

# CHAPTER 1

## Introduction to the micromorphology and function of the ocelli and surrounding structures in the Oriental Hornet

### *General introduction*

In the underlying study of the hornet *Vespa orientalis* (Hymenoptera, Vespinae), the cuticle, the head with its different organs and the abdominal yellow stripes play an important role.

An external view of the head of the hornet shows the compound eyes, positioned at the left and the right side of the head. Furthermore, three simple dorsal eyes or ocelli, two lateral and one median, are positioned in a triangle on the top of the head at some distance above the frons i.e. on the vortex. Two antennae are seen at both sides of the frons (Fig. 1.) At an internal view of the head, the three ocelli, surrounded by a large number of hair cell structures in the frons area can be seen. The hair cell structures are covering the internal surface of the cuticle of the hornet, in particular surrounding the pore canal openings, pores which contain a photoreceptor. Besides that a large amount of muscle tissue is present, within the head as shown in Fig. 2.

### *Objectives of this study*

The hornet is known to forage at a distance of several kilometers from the nest. For this purpose well developed orientation and navigation systems are needed. In the past some observations and behavioral experiments concerning the problems of orientation and navigation were performed. From these it was deduced that the orientation capacities towards gravity and light are temperature dependent. Therefore, we started our research by investigating the thermore-

gulation and the source of electric energy of the hornet, whereafter the specific organs of graviception were studied in more detail, in order to formulate our concept of orientation and navigation of the hornet and the role the ocelli.

*In chapter 1* an overview is given of the various concepts, macroscopic and ultra-microscopic structures dealt with in this study. *In chapter 2* and part of *chapter 3*, the thermal homeostasis is discussed; thermoregulation is achieved by the well known thermoelectric mechanism (Seebeck). *In chapter 3*, the source of electric energy is dealt with, which is a photovoltaic system. *In chapter 4*, we describe the micromorphology of the sensory cells of the Ishay organ, the main organ of graviception. *In chapter 5*, the micromorphology of the ocelli and its function as a main organ in dim light is discussed. *In chapter 6* we discuss the issues of orientation and navigation of the ocelli and the surrounding organs.

### *Appearance of Vespa orientalis*

The Oriental hornet *Vespa orientalis* (von Linné, 1771) is a social insect which founds an annual (or semi-seasonal) colony during the spring. These colonies usually prevail during the warm season only and are all comprised most of the time, of females only, as well as the progeny of one fertile female, namely, the queen. Only during autumn, just before termination of the life cycle, do males make their appearance.

