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Arthropod Structure & Development 34 (2005) 419–428

ARTHROPOD STRUCTURE & DEVELOPMENT

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Morphology of the prothoracic discs and associated sensilla of *Acanthocnemus nigricans* (Coleoptera, Acanthocnemidae)

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Received 8 October 2004; received in revised form 16 June 2005; accepted 27 June 2005

Abstract

The Australian 'little ash beetle' *Acanthocnemus nigricans* (Coleoptera, Cleroidea, Acanthocnemidae) is attracted by forest fires. *A. nigricans* has one pair of unique prothoracic sensory organs and it has been speculated that these organs may play a role in fire detection. Each organ consists of a cuticular disc, which is fixed over an air-filled cavity. On the outer surface of the disc, about 90 tiny cuticular sensilla are situated. The poreless outer peg of a sensillum is 3–5 μm long and is surrounded by a cuticular wall. One ciliary sensory cell innervates the peg. As a special feature, the outer dendritic segment is very short already terminating below the cuticle. A massive electron-dense cylindrical rod, which most probably represents the hypertrophied dendritic sheath, extends through the cuticular canal connecting the tip of the outer dendritic segment to the peg. The dendritic inner segment and the soma are fused indistinguishably. Thin, leaflike extensions of glial cells deeply extend into that conjoint and considerably enlarged compartment which also contains large numbers of mitochondria. In summary, the sensilla of the sensory disc of *A. nigricans* represent a new type of insect sensillum of hitherto unknown function. The possible role of the prothoracic sensory organ in fire detection is discussed.

Keywords: Ciliary sensillum; Mechanoreceptor; Infrared receptor; Thermoreceptor; Pyrophilous insect; Pyrophilous behaviour; Fire detection

1. Introduction

Acanthocnemus nigricans is a small dark beetle having a body length of only 3–6 mm. The species *nigricans* is the only recent species within the genus *Acanthocnemus* and is distributed all over Australia. Since the middle of the 19th century *A. nigricans* has also been found on other continents like Asia, Africa and Europe (Lawrence and Britton, 1994). Most probably, the reason for this recent expansion all over the world is the commercial export of Australian wood or cereals infested with *A. nigricans*. Therefore, the species can be also regarded as a cosmopolitan to warmer parts of the Old World (Champion, 1922). In contrast to its inconspicuous appearance, *A. nigricans* shows a remarkable behaviour as beetles of both sexes are attracted by forest fires. The beetles invade a freshly burnt area immediately and approach areas where glowing remnants of trees or hot ashes are still present (Champion, 1922; Schmitz and Schmitz, 2002). The beetles often land very close to spots with still high surface temperatures. After a short period of quickly running around, the beetles hide in small openings in the ash or under the bark of burnt trees. The reason for this so-called pyrophilous behaviour is unknown but it can be speculated that the described 'hot spots' serve as meeting places for the sexes. Most probably, the females deposit their eggs into the ash or under the bark of burnt trees. Currently, the larval food is unknown. Because it is reasonable to suppose that larvae were exported out of Australia inside wood (see above), it is very probable that the cambium layer of freshly burnt trees represents the primary source of food for the first instars.

In two pyrophilous genera of buprestid beetles, *Melanophila* and *Merimna*, unique extraantennal sensory organs have been found which are used in fire detection. Beetles of the genus *Melanophila* have two pairs of metathoracic infrared (IR) organs which contain about 70 arch-shaped photomechanic IR sensilla (Evans, 1966a,b; Vondran et al., 1995; Schmitz et al., 1997). The Australian 'fire-beetle' *Merimna atrata* has one to three pairs of abdominal IR receptors (Schmitz et al., 2001; Mainz et al., 2004) which

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doi:10.1016/j.asd.2005.06.001

are innervated by thermoreceptive multipolar neurones (Schmitz and Trenner, 2003). Therefore, the receptors function as microbolometers. However, the prothoracic sensory organs in *A. nigricans* are located on a different part of the body and, moreover, are fundamentally different from the IR receptors of the pyrophilous buprestid beetles. *A. nigricans* possesses two prothoracic sensory organs which are located directly anterior to the coxae of the prothoracic legs. Each of the organs consists of a tiny cuticular disc (diameter 110–185 μm), which is held by a lateral cuticular stalk above an air-filled cavity. First morphological investigations have already shown that the disc is filled with the somata of many sensory cells, which contain large numbers of mitochondria. By these findings, a sensory function of the disc was made very probable (Schmitz et al., 2002). Additionally, on the outer surface of the disc, small pegs were discovered which represent the cuticular apparatus of sensilla. In the present paper, we describe the morphology of the cuticular sensilla in detail. The possible role of the prothoracic sensory organ in fire detection is discussed.

2. Material and methods

2.1. Animals

Adult beetles were collected in 2002 and 2003 on freshly burnt areas in Western Australia. Animals were kept for several weeks in plastic boxes and fed with raisins, peanuts and walnuts; drinking water was given ad libitum.

2.2. Scanning electron microscopy

Twelve beetles were air-dried and glued on holders by Leit-Tabs (Plano, diameter 12 mm) with either the dorsal or the lateral side. Sensory discs from seven beetles were isolated and cleaned by sonication in a mixture of chloroform/ethanol (2:1) for 2 min. Discs were air-dried again and mounted on holders in an upright position which allowed examination from all sides. Specimens were sputtered with gold and examined with a Cambridge Stereoscan 200 SEM and a LEO 440i (Leica, Bensheim, Germany).

