Navigation organs of the oriental hornet
Rosenzweig, Eyal

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CHAPTER 3

Hornets Yellow Cuticle Microstructure: A Photovoltaic System

Abstract

This paper describes cuticular structures on the abdomen of the Oriental hornet (Vespa orientalis, Vespinae, Hymenoptera) in the region of the yellow stripes. A cross section in this region reveals the cuticle to resemble a notebook with more than 30 pages, the topmost pages (analogous to layers) being the thicker (up to 5 µm or more in thickness), while the ones underneath are gradually thinner.

The exterior of the cuticle displays pores which are dispersed at distances of 10-50 µm apart. These pores are actually cuticular depressions which frequently possess eaves on their cephalic side whose internal diameter is 13 µm near the surface but further down, in the region of the yellow pigment and the hypocuticle, this internal diameter broadens to about 20-30 µm. These pores thus extend from the exocuticle down to the hypocuticle. In the spaces between the pores in the endocuticular region there are sinuses. Within these sinuses granules of yellow pigment are located. As for the pores, each of them represents the external outlet of a canal that is perpendicular to the cuticle. The canal walls are composed of the same layers making up the cuticle. Structurally, the canal encasing the pore resembles an upside down arrow. This arrow extends to about 35-40 µm in depth and is narrow and hollow in its upper part, the shaft, for about 13 µm, broadens into the shape of an onion in its lower head part (some 20-30 µm in diameter). Down to its tip it becomes slightly sharpened to close at the hypocuticle by forming a concentric, dome shape structure that terminates in a nippleshaped protuberance.

Permeating through all layers of the cuticle are hemolymph, nerve fibers and tracheae. The parallel lamellae associated in the cuticle give the impression of an electrical capacitor.

The present article discusses the structure of the cuticle as a photovoltaic system in which the endocuticle lamellar layer and yellow pigment serves as a solar cell linked to an electrical capacitor. The manner whereby light energy and heat are collected, converted into electric energy, accumulated, transformed and used by the hornet is discussed. We assume that this source of energy is used for their thermoregulation by thermoelectric circuits.

Introduction

Previously we have described various electric properties in the cuticle of social wasps and hornets, in particular those of the Oriental hornet (Vespa orientalis, Vespinae, Hymenoptera), which suggested that the cuticle of hornets, the silk produced by the pupating larvae, and the comb walls glued by hornet saliva behave like an organic semiconductor with traps. Supporting this idea are the following observations: photoelectric properties (Ishay and Croitoru, 1978); electrical resistance in various species of Vespinae and

Polistinae (Croitom et al., 1978); the effect of hornet venom on the photoelectric properties (Ishay et al., 1979); photoelectric properties: a mathematical model (Ishay et al., 1980); thermoelectric [Seebeck] properties (Shimony and Ishay, 1981a); pigment granules in the tegumental yellow stripe (Shimony and Ishay, 1984); temperature dependence of the electrical resistivity of the hornet cuticle (Ishay and Shimony, 1982; Ishay et al., 1982; Ishay et al., 1983; Ishay et al., 1990); electrical capacitance (Shimony and Ishay, 1984); the influence of xanthines (Rosenzweig et al., 1985; Ben-Shalom et al., 1988) and thermoelectric current of the hornet cuticle and the hornet comb (Ishay and Litinetzky, 1996; Ishay and Shmuelson, 1996); and luminescence properties of the cuticle (Ishay et al., 1987) and of the silk cocoon (Ben-Shalom, Shimony and Ishay, 1990). All the above were properties that were measurable under laboratory conditions on cocoon silk, comb walls and on the cuticle of live (anesthetized) or dead hornets, that usually were killed by freezing shortly before the measurement.

The measurements were performed on the stripes of the abdominal cuticle of the hornets on the dorsal side or on the frons or clypeus plates. The stripes on the 4th and 5th abdominal segments partly contain pigment cells situated above the basement membrane and filled with yellow pigment granules (Becker, 1937; Ziegler and Harmsen, 1969). In social hornets (Vespinae) there are stripes with a colored pigment differing from the background coloration of the rest of the cuticle which normally is brown or in shades between red and black (Fig. 1). The colored stripes contain pigment granules underneath the translucent cuticle where light sensila were detected (Ishay et al., 1986). These granules are cylindrical in shape and in V. orientalis they comprise of what seems to be spores of a symbiotic fungus (Ishay and Shmuelson, 1994). In the hornet the pigment is of a prominent yellow color but in other hornets or wasps the pigment can appear in various shades of green, beige, black (Vecht, 1957, 1959; Ishay et al., 1967; Kemper and Döhring, 1967; Wilson, 1971; Matsuura and Sakagami, 1973; Spradbery, 1973; Edwards, 1980; Akre et al., 1981; Brian, 1983; Matsuura and Yamane, 1990).