The complete life cycle involves the following

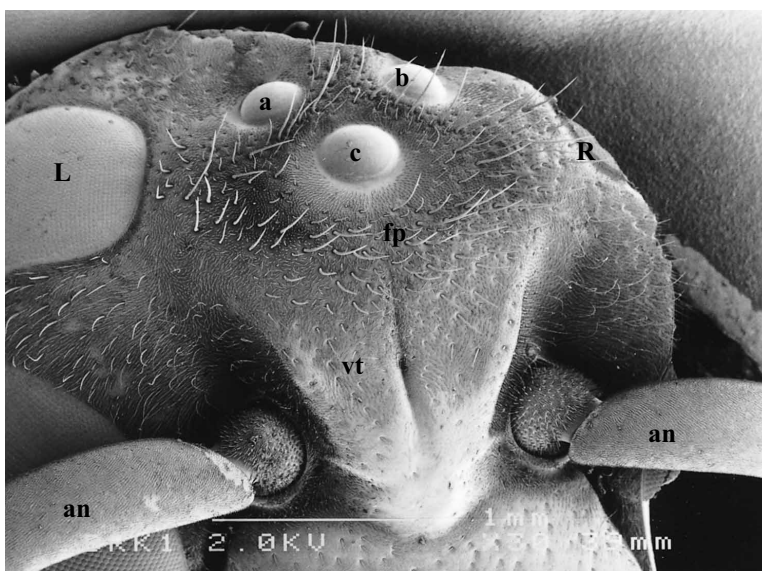


Fig 1

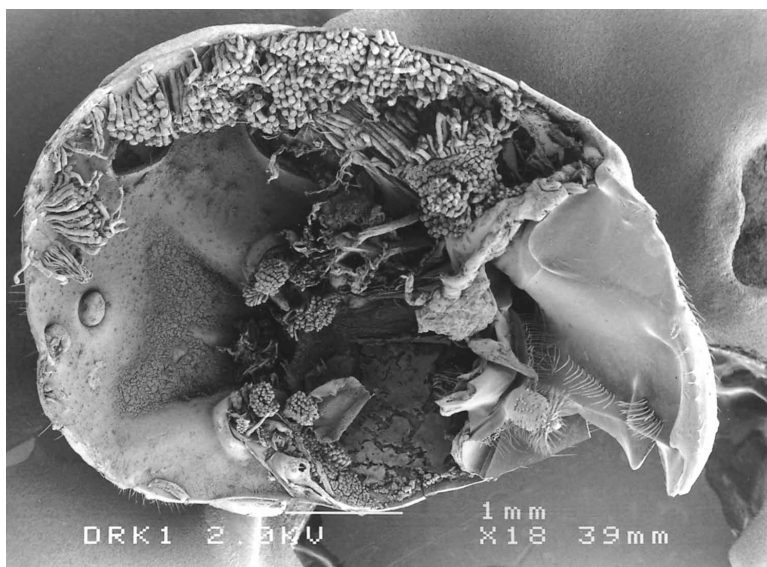


Fig 2

Fig. 1. Overview of the head of the hornet *Vespa orientalis*, observed from the outside, with two compact eyes (L, R), two lateral ocelli (a,b) and one medial ocellus, vertex (vt), snout with frons plate (fp) and two antennae (an). Bar= 1mm.

Fig. 2. Overview of inside of the head after removing part of its contents showing lateral (a) and central ocellus (c), second lateral ocellus hidden by hair cells. Particularly at the periphery muscle fibres (mf). The frons plate (fp) is covered with hair cells, which are barely visible at this magnification. Bar= 1 mm.

stages, to wit: a fertilized queen which emerges from hibernation during February-March to found a nest in an empty cavity, usually an abandoned rodent burrow, where it proceeds to oviposit her first eggs in an embryo comb and nurses these till eclosion of the initial workers. Thereafter, the handling of the brood is gradually relegated to the workers, while the queen engages henceforth only or primarily in oviposition.

Much information has accumulated in recent years on the biology of this and related species or genera of hornets and wasps (Ishay, 1967; Wilson, 1971; Guiglia, 1972; Spradbery, 1973; Edwards, 1980; Matsuura and Yamane, 1990). It turns out that the life cycles of the various species are fairly similar, except for some primarily local or ecological differences. The salient, common features among these hornets are the following : (a) all of them are predators, and the larger species within the genus *Vespa* constitute in their area of distribution an enemy of the honeybee. (b) all of them are estival, so that by winter only fertilized queens survive, which are intended to found a new colony in the spring. (c) if the hornets are active outside the nest mainly during the daytime and in the evenings in the summer; an activity started during the daytime may continue to completion in the dark. Darkness prevails within the nest, as well as a rather fixed temperature and humidity, and these conditions are strictly controlled or adhered to by the resident hornets. Furthermore, all the combs constructed within the nest are orientated in the direction of the earth's gravitational force.

### ***The importance of illumination to vespan life***

It was found (Ishay *et al.*, 1980) that optimal hornet longevity occurred under outside daylight illumination; second-best was under room daylight illumination. Under these conditions hornets, *Vespa orientalis*, lived significantly longer than under constant light

or darkness. Addition of proteins to the diet usually did not contribute to the longevity beyond that obtained with a sugar diet alone, but did promote enhanced building of cells and better nursing of the brood.