2.3. Light and transmission electron microscopy

Sensory discs of 10 beetles were isolated and immediately immersed in iced glutaraldehyde fixative (3% glutaraldehyde in 0.05 mol l^{-1} cacodylate buffer, pH 7.1; osmolarity 380–400 mosmol l^{-1}) and fixed overnight. The discs were then washed in buffer, postfixed with 1.5% OsO_4 in the same buffer, dehydrated through an ascending ethanol series and embedded in Epon 812. Semithin and ultrathin sections were cut with a Reichert Ultracut Microtome using glass- or diamond knives. Semithin sections (0.5 μm) were stained with a 0.05% toluidine-blue/borax solution and examined with a Leitz DM RBE light microscope. Uninterrupted series of sections through three sensilla were taken as a basis for the reconstruction of a single sensillum (shown in Fig. 6).

Additionally, we made sections parallel to the outer surface of the disc to obtain cross sectional profiles through the cuticular parts of the sensilla. Digital images of the sections were taken with a Nikon Coolpix 5000. Ultrathin sections were stained with uranyl acetate and lead citrate and examined with a Zeiss EM 109 TEM.

2.4. 3D-reconstruction of the sensory disc

To investigate the number and position of sensory cell somata inside the sensory disc, a series of 210 semithin cross-sections was cut through a single sensory disc. The digital images of the sections were stored on a PC and the software Amira (Version 3.0, TGS Inc., San Diego, USA) was used for 3D reconstruction. Due to inferior quality, 35 out of the 210 images could not be used. Therefore, the distances between images were adjusted individually to compensate for the loss of those sections. The outer cell membranes of the somata could not be traced and identified reliably. Therefore, we used the nuclei and nucleoli of the sensory cells for soma identification. To guarantee automatic identification by the software, nuclei and nucleoli as well as the cuticle were coloured in each section using a digitizing tray.

3. Results

3.1. The prothoracic sensory organs

One pair of unusual organs is located on the prothorax in both sexes. The two organs are situated directly anterior to the coxae of the prothoracic legs (Fig. 1(A) and (B)). The most striking component of an organ is a more or less round cuticular disc, which is somewhat sunken into the surface of the prothorax. At its posterior edge, the disc is held by a stalk which originates at the dorso-anterior border of the coxal cavity (Fig. 2(A) and (B)). When analysing the composition of the cuticle of the stalk, we found no morphological exceptions, which may indicate any flexible properties. Below the disc, a hemispherical air-filled cavity is situated. Because the opening of the cavity is somewhat larger than the diameter of the disc, exchange of air between the cavity and the outside is possible (Fig. 2(A)). The disc, which has been found to be innervated by sensory cell somata (Schmitz et al., 2002) represents the actual receptor, whereas the cavity can be regarded as an auxiliary structure.

3.2. Outer morphology of the sensory disc

A sensory disc has a diameter of 110–185 μm. The size

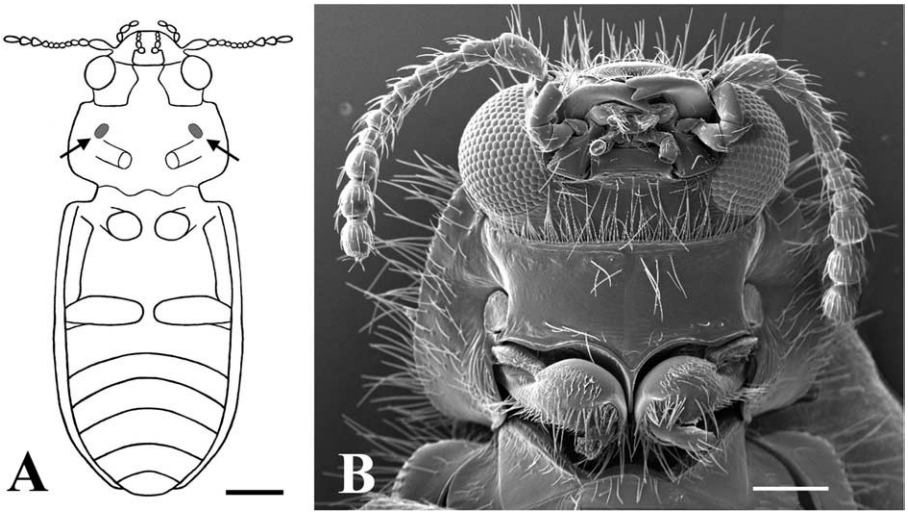


Fig. 1. (A) Schematic drawing of *A. nigricans* (ventral view, legs omitted). Arrows point to the prothoracic organs (bar 500 μm). (B) SEM image of the head and the prothorax seen from the ventral side. The organs are situated in front of the coxae of the prothoracic legs (bar 200 μm).

roughly correlates with the size of the beetle. In some beetles, the outer surface appears slightly curved inward whereas the surface of the underside is always bulged out convexly (Fig. 2(C) and (D)). The stalk shows an oval cross section with an inner diameter of about 30 μm.

Numerous small sensilla can be found on the outer surface of the disc (Fig. 2(B)). However, the sensilla are not evenly distributed. Most sensilla concentrate within an anterior semicircular area on the upper surface (Fig. 3). Some sensilla (about 13%, $N=9$ discs) were even found on the anterior edge of the disc (Figs. 2(C) and 3). We never found a sensillum on the underside. Most probably, all sensilla belong to the same type and can be identified by their cuticular apparatus, which consists of a small cuticular peg surrounded by a socket wall. At its base, the peg has a diameter of about 1 μm and a total length of about 3–5 μm (Fig. 4(A)).