After numerous cuticular properties were characterized, it was found that active or narcotized, live as well as dead hornets, produce voltages of several hundred mV, a current of up to several mA, and the appropriate power. The electric resistance of the hornet cuticle suggests the properties of semiconductors where the electric carriers are electrons or holes (Hannay, 1959; Cope, 1965; Kittel, 1968; Watson, 1969; Gutmann and Lyons, 1981; Gutman et al., 1983; Ishay et al., 1991), apart from their being endowed with a very large electric capacitance relative to their mass. Of hornet components examined, the cuticle (and also the silk produced by the pupating larvae) has a very complex chemical and structural constituent which hinders observations during its formation (Rudall, 1963; Locke, 1966; Anderson, 1974, 1979, 1985; Neville, 1975; Filshie, 1982; Schaeffer et al., 1987).

The studies mentioned and numerous others deal with the biochemistry of the insect cuticle or with its formation. In the present study we concentrated on the structure of regions in the abdominal cuticle on which we have previously performed electric measurements and which we intend to provide a better understanding for the observed structures and the functional role they may possibly fulfill. We already know that the hornet cuticle and pupal silk pick up solar energy and convert it into other forms, as into electric energy which is probably used, interalia, for cooling or warming the nest or for other daily needs (Ishay and Barenhoiz-Paniry, 1995).
Materials and Methods

Transverse stripes of cuticle from the abdominal segments 4 and 5 at their dorsal (yellow) side were taken from anesthetized or dead hornets, see Figure 1. Strips detached from their cuticle were fixed in a 0.1M cacodylate buffered glutaraldehyde solution (pH 7.4; 2 hrs) for light microscopical (LM) observation (Diavar, Reichert, Austria). For conventional scanning electron microscopical (SEM) observation, strips were postfixed in a 2% osmium tetroxide solution in the same buffer for 4 hrs, dehydrated in ethanol, critical point dried in liquid CO$_2$ and sputtercoated with 10-15 nm Au/Pd. Samples were investigated in a JEOL SEM (type 35) or a Cambridge stereoscan (type 1805) operated at 15-25 kV.

For field emission scanned electron microscopy (FE-SEM), glutaraldehyde prefixed strips were immersed in a mixture of arginine HCl, glycine, sucrose and sodium glutamate (2% each) for 16 hrs at RT, followed by rinsing in distilled water (3x). Subsequently strips were immersed in a mixture of tannic acid and guanidineHCL (2% each) for 8 hrs at RT, rinsed in distilled water 3x) and immersed for 8 hrs at RT in a 2% Os$_4$ solution in distilled water, as described previously (Kalicharan et al., 1992; Jongebloed et al., 1996). Finally strips were dehydrated in ethanol and critical point dried in liquid CO$_2$ and sputtercoated with only 23 nm Au/Pd. Samples were investigated in a JEOL FE-SEM, type 6301F operated at 2-3 kV.

Results

In Figure I is shown a macroscopic image of the abdominal segments 4 and 5 at their dorsal side in two hornets. Figure 2 presents a crosssection of abdominal segment no. 4 from its dorsal aspect in SEM. The figure shows a general view of the cuticle, with the epicuticle on top and beneath it the exocuticle which is constructed as a trabecular layer and the endocuticle which is a lamellar layer. Underneath the endocuticle are the sinuses compris

FIGURE 1. V. orientalis, showing their abdominal segments. Part of segments 4 and 5 are usually of a yellow color. The hornet on the left with the extruded stinger (a) has been damaged, probably during the collection from the field and consequently the two yellow abdominal segments display black areas of hemorrhage, whether on the left in segment 4 or on the right in segment 5. (x3)
ing the cavernous layer (c) and at the bottom are the hypocuticle (h) and the basement membrane (b). Additionally, one can see that in the bottom part, within the cavity of the sinuses, there are ‘pillarettes’, or actually extensions of the pore canals (pc) which pass from the epicuticle to the hypocuticle. (the yellow pigment granules were removed during the preparation for SEM viewing.)