*Vespa orientalis* hornets perceive the conditions prevailing around them via sensory organs attached to their cuticle. Their various external sense organs are covered with a layer of cuticle so that the latter mediates between them and the environment. The cuticle thus is an active mediator and it is therefore worthwhile to attempt to measure or assess the disparate properties of such cuticle. In an earlier report we described the photoconductive phenomenon which occurs on the "yellow strips" of the cuticle of *Vespa orientalis* (Ishay and Croitoru, 1978). It was shown that following an initial exposure to light of the yellow strips, of living as well as dead hornets, their resistance increases until it reaches a saturation value. At this stage the irradiated cuticle of the hornet acts like an organic photoconductor (Inokuchi and Akamatu, 1961), i.e. the cuticular resistance increases when the light is turned off and then decreases upon renewed illumination; this effect proved to be reversible.

We were interested in investigating whether the observed photoconductive phenomenon conforms to the general behavior of organic semiconductors under the same conditions. What is the possible impetus of the photoconductivity in the yellow strips on the daily activity of the hornets ?

In a '*Vespa orientalis*' nest, a fairly high and fixed temperature (29-30 °C) is usually present (Ishay *et al.*, 1967; Ishay and Ruttner, 1971; Ishay, 1973). The nest is situated in darkness or at least no direct penetration of light occurs. Thus, the hornet has an optimal temperature within its nest for carrying on its diurnal activities, and when exposed to sunlight, outside the nest it has the readiness for conductivity of an intrinsic semiconductor (Ishay *et al.*, 1980). It follows, then, that this

photoconductive property of the cuticle is dependent also on the temperature, which prompted us to assess the changes in the vespan cuticle resistance to electric current in relation to temperature.

In these investigations of the electrical resistance of hornet cuticle a correlation was found between temperature and cuticular resistivity in a relatively large group of hornets (49 in all), which again points to the cuticle as being an organic semi-conductor (Meier, 1974; Sachse, 1975). This basic property of the hornet cuticle is dependent neither on the pigment color nor on the age of the hornet.

### ***Cuticular resistance***

Measurements in the course of this study were all made in the dark. There is a difference in the electrical resistance of vespan cuticle exposed to the same temperature, depending when the measurements are made during warming or during cooling. This phenomenon -hysteresis- appears only when measurements are made in the dark.

Investigations on this phenomenon in hornets have revealed the existence of a hysteresis loop, which is obtainable upon measurement of a complete cycle within any temperature range between - 35 °C and + 50 °C (Ishay et al., 1982; Ishay and Shimony, 1983; Shimony and Ishay, 1984). This has been defined as "thermal hysteresis ". Some insects have proteins which produce a thermal hysteresis (Ishay et al., 1985).

The worker hornets do not hibernate and it seems that the occurrence of thermal hysteresis in the hornet's cuticle points to the possibility that their cuticle is endowed with memory, since at the very same temperature the resistance can differ depending on whether the cuticle is in the process of cooling or warming.

It is likely that the sentinel hornets (Ishay et al., 1967), when probing the entering or departing hornets with their antennae, can gauge, among other things, the resistance level

of their cuticles and thereby possibly the protocol of their flights as well as their feeding status. Thus, it appears that the normal cuticle, beside reacting to electrical current, as do organic semiconductors, has an advantage over the latter in that it stores some kind of memory and therefore provides information to nestmates.

The origin of this behavior of the cuticle resides probably in the polarity of some magnetic (or electric) elements in it (some magnetic or electric domains). The "fat" hysteresis loop obtained between the warming and the cooling lines in the control experiment (i.e. the space between these two lines) represents the energy investment (or gain) in these cuticular elements which, by changing their polarity and their spatial orientation or both, set up a net magnetization parallel to the field applied to them (Rosenzweig et al., 1985).

Resistance is an important feature of semiconductors, however, to understand the biological importance of hornet cuticle as a semiconductor, there was need to perform also measurements of the spontaneous voltage and current, that is, the voltage and current not created by the cuticle in response to an external electric current, inasmuch as these measurements can inform us regarding the intrinsic properties of the cuticle as a semiconductor. Additionally, we examined also the response of vespan cuticle to charging by an external voltage source.