3.3. Morphology and ultrastructure of the sensilla

Cross and longitudinal sections through the sensilla revealed that the small cuticular peg mainly consists of massive cuticle. Neither pores nor a lumen inside the peg were found (Fig. 4(A)–(C)). From below, a rod consisting of electron-dense material is connected to the base of the peg (Fig. 4(C)). The rod has about the same diameter as the base of the peg and the electron-dense material continues into the centre of the peg (Fig. 4(B) and (C)). The rod passes through the canal which extends from the proximal base of the peg to the lumen inside the disc (Fig. 4(C) and (D)). Even at higher magnifications of 85,000× the material shows a homogeneous appearance (Fig. 4(E)). Most probably, it represents the hypertrophied dendritic sheath, which has displaced the dendritic outer segment within the canal. A few micrometers below the inner opening of the canal, the rod becomes hollow and the tip of the dendritic outer segment (DOS) can be found inside (Fig. 4(F)). The short DOS has a diameter of less than 0.5 μm and contains only very sparse neurotubuli. No tubular body was found inside the DOS.

A ciliary constriction subdivides the DOS and the dendritic inner segment (DIS). However, because the DOS already shows a small diameter, there is no decrease in diameter from the basal part of the DOS towards the ciliary constriction. Also we found no clear evidence for the existence of an inner receptor lymph cavity around the ciliary constriction. Two basal bodies were found just below the constriction (Fig. 4(G) and (H)). The basal bodies are interconnected by root filaments which do not extend further into the proximal region of the DIS. Below the ciliary constriction the DIS broadens (Figs. 4(G) and 5(A)). As predominant features, thin, leaflike processes of glial cells deeply extend into the DIS (Figs. 4(G), 5(A) and 6) and a large number of mitochondria were always found inside (Figs. 5(A) and 6).

The soma region could be easily identified by a large nucleus (Fig. 5(A)), but the DIS and the soma are not clearly distinguishable as they show the same structural features (i.e. thin but deep invaginations of glial cells into their common enlarged compartment and lots of mitochondria, Fig. 5(B) and (C)). We found three enveloping cells (most probably representing the tormogen, trichogen and thecogen cell, Fig. 4(D), (F) and (H)) which enwrap the dendrite and the distal region of the soma cell. Therefore, most of the large cell soma is enveloped by a thin glial layer. In general, 2–3 nuclei of enveloping cells were found in the region of the ciliary constriction (Fig. 6). Due to the extreme entanglement of cell material inside the disc, an unequivocal identification of single enveloping cells could not be made. Based on a series of ultrathin sections through a total of three sensilla, a graphical reconstruction of a single sensillum was made (Fig. 6). The distribution and