Figure 3 presents a section through the cuticle of abdominal segment 4 (displaying a strip of yellow pigment). In the epicuticle several depressions can be seen, which are the pores (p). At the base of the lamellar endocuticle one can see the clump of yellow granules deriving from the pigment cells that occupy the spaces within the cavernous layer. In Figure 4 we see a cross section through the exocuticle and more interiorly, also through the endocuticle. The two uppermost layers in the section are the thickest. The endocuticle (the lamellar layer) is composed of 30 or more lamellae which become attenuated (thinner), the deeper we proceed (i.e., the closer to the abdominal cavity). Thus, the upper layers are about 5 µm in thickness whereas the lower layers are only about 1/3 µm thick. Generally, the lamellae are arranged in parallel shapes with a clear demarcation between two adjacent ones, however, at intervals of several µm one discerns also trabeculae which interlink two or more lamellae. Clear separation between the various layers can be seen in Figures 11 through 18. We need to point out that ‘our’ hornets were collected from a natural nest in the field by a method described earlier (Ishay, 1964) and among them were specimens inadvertently damaged, their cuticle showing a black spot indicative of oxidized hemolymph. In cases where the segment is damaged, whether the yellow distal part selectively or both the yellow and the brown
FIGURE 3. Cross section (fracture) through yellow cuticle. On top, in the epicuticle, one sees a number of apertures, pores (p). On closer inspection one can detect the layers of the endocuticle, which are laminar and separately beneath them there is a mass of yellow pigment granules (yg) located within the sinus of the cavernous layer. Underneath all this, one can vaguely make out the bottom part of the cuticle. c = cuticular layers. Bar = 10 µm.

FIGURE 4. The previous figure, tilted upside down (180°) and at twice magnification. Now one sees the exocuticle with the trabeculae (tb) arranged longitudinally. This is the trabecular layer. This layer and the one immediately below it are each about 5 µm in thickness. The further one proceeds downwards (i.e., the closer to the inner side of the gaster) the thinner become the layers of the endocuticle, which we arranged in laminar fashion. Bar = 5 µm.
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 FIGURE 5. Figure showing apertures of the pores (p) from the top. Diameter of the pore aperture is about 1-2 µm and they are dispersed at intervals of 10-50 µm or more. The pore is actually located within a depression and usually possesses a cave in the cephalic direction (which here is to the right). Between the rows of pores are interspersed setae (s). Bar = 10 µm.

parts (see Figure 1), then there is blackening of the entire segment, which tests to the presence of hemolymph that has come in contact with oxygen (as occurs during any external injury).

In Figure 5, the exterior of the cuticle, that is, the epicuticle is seen. At intervals of 10-20 (or sometimes 10-100 or more) µm one discerns pores (p) which are shielded on the cephalic side by eaves (i.e., light can be transmitted inside the pore from the upper or posterior side only). Between each two rows of pores, we can see setae(s). The top layer of the epicuticle is arranged in the form of shingles (or scales). Figure 6 presents a section through the epi and exocuticle. The epicuticle (ep) is built as a continuous plate of about 1 µm in thickness; it comprises the topmost layer of the cuticle which comes in direct contact with the environment. Underneath this plate there is the exocuticle, which is comprised of trabeculae that are arranged perpendicularly to the upper plate. The trabecular layer is about 5 µm thick.

The outlet of the pore (p) is located in this region. At the top, one can see a part of the canal that surrounds the pore, the so-called pore canal (pc) and more in depth the hollow area of the pore which here is less than 1 µm in diameter.

In the lower portion of the cavernous layer the pores broaden out into a sort of pedicle as shown in Figure 7. After removal of the hypocuticle from the bottom of the pore Figure 8, the various layers (c) comprising the pore canal are exposed. Here, too, one discerns the sealed terminus of the pore canal (pc) with the gap remaining to admit light (1). The maximal width in this region is about 20 nm. At this depth one can discern strands which interconnect the tips (lower side) of the various pores. These interlinking strands apparently are tracheae (tr), Figure 9. Closer to the exterior of the inner surface of the cuticle (i.e., to the abdominal cavity) one can see, under proper illumination, a reflection of the light shining through the cuticle on the other side. Between the lightadmitting gaps around the pores there are delicate fibers, apparently the fibers of neurons and bipolar cells (bp),
FIGURE 6. Section (fracture) through the executicle (or trabecular layer). Between the various rifts that pass here from below, first is seen a part of the pore (p). Then one can see the pore canal (pc), which is rounded and extends to a depth of 4.5 µm. ep = epicuticle. Bar = 1 µm.

