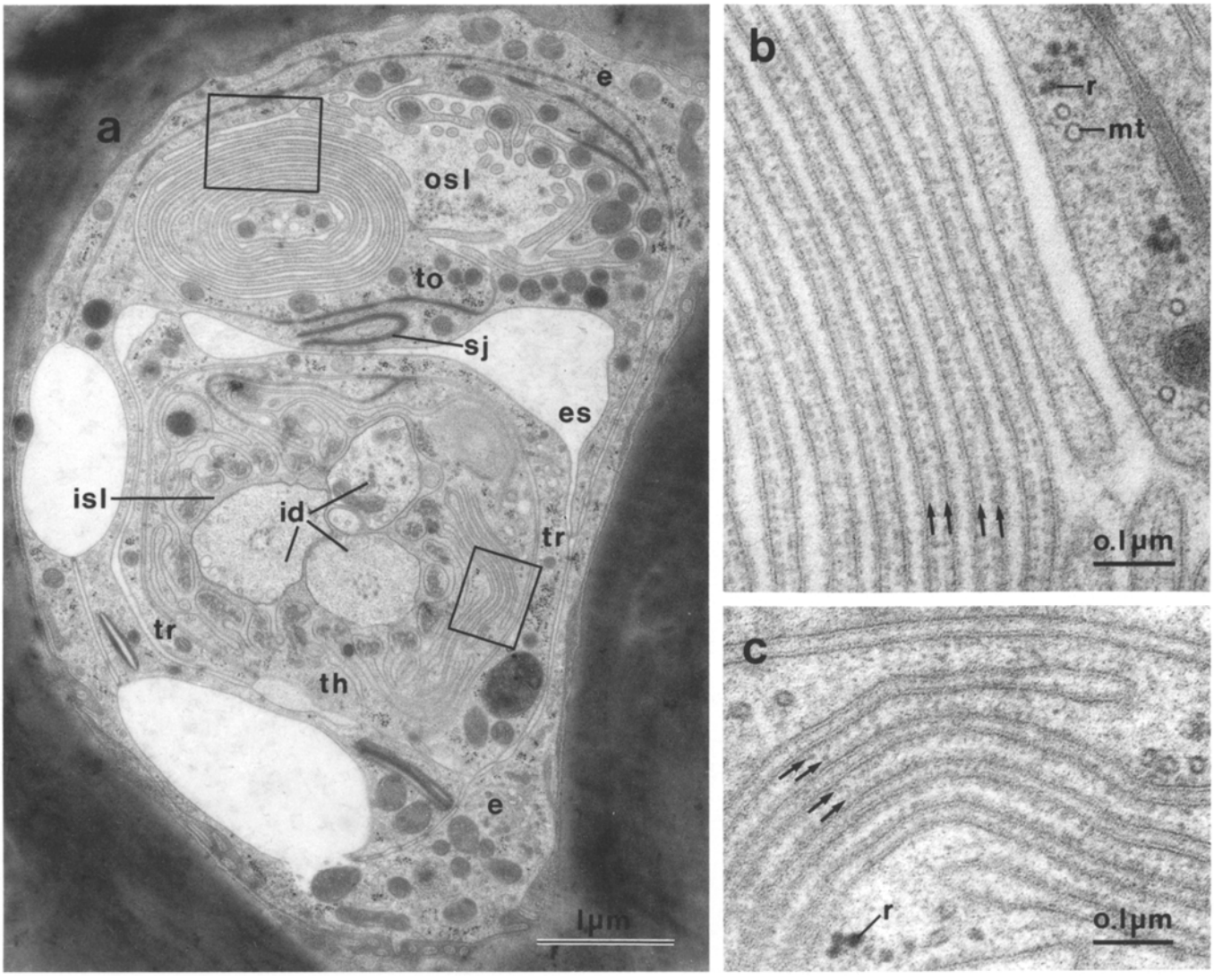

Fig. 4. **a** *Bombyx mori*, cross-section of s. styloconicum at subciliary level. A small inner sensillum-lymph space (*isl*) is discernible around the inner dendritic segments (*id*), continuous with the cisternae of the labyrinth of the thecogen cell (*th*). The trichogen cell (*tr*) at this level forms an incomplete envelope without apical lamellae. The outer sensillum-lymph cavity (*osl*) is now entirely bordered by the tormogen cell (*to*). Large extracellular spaces (*es*) are also seen between the basolateral membranes of trichogen, tormogen, and epidermal (*e*) cells. Septate junctions (*sj*) are seen between all sensillar cells; those around the inner dendritic segments are found a few µm more proximally. **b** Lamellae of tormogen cell (*upper boxed area* in **a**) at higher magnification showing portasomes (*arrows*). **c** Lamellae of thecogen cell (*lower boxed area* in **a**) with portasomes (*arrows*). Other symbols as in Fig. 2. a ×20000; b, c ×120000

Portasomes (Harvey 1980), the membrane particles thought to comprise ATPases involved in ion transport, are found on the apical membranes of all three auxiliary cells of the styloconic sensilla, at least in *B. mori* where cryofixation allowed for better tissue preservation (Figs. 2b, 4b, c). They are most prominent on the deeper membrane invaginations, whereas the more distal microvilli often lack portasomes (Fig. 5b, c). In the chemically fixed specimens of *A. pernyi* and *A. polyphemus* portasomes were unequivocally identified only on the membranes of the thecogen cell labyrinth. Accumulations of mitochondria are found close to the labyrinths and even within the lamellae of both genera (Fig. 5a).

In the s. trichodea of *B. mori*, on the other hand, portasomes were only observed on the apical membrane of the trichogen cell, even in cryofixed specimens (Steinbrecht and Gnatzy 1984).

Table 3. Volume of auxiliary cells (µm³)