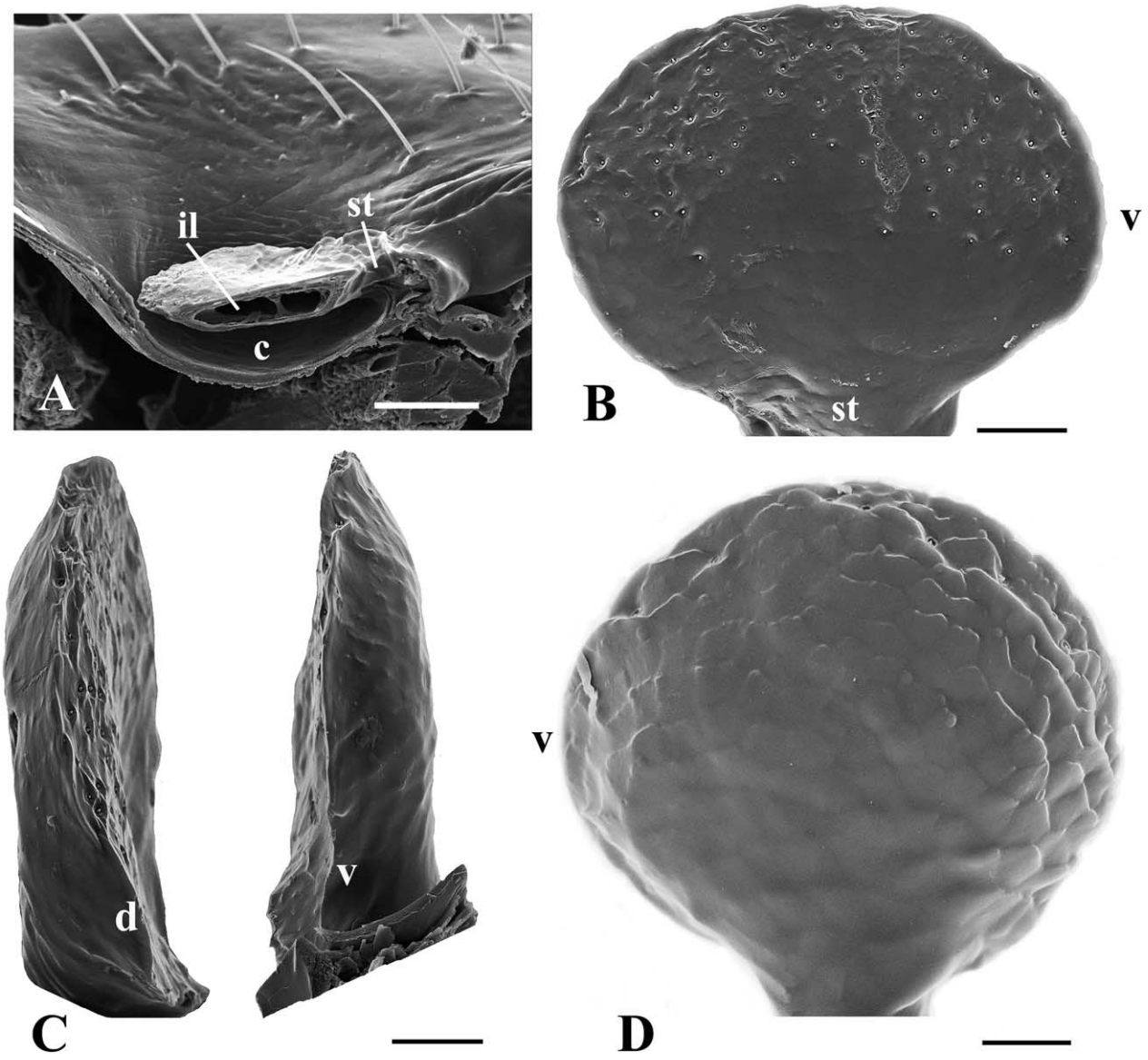


Fig. 2. SEM images of a prothoracic organ and an isolated sensory disc. (A) Organ cut open in the ventral region of the disc. The inner lumen of the sensory disc (il), the stalk (st) and the cavity (c) below the disc are visible (anterior on the left, bar 50 μm). (B) Topside of an isolated sensory disc. The posterior stalk (st) is situated below. Numerous small sensilla are located mainly in the anterior region of the upper surface (ventral edge (v) on the right, bar 25 μm). (C) Lateral view of the sensory disc onto the dorsal (d) and the ventral edge (v), respectively. Some sensilla can be found at the sharp bend between the upper and the bottom side (bar 25 μm). (D) Bottom side of the sensory disc. In general, no sensilla could be found here. However, in some specimens, a few sensilla were discovered directly below the upper side (ventral edge v on the left, bar 25 μm).

arrangement of sensory cell somata inside a sensory disc is provided in Fig. 7.

4. Discussion

4.1. Classification and proposed function of the sensilla

It is generally accepted that the *bauplan* of the cuticular apparatus and its interaction with the sensory dendrite is highly modality-specific in an insect sensillum (Steinbrecht et al., 1989). Therefore, the detailed study of the morphology of a sensillum gives valuable insight into its possible function, e.g. chemoreception, mechanoreception or thermo-/hygroreception. When analysing the *bauplan* of the small sensilla found on the sensory disc (in the following called ‘disc sensilla’) it turned out that these sensilla cannot be easily classified into one of the known categories mentioned above.

The lack of any lateral or terminal (i.e. tip) pores in the cuticular peg and the absence of an inner lumen inside the peg into which the DOS could extend (Steinbrecht, 1997; Ozaki and Tominaga, 1999) exclude a function of the disc sensilla as an olfactory or gustatory receptor. Additionally,

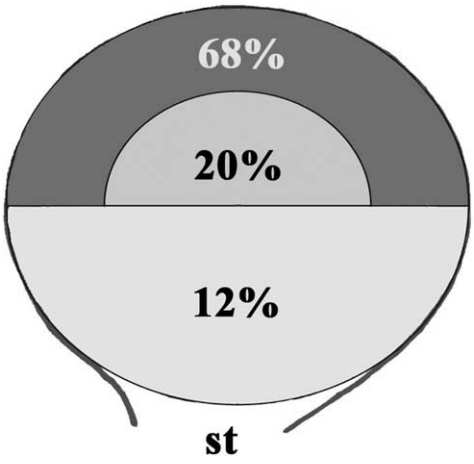


Fig. 3. Distribution of the sensilla on the topside of a schematized sensory disc. Sensilla which are located on the edges are included. Nine discs taken from seven beetles were analysed. The stalk (st) is situated below. Most sensilla (68%) concentrate within the anterior semicircular area (coloured in dark grey).