FIGURE 7. The pore canal (pc) in the region of the cavernous layer. From the top one sees the bottom layers of the endocuticle. Note that in the lower part of the endocuticle the canal commences at top at a diameter of 1.5-2.0 µm but becomes much wider further down. This is the region in which the photoreceptor cells are encountered. Bar = 1 µm.
FIGURE 8. Cross section (fracture) through the lower part of the pore canal (pc), in the region where the central concentric layers (c) are already closed but in a brief eccentric region (off-center, to the right) there is still an opening (L). Around the pore canal there are granules of yellow pigment (yg). Bar = 1 µm.

FIGURE 9. After scraping off the layers of the hypocuticle at a slightly lower level than that shown Figure 8, we can see the still not closed layers of the pore canal, probably the tracheae (tr). Bar = 10 µm.
FIGURE 10. An image of the reflection of light passing through the pore canals on the bottom side the cuticle. The picture was taken through a light microscope in the region above the basement membrane. The picture shows clear circles (see arrow) which are the emergent light beams. Around them there are dark circles (see arrows) representing a ring of tracheae and nerve fibers as well as nerve fibers that reflect through the basement membrane and include also bipolar (bp) cells. Bar =10 µm

FIGURE 11. After removing a number of layers of the hypocuticle, one sees the boutons of the scaled-off photoreceptor (arrow), pc-pore canal; h-hypocuticle; tf-tracheal tube. Bar = 100 µm.
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Figure 10. Thus, these neural-like fibers are located between the basal membrane and the hypocuticle, whereas the tracheae are situated here, also more deeply, between the hypocuticle and the cavernous layer.

A broader view of the basis of the cuticle in these regions is given in Figures 11-16. In Figure 11, where the basement membrane and several layers of the hypocuticle had been removed, we can see thick fibers that penetrate between the layers, the tracheal tubes (tt). We can also see the termini (sealed) of the pore canals (pc) interspersed between the thin layers of the hypocuticle. In Figure 12, we see at higher magnification at ‘a’, very thin layers of removed hypocuticle (h) and underneath them rounded, papilliform bodies, which are the termini of the pore canals (pc), and around a ‘sea’ of yellow granules (yg). We can also observe traces of tracheae (tt).

In Figure 13 details of a completely sealed single pore canal (pc) can be seen. This sealing is only gradually can be judged from the thin concentric layers at the distal end of the pore canal (a) and above them the internal layers (b) which are higher up and responsible for the sealing, with a single strand (s). The lower, concentric layers gradually merge into the plates of the hypocuticle (h). The image shows five of these leaflike layers around the pore canal. One can also see the yellow pigment granules (yg). When we remove the ‘lid’ of the pore canal (pc) in its eccentric region we notice, that it is surrounded by granules of yellow pigment (yg) and that the various layers composing the pore canal are rather sparse and gapped, leaving room for the passage of light (see Figures 8, 9, 10) between the hub of the pore canal and layer 1 and between layer 1 and layer 2 (from the center). The cuticular layers here are rather thin and the exterior most conjoin to form horizontal plates where previously they were arranged vertically. Figure 15 presents a detail of the cuticular plates, taken from the eccentric region which trans

FIGURE 12. One can discern the closure boutons (arrow), with one of them (a) surrounded by granules of yellow pigment (yg). This “bouton” remained intact (a); besides a broad part representing the closure area it possesses also a short and narrow papilliform extrusion (arrow) of avery small diameter. “is latter is the contact point through which apparently drains the electric energy stored in the capacitor in the upper cuticle. For greater detail consult text. pc-pore canal, tt-tracheal tube, h-hypocuticle. Bar = 100 µm.
FIGURE 13. At higher magnification than at Figure 12 we see a “bouton” whose central part is sealed. Here one finds the thick layers of the hub of the pore canal, whereas the thinner layers (a) stemming from the interior of the cuticle (the lamellar layer) recurve to “open” anew after the closure so as to form the hypocuticle (h). Around the pore canal (pc) and below the hypocuticle, one sees an abundance of yellow granules (yg). b-internal layers of the pore canal. Bar = 10 μm.