### ***Thermoelectric and photoelectric currents***

The spontaneous current in the cuticle of the studied specimens ranged between 30-40 nAmp under conditions of darkness, whereas under illumination the current drops to near zero. Upon warming up to 28-29° C, the current rises to 50-200 nAmp, however, after a while, it declines, regardless of whether the temperature is held steady, continues to rise or is lowered.

In light, the current values are lower than in darkness and this under all conditions. When the specimen is charged with an electric current under fixed temperature, the current attains several nAmp in darkness, but is usually less than that under illumination by about one order of magnitude. The capacitance values range between 1-7 mFarad both in light and in dark.

Within the temperature range used by us (8-30°C), we found the cuticular response to be negative photoconductivity (Ishay *et al.*, 1987), meaning that upon exposure to light, the electrical conductivity decreases (while the resistance increases).

The same could be observed when charging the cuticle with electrical current, namely, that charging in the dark attains discharge current values which are by one order of magnitude higher than those during charging in light. Interestingly, the capacitance values under both conditions are not very different and generally are in the same range as those published later for the hornet cocoon silk caps (Ishay *et al.*, 1994).

The rise in electric current upon increase in temperature is intrinsic, in that with increasing thermal energy more electrons arrive from the valence bond or, since the cuticle is doped with various metallic impurities (Ishay *et al.*, 1982), electrons are donated to the conduction band until depletion occurs and after a while (depending on previous conditions of the cuticle, the temperature, the relative humidity and probably the composition of gasses as well as other conditions not known yet) the conductivity diminishes.

In cooling as well, there is a decrease of the conductivity owing to the fact that fewer electrons receive the energy needed to jump to the conduction band (MacDonald, 1962). The optimal conductivity is at 28°C - 29°C which is also the optimal temperature of the hornet nest everywhere (Ishay and Ruttner, 1971; Heinrich, 1981).

Interestingly, at temperatures above optimal, that is above 28°C, the conductivity starts dropping. The slope of this decrease varies from the slope of illumination or that for cooling and all of them vary from the slope of warming, meaning that there is a hysteresis between each of them. This phenomenon was noticed earlier when measuring the resistance values upon warming versus those values upon cooling the cuticle (Rosenzweig *et al.*, 1985) and is a known feature in other organic ferro-electric materials like thiourea or nucleic acids (Gutmann and Lyons, 1981; Gutmann *et al.*, 1983). The reason for the drop in the current level, when warming beyond 28°C is probably phonon drag and/or phonon scattering (MacDonald, 1962; Ibach and Lüth, 1991).

In another study (Ishay *et al.*, 1997), we found that exposure of a part of the cuticle to light caused a sharp increase in voltage, when measured between the illuminated and the dark part of the cuticle. The direction of this voltage was reversed when the other part of the cuticle was illuminated. This voltage was found to be linearly dependent on the intensity of the incident light for relatively low light intensities of a few mW/cm<sup>2</sup>. However, this light-induced voltage was much higher if the light beam was directed at the back part of the cuticle strip than in the case where the front part of the cuticle strip was illuminated by the same light beam.

The spectral dependence of this effect was also investigated and the maximum of the relative quantum efficiency was found in the spectral range of 360-380 nm. It appears, that the cuticle might act as a biological solar cell. From the foregoing, it appears that hornet cuticle amounts to a photovoltaic cell which releases electric current in dependence upon the temperature. The accumulated energy serves partly to maintain homeostasis of the hornet's temperature by way of a Seebeck effect.

