Journal of Optoelectronics and Advanced Materials Vol. 4, No. 1, March 2002, p. 135 - 145

THERMOELECTRIC CONVERSION AND SPECIFIC HEAT OF HORNET COMBS

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Social wasps belonging to sub-family Vespinae (Hymenoptera) build brood combs made up of hexagonal cells, all of which have their outlet facing in the direction of the gravitational force. These combs are built of organic and/or mineral matter, each grain of which is enwrapped in saliva secreted by the building hornets. The enwrapping hornet saliva hardens rapidly into a tough polymer that binds together the building materials collected from the surroundings. The combs are intended to rear the brood from egg to imago. The comb cell walls possess electric properties which in part have already been elucidated. It has been established that the cell walls behave like a thermoelectric material in that with rise in temperature between 20-30°C there is increase of the electric current from 0 to 150 nano amperes (nA). Additionally, the specific heat of the comb has been measured and was found to be (in the range of 20-70°C) 0.72-0.85 J/g.K. For comparison purposes, analogous measurements were taken from the silk produced by the pupating larva inside each brood comb. The specific heat of the silk was found to differ markedly (two times higher) from that of the cell walls, while the electrical charge of the cell wall is higher than that of the silk cap by more than one order of magnitude The possible reason(s) for this disparity is discussed.

(Received August 30, 2001; accepted March 4, 2002)

Keywords: Specific heat, Hornets, Combs, Organic polymers, Thermoelectric properties

1. Introduction

Most of the species of subfamily Vespinae found an annual nest in the spring. The embryonal nest is started by a fertilized queen that had successfully undergone a winter hibernation. The nest is variously errected subterraneously (as in the species *Vespa orientalis*, and some of *Paravespula germanica* and *P. vulgaris*), in the hollow or branches of a tree, on a roof corner or attic or in any other available hollow space. The majority of species founding their nests in high (above-ground) places utilize building materials collected from the environment, primarily, cellulose, whereas species that nest subterraneously rely mainly on grains of soil available in abundance in the selected milieu. Whether soil particles or cellulose, these building materials are masticated by the female hornets (queen or the adult worker hornets) and in the course of this oral mastication are mixed with saliva. The resultant mash or dough serves to build the layers in the cell walls and gradually the entire cells and also the nest envelopes. Eggs deposited in the comb cells give rise to the brood and the structure housing this brood is fairly rigid because the building hornets' saliva hardens rapidly. Many details on the building of hornet nests are available in the literature, e.g. vide Ishay et al. (1967), Wilson (1971), Giuglia (1972), Spradbery (1973), Edwards (1980) and Matsuura and Yamane (1999). The comb cells of hornets resemble an inverted goblet. What we have, roughly, is an hexagonal tube sealed at the one end by the roof and the six converging sides but left open at the (bottom) end. Usually the queen, but at times also a worker hornet, deposits a single egg on one of the inner side walls of the cell, from which a larva hatches, grows and ultimately pupate. To pupate (at the end of) the 5^{th}-instar larva spins a silk weave to build a silk cap that properly seals the silk cocoon and subsequently it turns around to spin a silk sleeve which is fastened onto the hexagonal side walls of the cell from the inside and extends up to the roof of the cell. That done, it again reverses to commence spinning a delicate weave upon the formerly spun sleeve and cap, thus completing the silk cocoon. The pupating larva can now metamorphose, and about a fortnight later, the imago eclodes. As the imago eclodes, it severs only the silk cap, leaving the rest of the silk cocoon intact, fastened to the inner walls of the cell. The workers that later come to 'clean' the vacated cell do not remove the silk coating, so that subsequent ovipositions are made on the very same silk bedding, on one of the inner walls. The present study was undertaken to elucidate the relationship ─ especially insofar as the physical properties associated with heat capacitance are concerned – between the comb cell wall and the larval silk weave, and this within the temperature range optimal for hornets.

2. Materials and methods

Combs were collected from the field as previously described (Ishay, 1975). On transfer to the laboratory, they were evacuated of all brood (ova, larvae and pupae) (Fig. 1(a,b), then kept at room temperature till the start of measurements. The combs were photographed via scanning electron microscope (SEM) as previously described (Jongebloed et al., 1999). Their thermoelectric properties were determined at a temperature of 20-30°C by a procedure in use in our laboratory (Ishay and Litinetsky, 1996; Ishay and Kirshboim, 2000).