	s. styloconica			s. trichodea[a]	
Bombyx mori	Sensillum No.			*Bombyx*	*Antheraea*
	1	2	Mean	Mean	Mean
Tormogen cell	801	944	873	350	378
Trichogen cell	308	326	317	959	907
Thecogen cell	1128	1210	1169	129	–

[a] Data from Gnatzy et al. (1984)

Due to the location of the styloconic sensilla on the tip of the antennal branch, in *Bombyx* the distance between peg base and basal lamina is about 50 µm, which is much longer than in s. trichodea (10–15 µm). Consequently, the

Table 4. Surface area of auxiliary cells (μm^2)

	s. styloconica							s. trichodea[a]	
	Bombyx mori			*Antheraea pernyi*[b]				*Bombyx*	*Antheraea*
	Sensillum No.			Sensillum No.					
	1	2	Mean	1	2	3	Mean	Mean	Mean
Tormogen cell									
apical membrane	3427	4364	3896	6956	5927	4881	5921	1395	835
basolateral m.	1186	1247	1216	–	–	–	–	703	512
Trichogen cell									
apical membrane	302	436	369	1381	1471	1052	1301	3036	1365
basolateral m.	1176	1262	1219	–	–	–	–	1202	634
Thecogen cell									
apical membrane	4482	3828	4155	6279	3549	6238	5355	29	38
basolateral m. (facing receptor cells)	1172	1115	1144	–	–	–	–	447	–
basolateral m. (rest)	2163	2476	2320	–	–	–	–	524	–

[a] Data from Gnatzy et al. (1984)
[b] Sensillum 1 and 2: *A. pernyi*; sensillum 3: *A. polyphemus*

Table 5. Volume of sensillum-lymph spaces (μm^3)

	s. styloconica			s. trichodea[a]	
Bombyx mori	Sensillum No.			*Bombyx*	*Antheraea*
	1	2	Mean	Mean	Mean
Inner sensillum lymph-space	163	158	160	4.8	4.5
Outer sensillum lymph-space					
within sensory epithelium	150	175	163	202	376
within sensory hair peg	0	0	0	50	603
total o.s.l.	150	175	163	252	979

[a] Data from Gnatzy et al. (1984)

extracellular diffusion pathways from the haemolymph to the presumed sites of uptake in the basolateral membranes of the auxiliary cells are longer. There are, however, large extracellular spaces and lacunae between the basolateral membranes of all auxiliary cells, in particular in the more apical regions (Fig. 4a).