FIGURE 14. A view from a plane lower than that of a pore canal (pc) closure. One notes that the cuticle layers (a, b and c) are concentric and gapped, with yellow granules (yg) around them. Bar = 10 μm.
FIGURE 15. A view of the thinner layers around the pore canal (pc) prior to the closure. In each cuticular layer a, b or c, whose thickness is less than 1/3 µm, there are two smooth walls and an apparently porous center. At various intervals (of 1 mm or more), we see apertures (tr) that traverse the cuticle and around them yellow granules (yg). lo-longitudinal pore, s-free space between two lamellae. Bar = 1 µm.

FIGURE 16. Cross section of the pore canal wall in the closure region. The thickness of the layers here is about 1/3 µm, and each layer displays two walls and a content-filled space in between. In some layers the inner part shows apertures (*) which probably serve for the passage of hemolymph. Bar = 1 µm
FIGURE 17. The region of a pore canal closure (pc) is shown and surrounded by thinner layers, which at the closure point ‘reopen’ to create the thin plates of the hypocuticle. Here, too, can be seen delicate apertures (tr) which traverse the width of the layers. All around one sees yellow granules (yg). Bar = 1 µm.

FIGURE 18. In some layers of the pore canal one gets a clear impression of the apertures which traverse the length of the cuticle (arrow). Bar = 1 µm.
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FIGURE 19. Preparation of a cuticle with yellow pigment from which the lower portion the hypocuticle had been removed. There is a clump of yellow granules (yg) at the basal surface of which one sees a crater which once housed the pore canals of. The crater is broad at this basal site and must have contained the photoreceptor cells. The entire structure is supported by cords (c) (1, 2, 3). Bar = 10 µm

mits light. We can see lacunae of several sizes in the center of the pore canal (pc) and also between the more distal plates (a, b, c). In each cuticular plate one discerns a central, porous, core which is flanked by two walls in sandwich fashion (s). Each plate shows both transverse (tr) and longitudinal (lo) hole which apparently are conduits for hemolymph. In Figure 16, we see at higher magnification a layer of plates in the dense region from which it is obvious that in cross section each cuticular plate is comprised of two very thin walls. Between the walls the porous plate, takes up most of the space. The thickness of each plate here is about 1/3 µm and its content is porous with numerous apertures, which seem to be necessary for the transport of hemolymph. An enlargement of what was shown in Figure 13 is given in Figure 17. At the upper margin and left side of the figure granules of yellow pigment (yg) can be seen, while at the center we can see in more detail the closure of the pore canal. At the margins the concentric plates of the canal are shown, which abruptly change their orientation from vertical to horizontal. Note, that only the thin plates undergo this change in orientation, conjoining to form the hypocuticle. Here, too, one observes apertures traversing the plates (arrows). Figure 18 provides a higher magnification of Figure 16. On the top right we see yellow pigment granules and to the left of these are visible part of the concentric plates which surround the pore. In some of these plates one can distinctly observe longitudinal apertures (1a). We also note that the pore canal separates between the mass of yellow granules (yg) and the cavity of the pore.

If we photograph the terminus of the pore after its closure point, that is, underneath the hypocuticle, we can observe that this pore canal termination becomes tapered toward the tip (as observed in Figure 19). The entire structure (i.e., the pore) is separated from the environment by a ring (b), yet is linked to the environment by delicate fibers (1, 2, 3). The tip of the pore canal (d) appears to have a diameter of 2-3 µm, which is about the width of the pore canal at its commencement in the exo and endocuticle. Viewed from below, the entire structure is seen to be supported by various cords (c) arising from the inner borders.
of the pore canal. When we evacuate (by vacuum) the content of the pore canal, we can see its encasing walls (Figure 20).

Figure 21 is a drawing of what the LM-SEM images have revealed. The pore canal, inner structure of the tip of the pore canal, the pigment granules and the various leaflike layers encasing the pore canal are shown.

**Discussion**

In the present paper, we have provided a detailed description of the structure of the hornet cuticle in the region of the yellow stripes, that are known, as a semiconductorlike material (Ishay and Croitoru, 1978). The upper portion of the epicuticle is flat and continuous, barring the region of the pores. As for the exocuticle, it has vertical structures, namely, trabeculae, which provide mechanical support. There are 30 or more parallel layers rolled around the abdomen, whose general shape from below resembles a cone. These layers which are transparent or translucent extend down to the region of the yellow pigment granules. The upper part of the abdomen is convex, producing a lenticular shape that focuses the lighted light on the inner, yellow pigment granules, i.e., similar to a ‘Fresnel lens’ (Maycock and Stirewalt, 1981). The cuticle is photovoltaic (Ishay et al., 1992), the voltage accumulates in the lower parallel lamellae whence it is transmitted to the walls of the pore apparatus. The multilayer walls are built as biological mirrors, i.e., they reflect the incident light due to their optical thickness of about onequarter of the wavelength of light (Land, 1972, 1981). This mechanism protects the content, i.e., the photoreceptor from overheating, and so also the whole insect body.