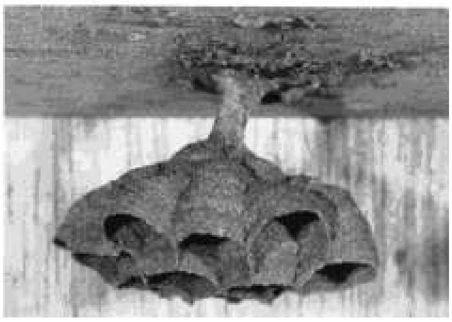

Fig. 1(a). Picture taken through light microscope of orientation comb in its natural state, that is, with the cell outlets facing toward the gravitational pull. The shown cells are devoid of brood. Note that the walls of the cells in the outer periphery are rounded, whereas those in the inner circles are already hexagonal and seen at approximately natural size.

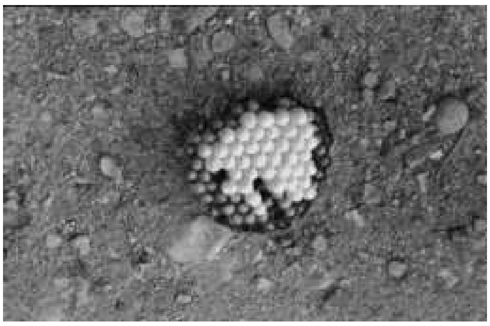

Fig. 1(b). View from below of a comb with brood. At center are the pupae with their white silk caps, and at the margins – the larval stages. Picture taken through light microscope at 1/4 × magnification.

Concerning these thermoelectric properties, we need to point out that our determinations were run in two series, namely, short-term determinations and long-term determinations. In the first instance, a cell-wall specimen from a naturally-built comb collected in the field is removed from storage under refrigeration (at 4 °C) and placed into a thermostat (Revco) where the temperature is varied between 20-30 °C for 15-20 minutes, and the onset of electric current is recorded automatically. Subsequently, as the temperature rises to 30 °C (peak current level), it is diminished to

20 °C, and so also the electric current drops. Roughly each couple of warming-cooling lasts about 35-50 minutes. In the second instance (the long-term procedure), the preparation removed from the refrigerator is first tested for inherent spontaneous electric current, at 30 °C, then discharged for 9-15 minutes till it either attains zero level or a plateau. Now the preparation is recharged by warming (i.e. left in the incubator at a fixed temperature of 30 °C) for one full hour, following which the discharged current is measured till it reaches starting level. For comparison purposes, we performed the same measurements also on the pupal silk caps.

The specific heat of comb cell walls was determined by the same method applied to the silk produced by the pupating larvae of hornets (Ishay et al., 2001). We should point out that to determine the specific heat one needs to crush the cell walls rather than leave them intact as in the thermoelectric determinations. Special attention was paid to ensure that the comb preparations were entirely free of any silk or any other element not present in the original comb.

Heat capacity C_p of the hornet comb material was measured as a continuation of our extended investigation of *Vespa*-produced materials (see Voronel et al., 1988; Chekhova et al., 2000; Ishay et al., 2001). The measurements were performed by a precise adiabatic computer-controlled calorimeter of Tel-Aviv University (see Voronel, 1974). A sample of dried and fragmented hornet comb material weighting 1.436 g had been packed and pressed into our preliminarily calibrated stainless steel container of 1 ml in volume. The heat content of the empty calorimeter was:

$$A_{cont} = 1.602 + 0.00115t - 1.3\times10^{-6}\, t^2 \text{ , J/K} \quad (1)$$

This expression includes also a heat content of two layers of copper foil pressed into the container to provide uniform distribution of heat within the poorly conductive sample.

3. Results and discussion

As can be seen from Fig. 1(a) (taken in profile) the combs are made up of cells shaped like an hexagonal tube, with the cell outlets facing down, that is, in the direction of the earth's gravitational pull (Ishay and Sadeh, 1975). As a rule, the color of the comb is like that of the surrounding soil, because the building hornets gather building materials from the environment and masticate it to form a mash in which the mineral or organic matter is macerated with their saliva and it is this mash or dought which is used to build the comb and its cells. This mash sets rapidly upon secretion and the collected particles in it are immersed in and held together by the hornet saliva, which is a relatively hardy, organic polymer. As seen in Fig. 2(a), the majority of particles embedded in the cell wall appear like tiny pebbles, having a diameter of 100-200μm. Fig. 2(b), taken from the roof of one of the comb cells reveals that the roof is multi-layered, with one layer comprised of the tiny pebbles (1) while its neighbor is made up of organic matter (2). This phenomenon is quite known in hornet comb building, where the combs are actually an intercalation of layers (for which see also Fig. 1(a)) (Ishay et al., 1995).