Discussion

I. Accuracy of data

The accuracy of the reported data relies on (i) the quality of tissue preparation (avoidance of swelling or shrinking) and (ii) the exactness of the serial reconstruction.

Cryofixation followed by freeze-substitution is the best way of tissue preparation for morphometry, if freezing damage can be avoided (for review cf. Steinbrecht and Müller 1987). Cryofixation was successful with antennae of *B. mori*, but not in the proximal regions of styloconic sensilla in *A. pernyi* and *A. polyphemus*. Nevertheless, it is very unlikely that the observed differences in apical membrane area between *Bombyx* and *Antheraea* are due to artefacts of chemical fixation.

The accuracy of the serial reconstruction is inversely proportional to the thickness of the section intervals. In order to reduce data acquisition to reasonable limits, fairly large intervals of 2 µm (exceptionally 3 µm) were used. The possible errors of the applied procedure have been extensively discussed and the conclusions tested by model calculations (Gnatzy et al. 1984, appendix). Considering the limitations of our procedure and the different degree of surface modulation (e.g., lamellae) of the various cell membranes, we estimated our values for surface area of highly folded cell membranes (e.g., apical auxiliary cell membrane, outer segment of type-2 receptor) to be the lower limit of the real surface, those of the basolateral membranes and dendrites to be correct within $\pm 25\%$, whereas the smooth spherical sensory cell somata might even be overestimated (by $\leq 40\%$).

The good coincidence of the data obtained from different sensilla (e.g., sensillum 1 and 2 in *B. mori*) should not mislead us to take the mean as a statistically representative value. Caution is necessary, since we know that morphometric data on sensilla may systematically vary with their location on the antenna (Steinbrecht 1970). Nevertheless, the quantitative differences observed between the thermo-/hygroreceptive s. styloconica and the olfactory s. trichodea are so obvious that there is no doubt about their significance. Moreover, the same trend is observed in the two genera *Antheraea* and *Bombyx* belonging to different families.

II. Receptor cells

Extracellular recordings from thermo-/hygroreceptive triads very often show a correlation of spike amplitude and response specificity irrespective of the electrode position;