**How is the cuticular photovoltaic system built-up ?**

The system is comprised of an air sac acting as a bellows and of primary and secondary tracheal ducts which pass along a series of photoreceptors and wind around the base of each photoreceptor to form individual tracheal loops. The respiratory rate changes in accordance with the ambient temperature and the physiological needs, so that within narrow limits, efficient thermoregulation is enabled by the conduction of air at the appropriate temperature. The temperature of the conducted air is determined in situ, by a process whereby accumulating electric energy in the cuticle is converted to thermal energy by a p-n junction system. Additionally, the membrane around the tracheae contains openings through which a product of an olfactory gland is evaporated, that apparently serves as a thermoregulatory pheromone. In temperatures below optimal the adult hornets (and wasps) commence to blow hot air around the developing brood (pupae) and thereby warm it to the desired temperature (Ishay and Ruttner, 1971), whereas when the temperature is higher than optimal, the adult hornets within the nest commence to ventilate the brood or the entire nest (Ishay *et al.*, 1967; Sadeh *et al.*, 1977). Thus, while the air sacs do contain the greater share of the air supply, the temperature of the air is determined according to need by its passage through the tracheal loops which gird the envelope of the photoreceptor. Here, each tracheal loop comes in contact with: 1) the cuticular envelopes of the photoreceptor – they are electrically of n type (i.e., electron donors) and 2) the yellow granules which are of p type (i.e., electron acceptors). The flow of air passing through the tracheal loop is thus exposed to this p-n junction where electric energy is stored, or caused to flow and this electric energy is transformed, according to need, into thermal energy which is utilized in thermoelectric circuits such as have been described originally by Seebeck and Peltier.

This process is geared primarily to provide thermoregulation of areas of the abdominal cuticle or other areas that contain extraretinal photoreceptors since it is crucial to keep the photoreceptors from overheating.

The thermoregulatory activity is important also for the entire nest, just as in vertebrates the excess heat produced in the striated muscles and the liver is transported via the circulation to all parts of the body.

**Additional information about the photovoltaic system**

In our subsequent studies the structure of the cuticle as a photovoltaic cell was dealt with in greater detail (Ishay *et al.*, 1992). Thus, we have provided some information about the structure of the hornet cuticle in the region of the yellow strips that are known already as a semiconductor-like 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 irradiated light on the inner, yellow pigment granules, i.e., similar to a 'Fresnel lens' (Maycock and Stirewalt, 1981).

The voltage accumulates in the lower parallel lamellae whence it is transmitted to the walls of the pore canals. These walls descend to below the yellow pigment layer whose granules absorb all visible light, except the wavelength of yellow (that is reflected) so that, most probably, underneath there is darkness. The thicker (upper) layers of the cuticle close off in the bottom part of the pore canal, while the thinner layers beyond the closure point re-expand and at an angle of 90°

form thin plates of the hypocuticle, sealing off the ‘sandwich’ from below. This photovoltaic system is active in daytime for most of the hornets’ lifetime, i.e., for workers several months during the warm seasons, while for the queens a whole year.

The ‘sandwich’ proper is comprised of about 30 (or more) horizontal layers that are doped with Si, P, S, Cl, K and Ca and smaller amounts of Mg, Fe and Zn, some of them electron donors and others electron acceptors. The parallel layers progressively attenuate from the exterior down to the yellow pigment layer, which is likewise horizontal. In the vicinity of the pore canal, however, all layers become vertical and contribute to the formation of 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 one-quarter of the wavelength of light (Land, 1972, 1985). This mechanism protects the content, i.e., the photoreceptor from overheating, and so also the whole insect body.

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 latter attenuates into nipple-shape 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, inter alia, to the nerves that support the pore. In the dark, the electric resistance, which in light was at a level of giga ohms ( $G\Omega$ ) drops down to a level of kilo ohms ( $K\Omega$ ) – a decrease of about 5-6 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 (Ben-Shalom 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 *Vespa 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; Ishay *et al.*, 1997). It follows, then, that hornet cuticle constitutes a combined system which integrates both photovoltaic and thermoelectric elements, and it is this system which regulates the micro-environment both of the sensory cells and their contained photoreceptors as well as of the nest cavity and the contained hornet population. The mentioned conditions are essential for proper development of the entire hornet colony. Thus, an appropriate temperature is crucial for vespan sensing of gravity inasmuch as hornets build their nest in the direction of the earth’s gravitational pull (Ishay and Sadeh, 1975, 1977).