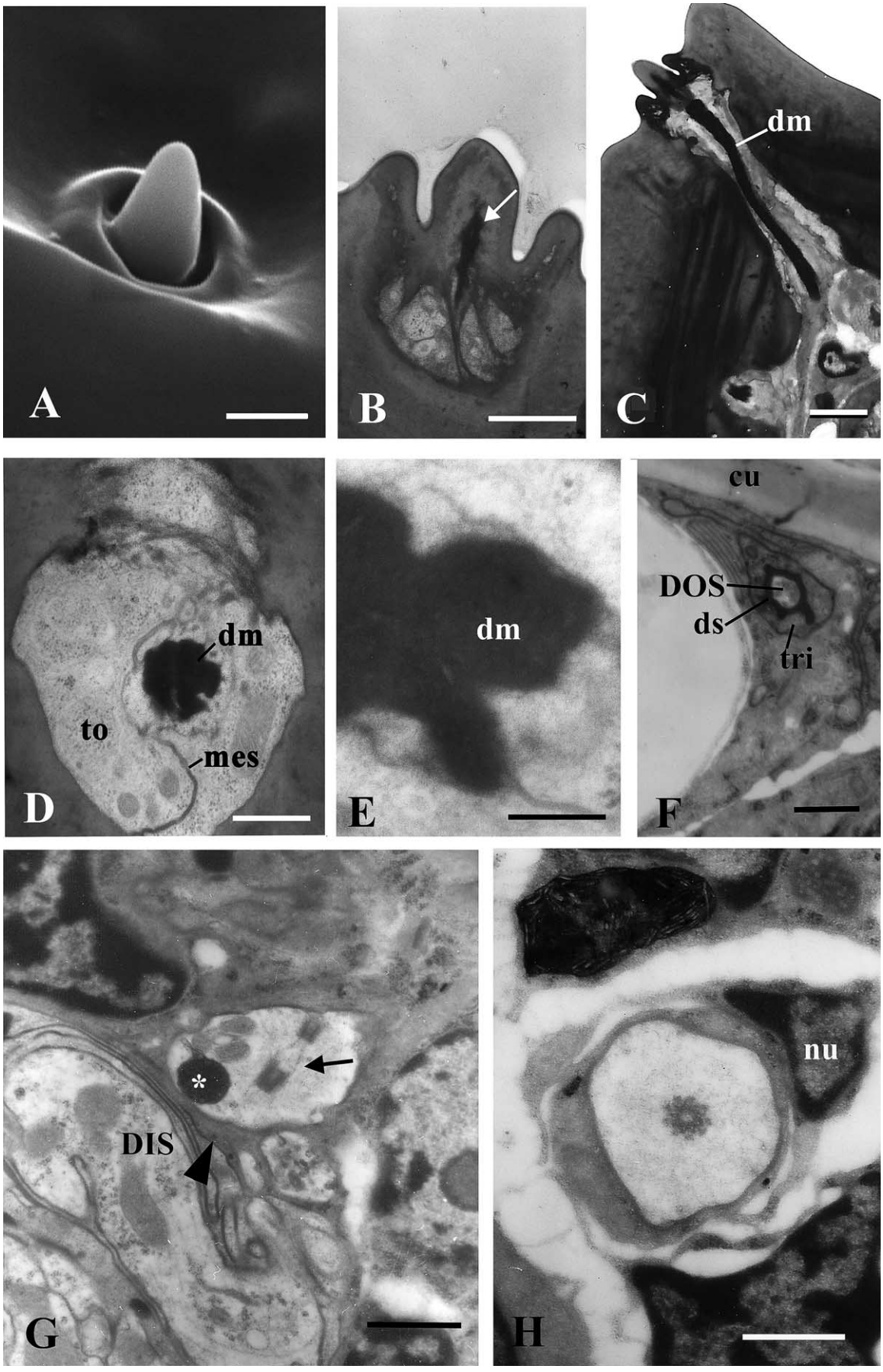
it is a typical feature of olfactory receptors that several sensory cells extend their DOS into the cuticular apparatus (Steinbrecht, 1984, 1999).

Mechanoreceptors (i.e. hair-type mechanosensilla and campaniform sensilla) are characterized by the specific linkage between the dendritic tip of a single mechano-sensitive sensory cell and the base of the cuticular apparatus (Thurm, 1964; Keil, 1997; Iwasaki et al., 1999). The cuticular apparatus is designed to be deflected (hair mechanoreceptors) or deformed (campaniform sensilla) in a predetermined and, therefore, directed way. Consequently, the adequate mechanical stimulus will cause a cross-compression of the dendritic tip which—as an important feature—contains a tubular body (Thurm, 1974; French, 1992).

When analysing the structure and possible interplay between the tip of the DOS and the small cuticular peg of the disc sensilla, it does not become evident, in which way the sensillum may act as a mechanoreceptor. The pegs are very short (3–5 μm) and therefore it is hard to imagine which kind of mechanical stimulus (i.e. touch or airborne sound) should be detected. Additionally, neither a preferred direction of deflection nor a tubular body inside the DOS was discovered. Moreover, it is completely enigmatic how the long electron-dense rod, which is placed between the peg and the tip of the DOS, can transfer any mechanical deformation of the peg to the DOS.

In insects, thermo- and hygroreceptive sensilla act as bimodal sensory organs (Steinbrecht and Müller, 1991). As a rule, two antagonistic hygroreceptor cells (a ‘moist’ and a ‘dry’ cell) are combined with a thermoreceptor cell. Such a thermo-/hygrosensitive triad of receptor cells within a given sensillum (Loftus, 1976) has been found in many insects reviewed by Steinbrecht, 1984; Altner and Loftus, 1985. The cuticular apparatus of thermo-/hygrosensitive sensilla is an inflexible and poreless peg or cone without a particular socket structure. The two hygroreceptive cells send their unbranched dendrites into the peg lumen. The dendrites fill the lumen of the cuticular apparatus almost completely and, therefore, are not surrounded by sensillar lymph. On the other hand, the DOS of the third, i.e. thermoreceptive, cell terminates below the base of the peg and often displays a unique lamellation or branching of its DOS. Poreless sensilla with inflexible sockets housing thermo-/hygro-receptors can be primarily found on the antenna. However, in *Periplaneta americana* a single unicellular type of this sensillum was found on the tip of the maxillary palp (Altner and Stetter, 1982). The sensillum shows the morphological features of a humidity receptor because the single unbranched dendrite extends into the inner lumen of the peg. Electrophysiological recordings ascertained a function as a hygro- and/or thermoreceptor (Altner et al., 1983). In the disc sensillum of *A. nigricans* we only found a single sensory cell showing an unbranched and considerably reduced DOS already terminating below the cuticle of the disc. Therefore, by means of its morphological features, the disc sensillum cannot be classified as a standard hygro- or thermoreceptor.