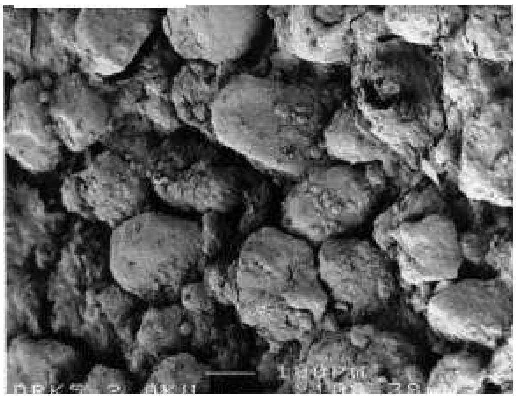

Fig. 2(a). Picture made via SEM of a segment of cell wall (×100). One can see tiny pebble-like particles of 00 – 200 μm in diameter and between them – the 'cement' comprised of adult hornet saliva which glue the particles and all other components together. Bar = 100μm.

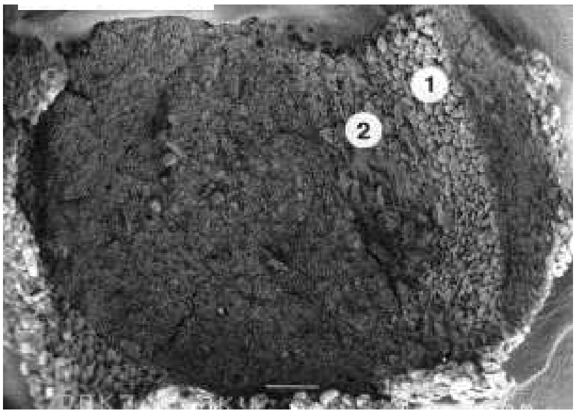

Fig. 2(b). Roof of a comb cell seen from inside: 1 - filling material comprised of tiny pebbles; 2 - filling material of an organic source. Bar = 1mm. Note that in other parts of the roof we also see such intercalation of the two filling materials.

Our short-term thermoelectric measurements were made both on combs collected from the field whose main constituents were minerals (Fig. 3(a)) as well as on combs built in the laboratory whose main building material was cellulose (as provided from paper towels offered to the hornets as building material) (Fig. 3(b)). In these two figures are given the results of thermoelectric determinations made at temperatures between 20-30 °C, and we note a rise in the current with each increase in temperature and likewise a decrease in current with each drop in temperature, down to the starting level. Ordinarily, the current level is in the range of nano Amperes, that is, 1.5-80 nA (10^{-8}A), and we note a significant difference in the current levels in the two types of comb. This disparity was subsequently confirmed on many repeat, comparative determinations. In this connection, we should point out that in the laboratory, the combs are built by hornets that had ecloded in the laboratory, and not by hornets from the field, that is, there are two distinct groups of building hornets and not surprisingly, therefore, the electric values from the respective combs differ not only in level but also in length of the cycle, with the field-built combs attaining the higher electric values. The reason for this disparity, we believe, is that the 'field' (natural) combs are composed mainly of minerals as opposed to the cellulose making up the 'laboratory' comb, and perhaps also because in the natural nest workers of various ages participate in the building and maybe their diet is more balanced and variegated than that offered to the laboratory' reared workers. Whichever the reason, the phenomenon of combs built by hornets from a qualitative standpoint occurs both among the field hornets and the laboraatory hornets, albeit from a quantitative standpoint and in terms of current intensity, there is discrepancy in favor of the field-built combs.