Regarding the question as to which light wavelengths are reflected by the cuticle, we need to note that the various cuticular layers range between 5 µm and 0.3 µm and possibly even down to 0.2 µm, in thickness (see Figures 4, 16, 17, 18). As is known, infrared light is emitted by radiation from a heated surface. The region from 0.75 µm to 1.2 µm is called the photographic infrared, because photographic emulsions still respond to radiation of such wavelengths. Arbitrarily, it is customary to divide infrared light beyond the photographic infrared into 3 ranges, namely, near infrared, at a wavelength range of 1.2-5.2 µm and beyond that, the far infrared, which ranges between 8-14 µm (between 5-28 µm the atmosphere is entirely opaque). On the assumption that thickness of the cuticular layers represents a quarter of the wavelength which it reflects, then the layers closest to (i.e., the innermost layers) reflect the near infrared (the photographic infrared) because 0.2 µm x 4 = 0.8 µm or 0.3 µm x 4 = 1.2 µm, but the outermost layers which are 5 µm thick are accordingly apt to reflect the waves of the far infrared (5 µm x 4 = 20 µm). It follows that the
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The hornet cuticle utilizes at least part of the visible spectrum as (electric) energy source, whereas the infrared waves which are a heat source are reflected, which enables the hornets to fly undisturbed in the daytime heat. Detection of infrared radiation, whether of terrestrial or remote stellar origin, is achieved in human technology either by relying on the energy state in semiconductors where a photon lifts an electron to a conductive state and the detection here is of the photon induced change of the conductivity of the detector type, or by relying on a semiconductor which contains a p-n junction, where an electronhole pair is formed in the vicinity of the junction (Kruse et al., 1963). The strong field on both sides of the junction separates between the two carriers so that a photovoltage is created. Such detectors are instigated on the photovoltaic effect (Hudson and Hudson, 1975) in the cuticle of hornets which is itself photovoltaic (Ishay et al., 1992) and also behaves as a semiconductor (Ishay et al., 1991). Thus the hornet cuticle possesses, theoretically, the ability to detect infrared radiation, whether it is for the purposes of gauging the temperature, or for recognizing nest mates in the darkness of the nest, or for the purposes of communication and navigation.

The pore apparatus includes the pore canal, whose hollow portion serves as a light guide for the photoreceptor (Goldstein and Ishay, 1996) while its walls conduct the electric energy formed in the illuminated portion to the bottom, darkened part of the photoreceptor (the bulbous head of the arrow). The latter attenuates into nippleshape in the region of the darkened hypocuticle. Here the electrical energy is transformed either into a current transmitted to the hypocuticle plates or into a combined voltage which is transmitted, interalia, to the nerves that support the pore. In the dark the electric resistance, which in light was at a level of giga ohms (GΩ) drops down to a level of kilo ohms (KΩ). a decrease

FIGURE 20. If one applies suction by vacuum to the region housing the photoreceptor cell, it is possible that the entire cell could be sucked out, leaving behind only the framework of cuticular layers making up the pore canal, in which the photoreceptor was originally enclosed. 1 = site of the photoreceptor; 2 = nerves and/or tracheae
Bar = 10 µm.
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of about 56 orders of magnitude (Ishay and Litinetsky, 1996). This difference prevents electrical current from flowing back into the photovoltaic cells, i.e., in this respect behaving like a diode (BenShalom and Ishay, 1989). The dielectric fluid permeating all the internal spaces is the hornet’s hemolymph which is transparent and of a yellow coloration (like that of the yellow granules). The hemolymph of *V. orientalis* adults has a pH lower than 7.0, i.e., is acidic; the osmolality range is between 321-593 mOsmole/kg and the specific gravity is 1.022-1.028 (Joshua et al., 1973). However, in cases of damage to the cuticle, the hemolymph darkens oxidizes, thereby preventing the transmission of light (Whitcomb et al., 1974).