In search for the possible function of the disc sensilla our attention was drawn on the finding that the enveloping glial cells send many processes deep into the lumen of the soma and the DIS. Furthermore, the soma and the DIS obviously form a larger functional unit which also contains many mitochondria. To our knowledge, these are quite unusual features for a sensory cell in a cuticular insect sensillum. Pronounced interrelations between enveloping cells and the stimulus perceiving sensory parts have already been observed in the trigeminal terminal nerve masses (TNMs) in IR-sensitive snakes. In crotalid snakes, specialized Schwann cells are tightly associated with the TNMs. The Schwann cells extend their cytoplasmatic processes into the interstices between the terminal processes and around the TNMs (Bullock and Fox, 1957; Terashima et al., 1970; Amemiya et al., 1996). Consequently, the fine terminal branchlets are heavily entwined with Schwann cells (Molenaar, 1992). The same phenomenon was found in the terminal dendritic mass (TDM) of the multipolar thermoreceptor innervating the abdominal IR organ in the Australian ‘firebeetle’ *M. atrata* (Schmitz et al., 2001). Here, several hundred small terminal dendrites are stuck together and are enveloped by thin processes of glial cells. Moreover, in the TNMs in snakes and in the TDM in *M. atrata* large numbers of mitochondria were found. Therefore, it seems to be an important feature of thermoreceptive sensory terminals, which are involved in IR reception to contain large amounts of mitochondria and to show invaginations of accessory cells. A nutritional role of the enveloping cells can be discussed. For this reason we propose that the soma and DIS complex may also act as a thermoreceptor in the disc sensilla of *Acanthocnemus*. In this case, the entire organ would function as a bolometer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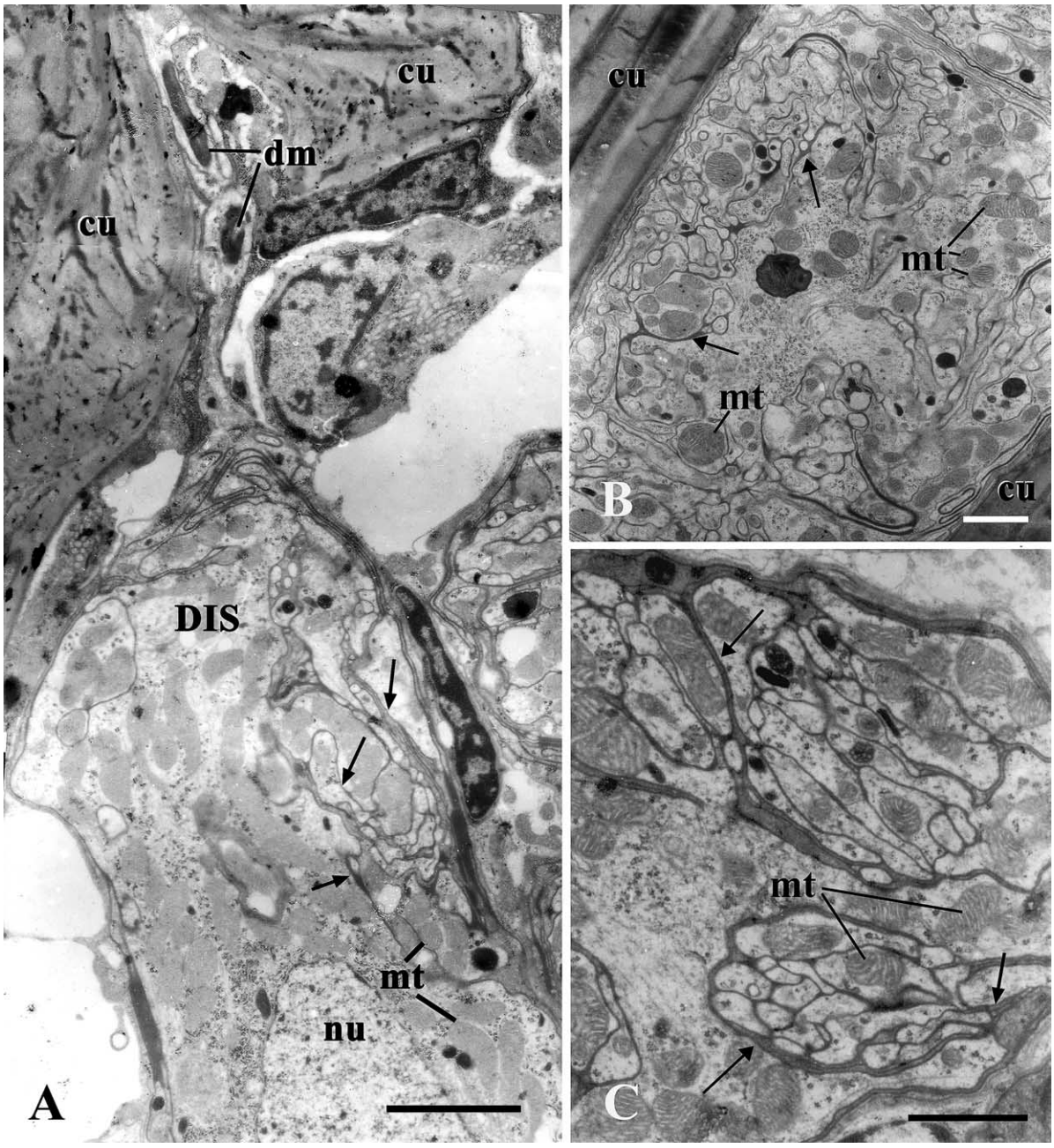

Fig. 5. (A) Longitudinal section through a sensory cell. Distally, the soma region with the nucleus (nu) continues into the dendritic inner segment (DIS). Note the deep invaginations of glial cells (identifiable by their darker cytoplasm) into the lumen of the sensory cell (arrows). Inside a canal passing through the cuticle (cu), the rod of electron dense material (dm) is partly visible (mt, mitochondria, bar 2 μm). (B) Soma of a sensory cell situated between the outer cuticle (cu, upper left corner) and the cuticle of the bottom side of the disc (lower right corner). Note numerous invaginations of (dark) glial cells into the protoplasm (arrows) and large numbers of mitochondria (mt, bar 0.5 μm). C Detail of a sensory cell soma. Various invaginations of glial cells into the cytoplasm can be observed as indicated by small arrows (mt, mitochondria, bar 1 μm).