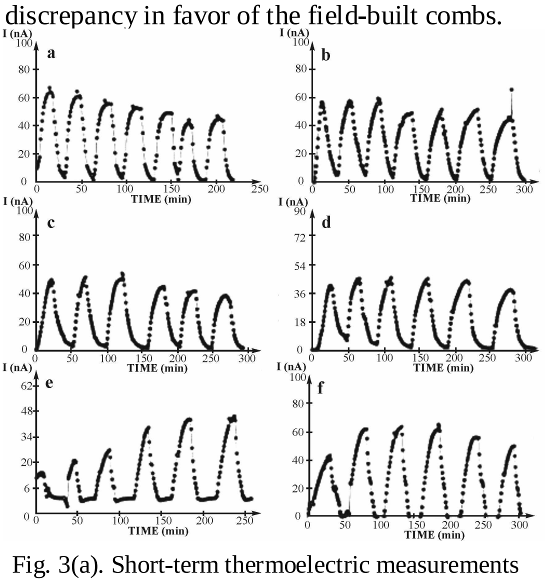

Fig. 3(a). Short-term thermoelectric measurements taken from the surface of a cell wall preparation (comb collected in the field).

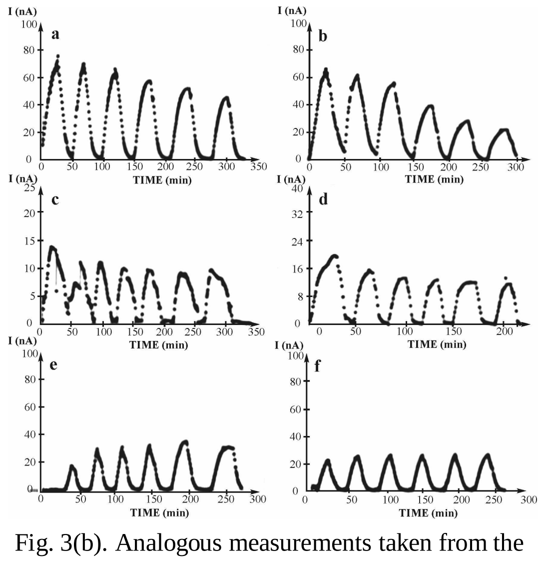

Fig. 3(b). Analogous measurements taken from the surface of a wall of a comb (built in the laboratory). For details consult 'Results and Discussion'.

As for the long term thermoelectric measurements of silk caps, these are shown in Fig. 4(a). Similar measurements from the walls of a field-collected comb are given in Fig. 4(b). As can be seen from the former (Fig. 4(a)) – the starting spontaneous current varies between 8-30 nA (i.e. 8×10^{-9} – 3×10^{-8} nA). Following charge (for 1 hr at 30 °C) and discharge also at 30°C, the starting levels range between 90-480 nA and the discharge lasts up to 150-350 min (2.5-5.8 hrs).

Analogously, in the comb wall preparations the spontaneous current was 8-150 nA, and the current level (after incubation for 1 hr at 30 °C) at the starting levels were 120-800 nA, and the duration of discharge was between 800-2700 minutes (33-112 hrs). The comparative findings for comb cell wall and silk cap preparations are summarized in Table 1.