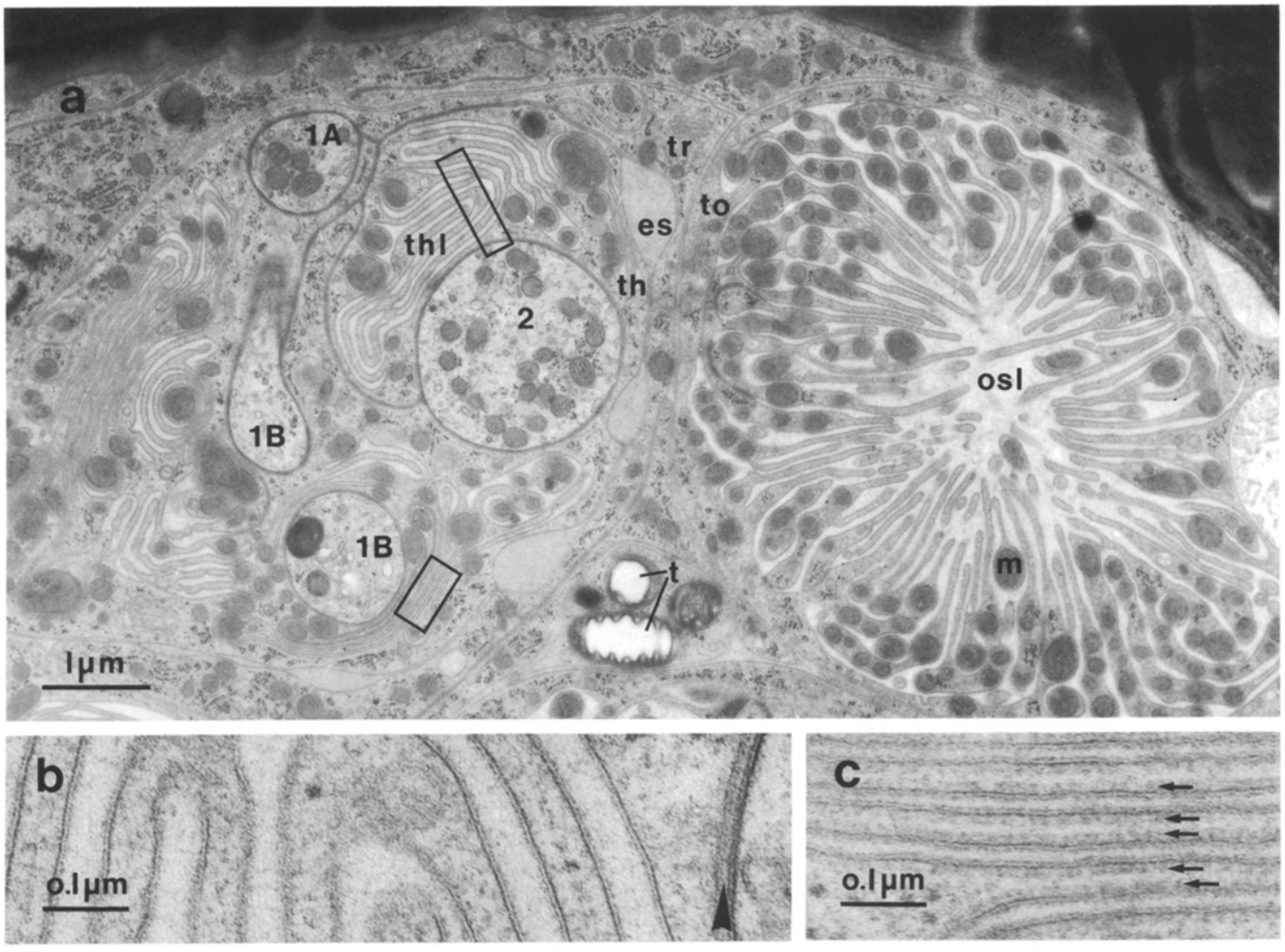

Fig. 5. **a** *Bombyx mori*, s. styloconicum cross-sectioned at level of inner dendritic segments. Note the larger diameter of the type-2 receptor (*2*) as compared to that of the type-1 receptors (*1A, 1B*), one of them (*1B*) forming 2 section profiles due to its curved course. The thecogen cell (*th*) completely wraps the dendrites, its apical plasma membrane is deeply folded forming the thecogen labyrinth (*thl*). Mitochondria (*m*) are abundant in the vicinity of the thecogen labyrinth and in particular in the basal parts of the lamellae of the tormogen cell (*to*). **b** and **c** *Boxed areas* of **Fig. 5a** at higher magnification. The apical plasma membrane bordering the thecogen cell labyrinth is not uniformly studded with portasomes (*arrows*). *Arrowhead* in **b** thecogen/receptor cell junction; *t* tracheole; other symbols as in Fig. 4. a ×15000; b, c ×120000

as a rule the response of the cold unit has substantially larger spikes than the moist or dry unit ("Ableit-Charakteristik") (Waldow 1970; Altner et al. 1978, 1981; Becker 1978; Tichy 1979; but see Loftus 1976). The same is true for *Bombyx* and *Antheraea* (J. Gödde, personal communication). The larger spike amplitude of the cold cell correlates well with the larger diameter of dendrite and initial axon and the larger volume of the soma of the type-2 receptor cell. A similar correlation has been established in the pheromone-sensitive s. trichodea of *Bombyx mori* (Steinbrecht 1973; Gnatzy et al. 1984) and in mechanoreceptive chordotonal organs of *Periplaneta americana* (Young 1970) and *Notonecta glauca* (Wiese and Schmidt 1974). More direct evidence that the type-2 receptor represents the cold unit is available for *Antheraea polyphemus*, where prolonged stimulation by sudden temperature changes resulted in selective degeneration of the type-2 receptor (Zimmermann and Altner, in preparation).