As described, the cuticle of the Oriental hornet is constructed in the manner of a photovoltaic cell incorporating or linked to an electric capacitor. It seems to us, that each hornet (and in this respect probably each bee or ant), as it departs the nest under insolation (i.e., sunlight irradiation), charges its capacitor (in fact, its numerous capacitors) and before attaining the maximal (breakout) voltage the insect must fly back to its nest and discharge some (or most) of the energy it has accumulated. This discharge includes also: O₂ released from the traps (see further) and, of course, the
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prey collected during the flight. The discharge is probably achieved through contact of its feet with the silk caps of the pupae which serve as a capacitor for the entire nest (Ishay and Barenholz-Paniry, 1995), or by probing adult homers, at the entry or inside the nest, with their antennae. As for the charge, this apparently is dependent on various factors such as humidity, temperature, light irradiation, age of the hornet and the like (Shimony and Ishay, 1984), and consequently the hornets outside the nest apparently must return to the nest at time intervals, correlated to the solar UV and blue radiation dose, which is different at different hours of the day even at the same location. It seems to us (Ishay et al., 1967), that during its lifespan each hornet is undergoing at least 3000-4000 cycles of charging and discharging and in this respect it resembles a good battery.

The stripes of yellow cuticle are built and function as a photovoltaic system (Ishay et al., 1992). The upper portion contains parallel transparent plates not unlike the photovoltaic plates in known solar cells (Maycock and Stirewalt, 1981), except that in hornets it is composed of 30 or more photovoltaic plates, which markedly enhances the efficiency of the system. The plates are thicker in the upper part of the cuticle, therefore more electric carriers accumulate in the thinner, lower plates. In this connection, thickness of the plates acts much the same as the gap between two consecutive plates, that means, the greater the gap or distance the smaller the capacitance. The electric charges in this case probably electrons settle on both sides of each plate because of the energy of photons which has boosted them from the valence band to the conduction band of the yellow granules layer (= the anode) and in light they get caught in some type of traps (perhaps O$_2^-$) that are formed in the cuticular plates (= the cathode). For further details on traps consult Gutmann and Lyons (1981) or Gutmann et al. (1983). The relative quantum efficiency of the light-induced voltage as a function of wavelength is highest at or around UV and blue light: the cuticle is luminescent and when irradiated by UV light at 290 nm the emission spectrum is maximal at 345, 450 and 510 nm and the Δ energy between the irradiated UV and emitted light is absorbed and converted to other forms of energy by the cuticle (Croitoru et al., 1978; Ishay et al., 1987; Ishay et al., 1992). At high noon, when the relative amount of UV light in the radiation impinging upon the earth is maximal, hornet activity is also at a maximum (Ishay and Lior, 1990). Additionally, we found that the short wavelengths (UV and blue) are the ones that exert the greatest awakening effect on hornets that had been anesthetized by ether (Ishay et al., 1994; Ishay and Levto, 1994; Kristianpoller et al., 1995; Goldstein et al., 1996).

In the sixties it was noted by one of us (J.S. Ishay unpublished observations) in a honeybee artificial flight room in the TelAviv University and subsequently confirmed in the flightroom of the Institute für Bienenkunde, Oberursel/Taunus, Frankfurt, Germany, that hornets are attracted to UV light and show a high tendency to fly or walk toward a UV light source even at daytime. Several electric UV grid devices are now commercially available for insect control (see Edwards, 1980). UV lamps are strongly attractive to wasps as well. The sunlight is radiated perpendicular to the cuticle at least in the upper part of the body. It traverses all the layers of the upper parts of the cuticle; in the region of the yellow stripes the cuticle itself is translucent and therefore the passing light is absorbed in the layer of the yellow granules. The thickness of this layer is about 5 µm and there the photons ‘push’ out electrons and set them free. The excess electrons move up and accumulate on the plates of the cuticle’s horizontal layers that become n-layers, because electrons have a negative charge. In the yellow pigment layer therefore, holes are created, it becoming the p-layer. As long as radiation falls upon the junction, electronhole pairs will be formed and
The length of each yellow granule is about 0.5 µm (Ishay and Shmuelson, 1994), i.e., of optimum dimensions for absorbing photons in amorphous silicon. Beyond the layer of yellow crystals light does not pass, so that the hypocuticle is in darkness (apart from the pores which do transmit light). Thus, charging of the cuticle is effected, with - at the exterior and + inside. By the mode of hookup described for the various measurements (Ben Shalom and Ishay, 1989), in more than 85% of the measured specimens, a positive voltage on the inner (i.e. lower) surface of the cuticle compared to its outer surface was found. The range of the obtained voltage was up to 0.4 V at open contacts, i.e., close to that of a usual photovoltaic cell and a short current range of 0.1-5 µA. The electric capacitance of the cuticle at 1000 Hz was about 0.6 nF as opposed to 3.0 nF at 100 Hz. This inverse relationship between frequency and the electric capacitance might point to the presence of polar substances possibly chargeable proteins or ion pumps. The findings suggest that the yellow stripes in the cuticle act as semiconductors of p-type while the brown stripes act like those of n-type (Shimony Benshalom and Ishay, 1984).