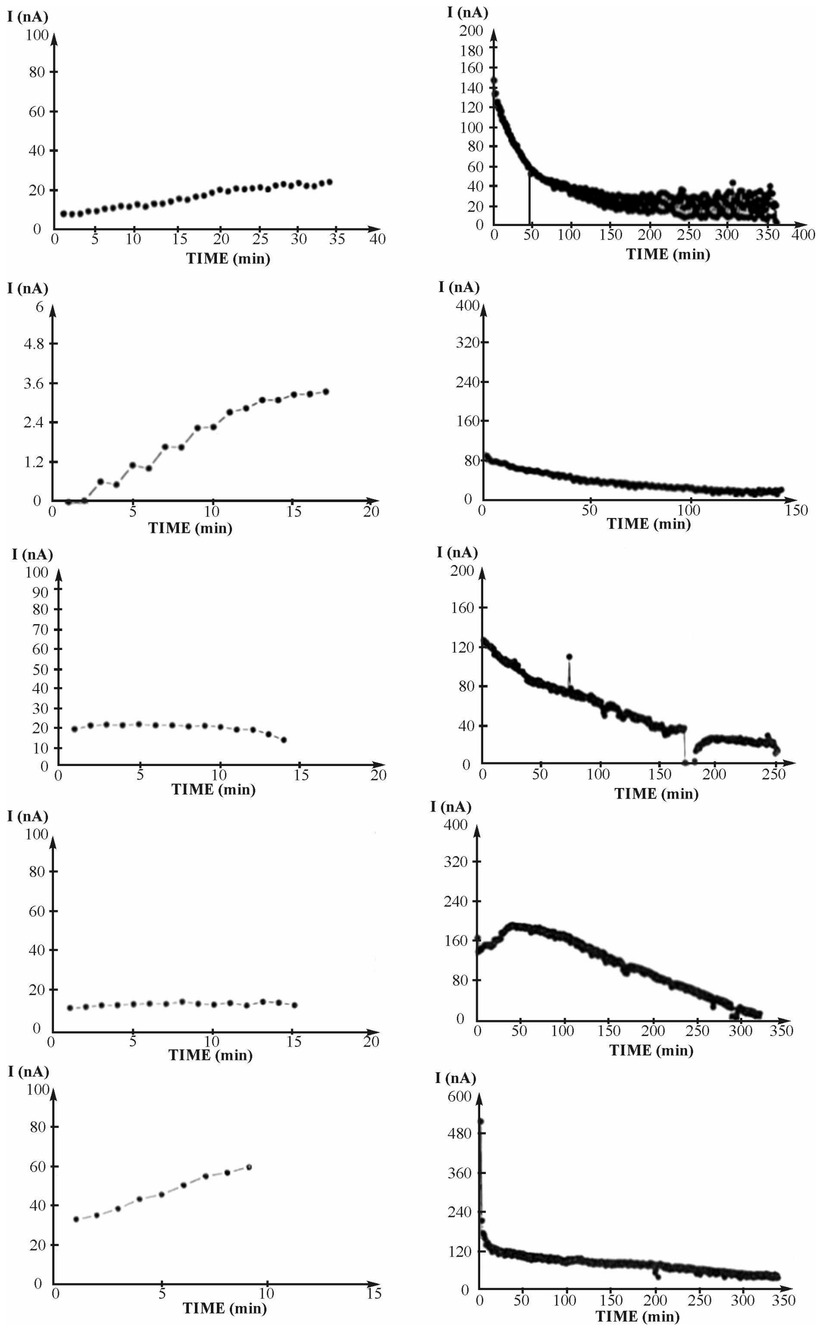

Fig. 4(a). Spontaneous current and discharge current (after charging for 1 hr) in preparations of silk cap. For details consult as before.

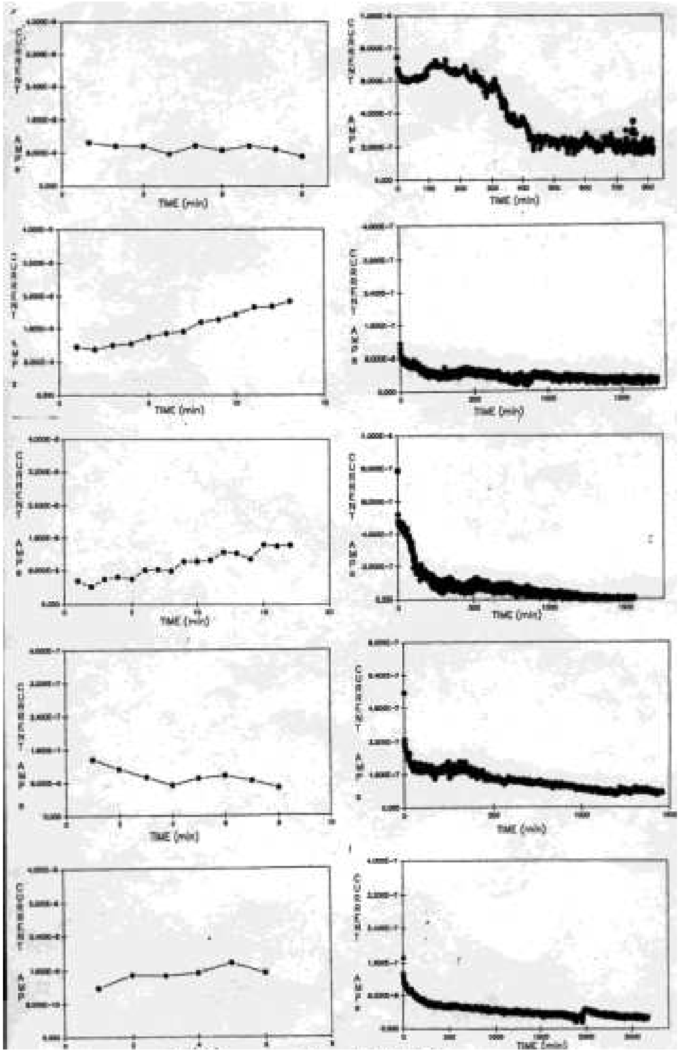

Fig. 4(b). Measurements of spontaneous electric current (on left) and the discharge current after 1 hr. incubation at 30°C (on right) of 5 preparations of comb cell wall. For details consult Table 1 and 'Results and Discussion'.