Fig. 4. (A) SEM image of the cuticular apparatus of a sensillum consisting of a small peg surrounded by a socket wall (bar 1 μm). (B)–(H): Ultrathin sections through sensilla at different levels. (B) Longitudinal section through the peg and the surrounding socket wall. In the centre of the peg electron dense material can be seen (arrow, bar 1 μm). (C) Longitudinal section through a sensillum located on the topside close to the anterior edge. The electron dense material (dm) can be traced up to the inner lumen of the disc (bar 2 μm). (D) Transverse section through a sensillum just below the peg. The electron dense material (dm) builds a compact rod. The outermost enveloping cells—most probably the tormogengen cell (to)—forms a mesaxon (mes, bar 0.5 μm). (E) Part of the homogeneous electron dense material (dm) at higher magnification (85,000×, bar 0.2 μm). (F) Cross section through the dendritic outer segment (DOS) below the cuticle (cu, cuticle; ds, electron dense material of the dendritic sheath; tri, trichogen cell; bar 0.5 μm). (G) Longitudinal section through the dendritic inner segment (DIS) of a sensory cell. Two basal bodies are located in the apex of the DIS. Note the root filaments (arrow) which extend from the distal (above) to the proximal basal body. Processes of a glial cell, identifiable by a darker cytoplasm, extend into the DIS (arrowhead). Asterisk marks a dense body (bar 2 μm). (H) Cross section through the distal basal body. The nucleus (nu) region of an enveloping cell (probably the thecogen cell) is visible (bar 1 μm).

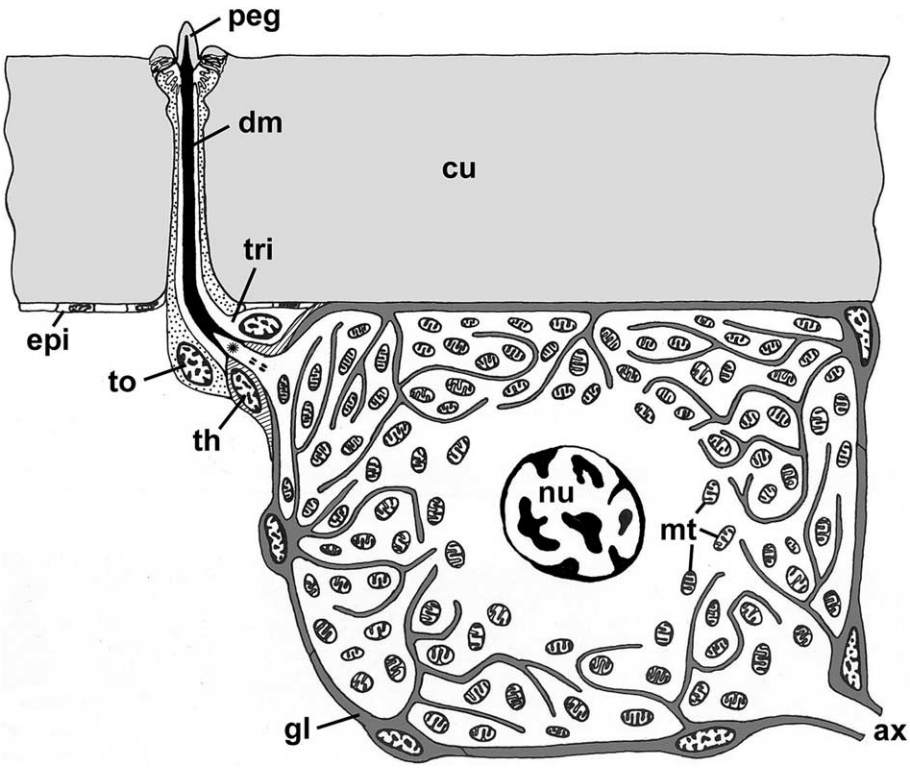

Fig. 6. Graphical schematic reconstruction of a sensillum of the sensory disc. The DIS is totally integrated into the apical region of the soma; two basal bodies indicate its distal ending. The short DOS is marked by an asterisk. Abbreviations: ax, axon; cu, cuticle; dm, electron dense material; epi, epidermis; gl, glial cell; mt, mitochondria; nu, nucleus; th, thecogen cell; to, tormogen cell; tri, trichogen cell.

(see below). Whether the DOS and the electron dense rod also play a role in the uptake of the thermal stimulus, or if they are obsolete, has to be investigated. However, it has to be pointed out that at the current stage of knowledge, other transduction mechanisms cannot be categorically ruled out.

4.2. The construction of the prothoracic organ provides insight into its possible function

The main component of the prothoracic organ is the tiny disc which contains the sensory equipment. The disc is located above an air-filled cavity and the narrow cleft around the disc allows exchange of air between the cavity and the outside. An inflexible cuticular stalk connects the disc to the prothoracic exoskeleton. Therefore, any active or passive movability of the disc seems impossible. However, vibrations of the disc cannot be ruled out. Provided that the sensilla have a thermosensory function, the organ can be regarded as a small bolometer (i. e. a microbolometer) with low thermal mass which is thermally insulated from the beetle's body. As a result, the disc will heat up quickly when IR radiation is absorbed. Correspondingly, after the termination of the IR stimulus, the disc will cool down very fast. The increase in temperature, which depends on the respective radiation intensity, can be measured by the thermoreceptors (Bleichmar and De Robertis, 1962).