Type-specific differences in the length of the dendritic segments, although often obscured by a high individual variation, are reported also from other insect species (e.g., *Cimex lectularius*; Steinbrecht and Müller 1976). Their functional significance remains open to discussion.

III. Auxiliary cells

When the cellular organization of s. styloconica is compared with s. trichodea, striking differences are observed in the auxiliary cells. Moreover, both genera, *Bombyx* and *Antheraea*, show the same peculiarities, and even in the quantitative data similar ratios are observed.

By far the greatest differences between the two types of sensilla concern the *thecogen cell*. Its apical membrane area in s. styloconica is even larger than the sum of all apical membranes in s. trichodea. In the latter (and also in the olfactory s. basiconica, R.A. Steinbrecht, unpublished) the thecogen cell is the smallest of all auxiliary cells, has no enlarged apical membrane and bears no portasomes. Altner et al. (1983) observed membrane infoldings or an apical labyrinth in the thecogen cells of np-sensilla of 11 species from 9 insect orders. In this context it may be of

functional importance that the inner and outer sensillum-lymph spaces are confluent in the s. trichodea of *Bombyx* and *Antheraea*, but are separated from each other in styloconic sensilla, not only by a thick-walled dendrite sheath but also by a cellular envelope of the thecogen and the trichogen cell up to the peg base, where it closely contacts the peg cuticle. From mechanoreceptors we know that the dendrite sheath alone is permeable to smaller molecules and ions (Keil and Thurm 1979), but in the present case a cellular envelope with its two membranes can regulate and possibly selectively block the exchange between the two sensillum-lymph spaces. It remains to be shown whether the complete cellular envelope of the dendrite sheath is a general feature of thermo-/hygroreceptive sensilla of Lepidoptera and other insect orders. At least for the s. styloconica of *Bombyx* and *Antheraea*, however, the equivalent circuit diagram as proposed by Thurm (1970) for mechanoreceptors and extended by Kaissling and Thorson (1980) for olfactory receptors has to be modified.

The extent to which the apical membranes of the various auxiliary cells bear portasomes obviously varies with the sensillum type. A correlation of these data with the efficiency of the electrogenic cation pump of the apical membranes, as can be measured by the transepithelial voltage or by the short circuit current, appears rewarding when the two types of sensilla are compared. What could be the function of the electromotor force produced by the trichogen and tormogen cell if the outer sensillum-lymph space does not contribute to the receptor current? Electrogenic cation pumps are well known from various other tissues with secretory or absorbing functions (reviewed by Harvey 1980). Of particular interest as an alternative interpretation is the involvement of such a pump in water resorption in the rectal pads of *Thermobia domestica* and *Lepisma saccharina* (Noble-Nesbitt 1977; Küppers et al. 1986). In this case, potassium is pumped into the subcuticular space and passively leaks back into the cell carrying water molecules alongside by electroosmosis. Such a mechanism would be useful for water conservation in all sensilla, in particular in hygroreceptors where optimal water balance should be essential for the precise functioning of the sensillum (Altner and Loftus 1985; Steinbrecht and Müller, in preparation).

The data of Gnatzy et al. (1984) on the area of apical auxiliary membranes in s. trichodea of *Antheraea* were found to be consistent with a high capacity of 27 pF observed electrophysiologically in these sensilla (de Kramer et al. 1984). The correlation was based on the usual specific membrane capacitance of 1 $\mu F/cm^2$ (Cole 1972). In the s. styloconica, inner and outer sensillum-lymph spaces are morphologically and probably also electrically well separated, a circumstance that does not allow the simple summation of all apical membranes for the calculation of a summated capacitance. However, the apical membranes facing the outer sensillum-lymph space alone should yield a capacitance of at least 40pF and 60pF in *Bombyx* and *Antheraea*, respectively. This should be directly tested by electrophysiological experiments evaluating the response to current transients. In general, examining the electrical circuitry of the thermo-/hygroreceptive s. styloconica in the same way as the olfactory s. trichodea (e.g., de Kramer 1985) should provide a valuable test for the validity of current hypotheses on sensillar function, because the two sets of morphometric parameters are so highly different in the same species.

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