From the tabular results we note that the starting charge levels in comb are significantly higher than in silk, while the discharge lasts many times longer in comb than in silk, these results pertaining to one hour of charging. We can suppose that in nature (long time high temperature) it persists through most hours of the day when it is warm outside.

Measuring the specific heat (Fig. 5). In this picture we can see the results of specific heat determinations on combs collected in the field. The specific heat at optimal nest temperature (29 °C) (Ishay and Ruttner, 1971) was about 0.77 J/g.K. The results of our C_p measurements of hornet comb wall within a temperature range of 20-70 °C are presented in Fig. 5 and may be fitted within a $\mp 0.5\%$ error by the equation:

$$C_p = 0.53 + 0.01663t - 3.887 \times 10^{-4}t^2 + 3.206 \times 10^{-6}t^3 \text{, J/g.K} \qquad (2)$$

Table 1. Comparison of electric charge values in comb cell wall and silk cap.

Comparison	Samples	Sample No. 1	2	3	4	5	Mean	Standard Deviation
Spontaneous starting level [nA]	Silk caps	10	0	20	10	35	15	5.916
	Cell wall	10	10	7	150	1	36	23.390
Peak values after 1 hr. incubation at 30°C [nA]	Silk caps	150	90	130	170	500	208	60.575
	Cell wall	800	120	800	500	180	470	114.717
Discharge duration till starting level (minutes)	Silk caps	350	150	250	300	350	280	30.550
	Cell wall	800	1500	1500	1500	2700	1540	225.929
Integral ($\int$) of the charge of electricity Q	Silk caps a)	$\int_0^{350} Q = 1.63\text{mC}$	$\int_0^{150} Q = 0.31\text{mC}$	$\int_0^{250} Q = 0.81\text{mC}$	$\int_0^{300} Q = 0.8 \pm 0.08\text{mC}$	$\int_0^{350} Q = 0.20 \pm 0.012\text{mC}$	0.75	0.252
	Cell wall b)	$\int_0^{800} Q = 17.9 \pm 0.4\text{mC}$	$\int_0^{1500} Q = 11.2\text{mC}$	$\int_0^{1500} Q = 6.8\text{mC}$	$\int_0^{1500} Q = 3.9\text{mC}$	$\int_0^{2700} Q = 6.7\text{mC}$	9.31	2.446
Net $\frac{b}{a}$ energy content	$\frac{b}{a}$	10.98	36.12	8.39	4.87	33.5	12.4	6.6318

Q = charge of electricity (integral of electrical current, A $\times$ s)

The heat capacity of the sample within this range is a monotonous function practically insensitive to the heating rate, thus unlike our previous results on vespan silk. This value of the specific heat of comb wall is rather low relative to that of other materials in the nest, such as the pupal silk, which is about 1.5 J/g.k, or about twice that of the comb.

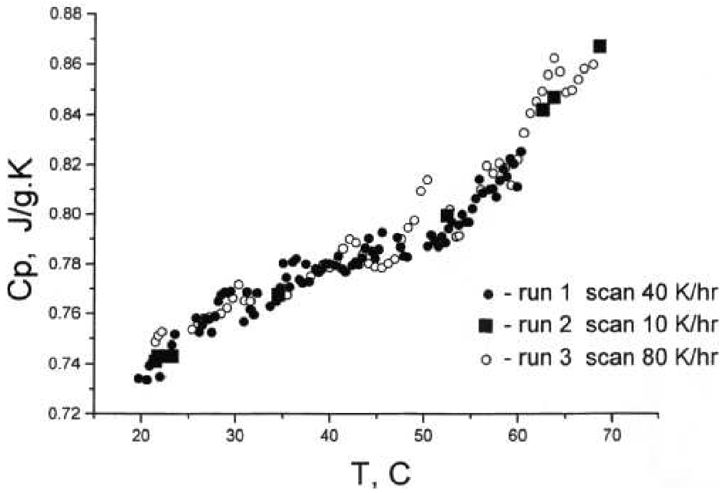

Fig. 5. C_p - t specific heat curve of comb cell wall in correlation with the temperature. Changes in the specific heat occur with changes in the temperature. At optimal temperature for hornets, the specific heat is 0.76 J/gK. With rise in the temperature there is increase in the specific heat so that at 70°C it attains 0.88 J/gk. In runs made at 10, 40, and 80 K/h there are some but not especially large changes. Curve for hornet comb: filled circles - run 1 with heating rate 40 K/h; solid line - polynomial approximation of these data: $C_p = 0.530 + 0.01663\times t - 3.887 \times 10^{-4} * t^2 + 3.206 \times 10^{-6}*t^3$, J/g.k; filled squares - run 2, obtained by very slow heating rate (i.e. equal to or less than 10 K/h); open circles - run 3, seen with about 80 degrees of Kelvin per hour.