### *Sensitivity to gravity*

The sensitivity to gravity has been examined in a number of studies. By their behavior at the start of building, it is clear that hornets display negative geotropism; however, the capacity to distinguish the highest geotropic point, i.e., the zenith which is exactly opposite the center of gravity, is probably not fully developed at eclosion but rather improves with time during the first 3 days of life. At eclosion, an inclination of 5° is sufficient to cause the hornets’ to start building at the point of inclination as if it were the highest point of the container. It is only after several days that the hornets are able to discern the highest point in any of the variously designed containers (Ishay, 1976).

Hornet workers, queens and males, aged 0-24 hours (i.e. juveniles) and 24 hours and more (i.e. adults) were tested by us for their res-

ponses to changes in the direction of the gravitational force while placed on a flat surface gradually tilted between  $0.5^\circ$  and  $180^\circ$ . The tests were run on non-blind and blind hornets, at temperatures ranging between  $18^\circ\text{C}$  and  $35^\circ\text{C}$ , in daylight as well as in the dark. Up to 18 hours of age, negative phototaxis prevailed among the hornets, which displayed a clear preference for remaining in the dark regardless of the geotropic position. Between 18-24 hours of age, there was gradual appearance of a sensitivity to change in the geotropic position. Beyond 24 hr of age, the hornets became sensitive to changes in their declinations, with workers becoming sensitive at a  $3\text{-}5^\circ$  declination, queens at  $4\text{-}5^\circ$  and males at a declination of  $8\text{-}19^\circ$  from the horizontal. Hornet response takes the form of an upward climb, to the highest point of the test surface. Such response required a temperature exceeding  $24.8\text{-}25^\circ\text{C}$  for workers,  $23.2^\circ\text{C}$  for queens and  $20.8\text{-}21^\circ\text{C}$  for males (Ishay *et al.*, 1986). It was found that as a group, the hornets respond even to a  $1^\circ$  inclination, but singly, the (maximal) sensitivity or response is only to an inclination of  $3\text{-}5^\circ$ . The hornets can build a comb (oriented towards the gravitational force) when their multifaceted eyes are covered; in fact the normal building activity is undertaken in the dark and even by hornets that had been blinded or had eclosed in the dark and had never seen any light. If part of the frons plate of hornets is damaged, there is no building whatsoever, or the building is meager and the comb direction is distorted. In other studies we investigated the sensitivity of hornets to gravitation also under conditions of hypergravitation, created on a specially designed centrifuge. We found that comb construction by hornets exposed to centrifugation at 1 to 2 days of age differed from that of hornets similarly exposed at 3 to 7 days of age. Juvenile hornets built their cells in the direction of the resultant force, whereas adults resisted the centrifugal force and tried to build in the direction of gravitational force (Ishay and Sadeh, 1975). Furthermore, hornets

eclosing from and developing in combs subjected to centrifugal spinning, built combs whose direction was affected both by rotation and by the resultant of the gravitational and centrifugal forces. In all instances of building, whether new, or restoration of the old, there was a relatively large deviation from the direction of the computed resultant. However, when the hornets were removed from the centrifuge they proceeded to build correctly, that is, in the direction of the earth's gravitational force regardless of their previous environmental conditions (Ishay *et al.*, 1989).

### ***The Ishay organ and its sensory epithelium - hair cell structures***

In subsequent studies we found that the high sensitivity of the hornet to directional changes in the gravitational force under differing of conditions is enabled by the presence of a complex sense organ sensitive to varying accelerations. This is the Ishay organ, which is located in the space between the frons plate and the anterior part of the cerebroganglion. In this region are also located the compound eyes (on both sides), the three ocelli (in the upper region) and a pair of antennae (in the lower region). In addition, the region is traversed at its base by nerves from the salivary glands and on both sides by muscles, the largest of which are the adductor mandibularis, the lateral pharyngealis, and the antennal muscles.