In principle, the construction of the prothoracic organ is very reminiscent to modern micromachined silicon microbolometers. Up to 80,000 of those sensors can be used to build a microbolometer array suitable for thermal imaging (i.e. IR thermography). A single minute microbolometer consists of a platelet of silicon nitride suspended a few μm above the underlying silicon substrate. The platelet is typically 50 μm square by less than 1 μm thick. Long thin supporting legs and a vacuum environment thermally isolates the platelet from the substrate, which serves as a heat-sink. Additionally, the legs support conductive films for electrical connection. Thermal radiation focussed onto the platelet will heat it up. The temperature of the platelet and therefore the intensity of the radiation can be measured by the change in resistance of an electrical resistor (most commonly vanadium dioxide, VO_2) deposited on the platelet (for detailed review see (Rogalski, 2002, 2003)).

Thermal IR detectors of the bolometer type are well known in IR sensitive boid and crotalid snakes (Bullock and Fox, 1957; von Düring, 1974; Molenaar, 1992). Analogous to the sensory disc in *Acanthocnemus*, the actual IR receptor in crotalid snakes consists of a thin membrane. Like the sensory disc in *Acanthocnemus*, the membrane is only 15 μm thick and, therefore, has an extremely low heat capacity. To achieve a good thermal insulation, it is suspended within a cavity inside the snakes head. The air-filled inner cavity underneath the membrane can be actively ventilated by a small duct directed to the outside (Lynn,

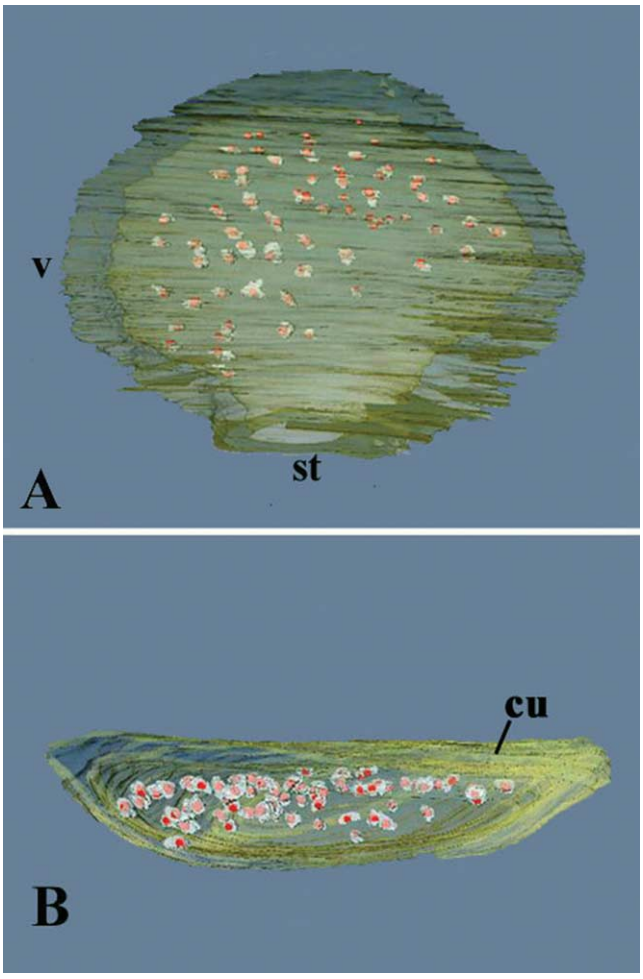

Fig. 7. Three-dimensional reconstruction of a sensory disc. (A) View onto the outer surface. The position of the somata of sensory cells is indicated by their nuclei (white) and nucleoli (red). The stalk (st) is situated below, ventral (v) is on the left. (B) View into a sensory disc from posterior. The outer surface is located above (cu, cuticle); the cuticle of the posterior half is omitted. Positions of nuclei and nucleoli of all sensory cells are indicated as in (A).

1931). The membrane consists of a central layer sandwiched between an outer and inner epithelial layer. The central layer contains enormous amounts of highly thermosensitive trigeminal nerve fibres (Bullock and Cowles, 1952; Bullock and Diecke, 1956; Bullock and Fox, 1957; Bleichmar and De Robertis, 1962; Goris and Nomoto, 1967; Hartline, 1974; De Cock Buning et al., 1981; Amemiya et al., 1996). The terminal nerves form so-called terminal nerve masses (TNMs, (Terashima et al., 1970; Amemiya et al., 1996)). The TNMs are the broadened unmyelinated endings of the terminal nerve fibres, which are arranged in a single layer directly beneath the outer IR absorbing epithelium. As a special feature, the TNMs contain large numbers of mitochondria.

If it should turn out that the sensory cells inside the sensory disc of Acanthocnemus nigricans work as warm receptors, another interesting structural and functional analogy between IR receptors in snakes and insects would be found.

Acknowledgements

Mike Cantelo and Brian Inglis from CALM*fire*, Perth, WA, enabled us to visit bush fires for the collection of beetles and supported us with all necessary equipment. Karl-Heinz Apel and Tobias Mainz helped us to collect the beetles. The Department of Environment and Heritage (Canberra) and the Wildlife Branch of CALM (Perth) issued the collecting and export permits. We are grateful to the NEES Institute for Biodiversity of Plants at the University of Bonn for the use of the SEMs. Mareike Rüdinger took some of the SEM pictures. The research was supported by grants from AFOSR and DARPA to H.S.

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