Another difference between comb and silk is that the specific heat of the former (depending on the temperature) is fairly monotonous, not showing much variability with hiking of the temperature up to 60 °C. Contrariwise, the specific heat of the silk displays much variability with rise of the temperature between 20-40 °C, within this temperature range, the specific heat rises. Fig. 6 presents both curves (for comb and silk) in the same graph. The points are our measurements and the curves present means for analogous material. Note that values for alumina, silica, limestone, clay and sand are close to those for comb, while polyethylene, paraffins, proteins, and chitin values are close to silk values. The difference between these two types of materials is obvious since the polymer materials have much greater specific heat (owing to their much more complex molecules) (Handbook of Data, 1975; Kikoin, 1976; Mark, 1996).

At face value, the composition of the mentioned materials, namely, comb and silk, would seem to explain their specific heat and the disparity between them. Yet, other explanations may come to mind. Thus remember that the silk is produced by the pupating larvae, which spend about two weeks in the cocoon up to maturation and eclosion. As for the comb, it is produced from organic or inorganic materials, or a mixture of both, and the glue that holds them together is the saliva produced by the adult hornets. Furthermore, the comb will survive the entire summer, which is the active season of hornets. Comparison of Figs. 2A and 2B reveals a difference in thermoelectric properties between the two types of comb, namely, the comb composed of strictly organic matter and the one comprised mainly of mineral matter. In fact, the determining factor is the thermic properties of the workers' saliva, the latter rapidly becoming a polymer. This said, we need mention also the possible contributory role of the filling material in the comb, which in those collected from the field is mainly mineral.

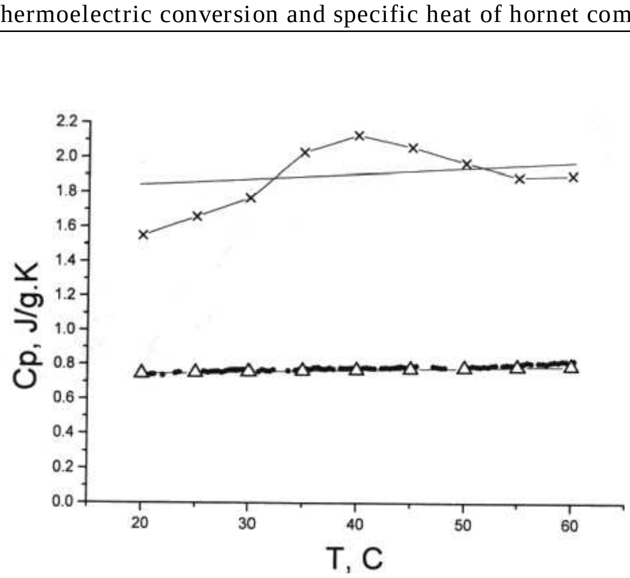

Fig. 6. Comparison between the specific heat (C_p) of comb (bottom line) and that of silk (upper cruciform line). One can see that the specific heat of silk is about twice that of comb throughout the measured temperature range. Comparison of C_p - t relation of new data with some inorganic and organic groups of material: filled circles - hornet comb (runs 1-3), solid line with open triangles - large group of minerals and inorganic components of soil (ordinary clay, sand limestone, concrete a.o.); upper straight line - specific heat at macromolecular organic substances such as polyethylene, paraffines a.o., generalized by this solid line with scatters about ±20%; solid line with crosses - measured in previous work on silk.