While exploring the interior of the frons plate in hornets and focusing on the structure of the conus, which intrudes inward from the sutura coronalis, we detected in the various layers overlying one another, yellow granules, stereocilia, bobs, and disc-like plates. The latter proceeding into the space of the acoustic box. The mentioned configurations are capable of some mobility and are thus not strictly statoliths.

The acoustic box is a very complex organ with weighted bobs of various configurations that may aid in gravity detection. Fibers and bobs



within the acoustic box are immersed within hemolymph which is enclosed by epithelium that may be piezoelectric. In insects, the acoustic box may serve a similar function to what mechano receptors serve in other invertebrates. The two components that can detect gravity are: (a) the external sensors of the head and especially those on the frons plate which are dry and static, and (b) those inside the acoustic box that are immersed in hemolymph. Finally, the fibers and bobs inside the box may also serve a mechano-receptive function (Ishay *et al.*, 1996).

In further studies, we focused on the morphology of the cilia which comprise the sensory epithelial element in the Ishay Organ (see below). To date three types of hair cell configurations with stereo- and kinocilia have been described by us in the head of the hornet; these were encountered at the vertex and frons regions adjacent to the three ocelli and are assumed to be part of the hornet's gravity detecting system.

The *first* and most common type of hair cell configuration (*type A*) was a cell surrounded by a septum, having a diameter of 30-50  $\mu\text{m}$ . Aggregates, of over 20 such hair cell groups together, formed a larger unit, 130-300  $\mu\text{m}$  in diameter, which was also enclosed by a septum. Many of these larger round units were, in turn, arranged in either angular or leaf-like clusters. The hair cells bore numerous cilia of 4.5-6.0  $\mu\text{m}$  long, and were themselves composed of smaller sub-units of about 7-8  $\mu\text{m}$  in diameter, which were not enclosed by a septum.

The *second* type of hair cell configuration (*type B*) was made of discrete cells with a diameter of approximately 12.5-14  $\mu\text{m}$ , located in the vicinity of the pore canal outlet of the peripheral photoreceptor. These single hair cells were either devoid of or only partially enclosed by a septum. Their cilia were 4.5-6.0  $\mu\text{m}$  long as well, but with a diameter of only 150-160 nm. On the exterior of each cilium a tubular system could be detected. Furthermore, the tips of adjacent

cilia were interconnected by a kind of fiber, bearing a spherical body in its middle.

The *third* type of hair cell (*type C*), present in the neighborhood of the second type of hair cell (*type B*), was chalice-shaped and had interconnecting fibrils comparable to those found at *type B* as well. We believe, that these 3 types of hair cell configuration along with the ganglion cells interconnecting their bases, are all components of the gravity organ of the hornet, the Ishay Organ, and together with the cuticular photoreceptors play a role in the navigation system of the hornet. We further conjecture that the described structures are engulfed by endolymph and that signals produced by each unit are conducted by neural fibrils to the hornet's central nervous system (Jongeblod *et al.*, 1999).

Graviception is important, also in vespan orientation during flight. The workers in the nest of the Oriental hornet depart the nest for the field in foraging flights that may take them as much as 5 km from the nest. Yet, even from such great distances they are able to navigate their way back in great precision. We believe the hornet's ocelli are contributory here. These ocelli are situated on the vertex plate in such a fashion that if we draw a straight line through each, we end up with an equilateral triangle. Each ocellus bears a convex cornea shaped as a hemisphere. The tangential planes of each ocellus create between them a pyramid of three equal sides. The arrangement of each ocellus on a different plane enables a panoramic visual coverage of practically all the 360° field of vision above and around the head. Assuming that these ocelli pick up polarized light, we surmise that hornets can sense the direction of the sun rays through them. However, to be able to determine the direction of the sun vis-a-vis the zenith, the hornet needs to orient itself in a position which is absolutely horizontal with respect to the earth's surface or, alternatively, with respect to hypothetical plane which is tangential to the earth's surface (Rosenzweig *et al.*, 1999).

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