The current was also measured (in dead specimens) in correlation with time in order to compute the electric charge in the hornet (Ishay et al., 1990). It was found that even after 24 hours of maximal current drain, the hornet is still not absolutely discharged. The drained current yielded an exponential curve that enabled computation of the electric capacitance app. 3nF, the chargeapp. 2.5 µCoulomb (µC) and the energyapp. 4.6 µjoule (µj). These measurements were performed at room temperature (i.e., 20-24°C) and at low relative humidity. Same measurements performed at the proper optimal conditions yielded results that were higher by 2-4 orders of magnitude (Ishay and Litinetsky, 1996). There is yet no information about these parameters in living specimens measured in optimal conditions. This ‘battery’ which charges itself with light energy becomes charged, of course, only when the hornets fly in (or are exposed to) the sun, and the closer the flights to noon time the faster the charging process, which means that the flying time is accordingly curtailed (because the hornets must return to the nest to get rid of the excess voltage before breakdown occurs in the ‘battery’). As known, the cuticle behaves as an intrinsic semiconductor and therefore it may be charged also in darkness at the optimal temperature where the activating energy is (Ea) = 0.536-1.859 eV.

In the hornet yellow cuticle there are in fact two systems of charging, namely, that of the upper cuticle where the resultant electric charge leaves through the layers of the pore canal to reach the hypocuticle, and that of the yellow pigment granules which ‘encounters’ the cuticular layers in the dark, lower region of the pore canal and conjoins with them to form a p-n junction. Another p-n junction is at every contact of yellowbrown stripe of the cuticle. It is tempting to locate the main junction at the ‘contact point’, the nipples on the boutons. The current or voltage which flows from this ‘solar battery’ can serve, while discharging, various roles, not all of which are presently known to us. Yet it stands to reason that electric energy is used via a Seebeck effect or other thermoelectric effects like Peltier and Thompson (already reported in hornets) (see Shimony and Ishay, 1981a).
ferent temperatures. Peltier discovered, in 1834, that when an electric current is passed through a junction between two electric conductors, heat is either absorbed or is emitted at the junction, depending on the direction of the electric current flow. Thompson, in 1857, discovered a third thermoelectric effect related to the already mentioned two: the absorption or evolution of heat when an electric current flows in a uniform conductor along which there is a temperature gradient.

The created electric energy heats or cools the air passing through vespan tracheal tubes, which are abundant between the plates of the hypocuticle (See Figures 9-12). Indeed in the hornet *V. crabro*, one can actually see a tracheal fing encircling each photoreceptor in its lower part (Shimony and Ishay; 1981 b), possibly contributing to maintenance of an optimal temperature around each pore which contains an extraretinal photoreceptor (Goldstein and Ishay, 1966) and thereby also contributing to self thermoregulation of each hornet during its flight. Even when the hornet flies in the hot sun in the hottest regions of the globe and at high noon (the period of main activity). The only time that hornets are seen to imbibe water is when building their combs (Ishay, unpublished). Yet the same mechanism can be activated, when necessary, to warm the brood (primarily the pupae) by blowing warm air from the spiracles (= the tracheal outlets) upon them (Ishay and Rutmer, 1971).

In connection with this intriguing prospect, we note that yellow stripes occur on all the species of social hornets and wasps, and in many species of solitary wasps, not to mention numerous other nonsocial insects of various taxa. Apparently the number of yellow stripes in the cuticle of social or solitary insects is low in tropic and subtropic regions however, increases with increase in the geographic latitude or increment in the altitude. Furthermore, yellow stripes are more abundant in males than in females and on the dorsum of the insects than on their ventrum and occur particularly on the abdominal segments.

We assume that there, they serve the same purpose as conjectured above.
References

Hornets yellow cuticle microstructure

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Hornets yellow cuticle microstructure