We believe the difference between silk and comb wall resides in the basic properties of these two materials and the different roles which they serve. The comb is the dwelling place of the brood, which develops from egg to adult. During the pupal stage, the pupa is separated from the comb walls – actually the comb cell walls – by a partition of silk. This silk, with its high specific heat, attracts heat and stores it, thus serving the encased pupa as quasi-incubator or thermos of a fixed, high heat – something the developing pupa needs because during most of its pupal phase it lacks muscles with which to warm itself. At least in the cap region, the silk cocoon is comprised of two distinct layers (Duncan, 1939) between which, we presume, there is a thin layer of air acting as an insulating material. The silk can also absorb water vapors or, alternatively, lose water, in accordance with the extant temperature (Ishay et al., 2001; Golodnitsky et al., in preparation), and thereby regulate the temperature and the relative humidity in the nest, apart from keeping bacteria from entering the cocoon (Shabtai and Ishay, 1998). To cool the nest during a warm day, the hornets 'hang' water droplets on the silk caps (Ishay et al., 1967), but not on the walls of the comb; this is done to obviate the risk of the comb walls absorbing water and rendering the comb a nidus for bacterial growth as well as attenuating its stability. It thus appears that the two materials under discussion, namely, silk and cell walls, also serve different functions. The comb affords stability, a medium for acoustic communication (Ishay and Sadeh, 1982), a reference point for gravity directed orientation (Ishay and Sadeh, 1975), an insulation from the immediate environment in thermic terms and a provision of a private niche (cubicle) for each of the developing brood, whereas the silk affords a private incubator for each pupa for a limited period of time. We know that the very same comb cell may provide successive housing for at least 3 generations of hornets developing from egg to adult. Yet each pupa spuns a complete (new) cocoon for itself, despite the fact that only the silk cap is removed during eclosion of the previous 'tenant'. Our results indicate that the polymer evolving from the saliva of the adult hornets (as well as the filling material in the comb) is of a low specific heat, just as are various inorganic and mineral materials. The reason for this is perhaps to ensure that the extra heat will pass easily to the silk encasing the pupa, but possibly also to enable the excess heat to convert to a slowly-discharging electric charge. Undoubtedly, the behavior of both the silk and the polymer in the comb is like that of an organic semiconductor (Gutmann et al., 1983), albeit with the following structural difference, to wit: the silk fibers are composed of an inner (core) fibril made up of fibroin proteins that extend longitudinally and an outer coating made up of sericin proteins arranged above and across the inner fibril (Ochiai, 1960; Rudall and Kenchington, 1971; Magoshi, 1979; Proudhome et al., 1985; Michaille et al., 1989; Ayub et al., 1994). We presume that the conduction of an electric charge is performed along the fibroin fibril, while the conduction of water (serving to cool the comb and enhance the relative humidity) is probably relegated to the coat or, else, the space between the core and the coat. Contrariwise, insofar as structure of the comb cell wall, we distinguish here a polymer that serves as a matrix, that is, an amorphous, plastic material to which layers can be accreted or from which layers can be depleted. In fact this is how the comb cell wall is built, that is, strips of material are added until the entire wall is completed, the while lending the comb cells an hexagonal shape in lieu of the rounded shape at the start of building (Ishay et al., 1982). The comb cell wall polymer is also elastic, as witness the fact that a natural comb, maintained in high (relative) humidity, is easily bent without breaking. Within the comb cell matrix are embedded tiny grains-pebbles, that is, particles of an organic and/or inorganic material whose diameter usually does not exceed 100-150μm. The entire structure displays the properties of a capacitor in that we have an insulating material encased within a conductive material. Such a capacitor has a lower specific heat than the vespan silk, but its electric charge is apparently higher than that of silk, and owing to its special construction, discharges no less and for a more extended period of time.

Furthermore, since the comb interconnects walls from all the comb cells, the transport of electric charge can be effected everywhere and from everywhere as needed (i.e., like an electric power plant), whereas the silk is usually exclusive per single cell only, serving primarily the individual needs of each spinning larva undergoing pupation.

In a previous study (Ishay and Ruttner, 1971) we ascertained the high and fixed temperature prevailing in the nest of the hornet *Vespa crabro*. To this end, we removed all the adult population from such a nest, and then measured the inside temperature continuously. We found that even 24 hours later, the nest temperature was still fairly constant and higher than that of the surrounding milieu, and only gradually – over a number of days – the temperature dropped slowly to finally equal the surrounding temperature. It stands to reason that the preponderance of the heat is contributed by the combs (cell walls and silk), in whose walls and silk there is gradual conversion of the stored electric charge into heat. We suspect that the interplay between the comb cell walls and the silk creates within the nest a thermoelectric microclimate-conditioner system. We look forward with anticipation to decoding the structure of the responsible polymers in the two cases.

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