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ORIGINAL PAPER

Gravity orientation in social wasp comb cells (Vespinae) and the possible role of embedded minerals

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Abstract Social wasps and hornets maintain their nest in the dark. The building of the combs by all Vespinae is always in the direction of the gravitational force of Earth, and in each cell's ceiling, at least one 'keystone' is embedded and fastened by saliva. The sensory mechanisms that enable both building of sizeable symmetrical combs and nursing of the brood in the darkness merit investigation, and the aim of the present study was to identify and characterize the 'keystones' that exist in the ceiling and in the walls of the social wasp comb cells. Bio-ferrography was used to isolate magnetic particles on slides. These slides, as well as original cells, were analyzed in an environmental scanning electron microscope by a variety of analytical tools. It was found that both the roof and the walls of each comb cell bear minerals, like ferrites, as well as Ti and Zr. The latter two elements are less abundant in the soil around the nest. Ti and Zr are known to reflect infrared (IR) light. IR imaging showed a thermoregulatory center in the dorsal thorax of the adult Oriental hornet. It is not known yet whether these insects can sense IR light.

Keywords Vespinae · Oriental hornet · Bio-ferrography · Titanium · Zirconium · Hafnium · Infrared

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Introduction

Social wasps and hornets maintain their nest in the dark (Duncan 1939; Guiglia 1971; Wilson 1971; Spradbery 1973; Edwards 1980; Matsuura and Yamane 1990). This is achieved by wrapping the nest in envelopes or by building the nest in a dark place, as beneath the ground. Even when the nest envelope is disrupted, the hornets are quick to repair the damage and restore darkness to the nest (Weyrauch 1935). In fact, repairing the nest envelope seems to be a high-priority task, which raises the question as to why it is so important for them to live in the dark.

Within the hornet's nest, combs are built that contain numerous cells, all of which have their outlets facing precisely in the direction of the gravitational force of Earth (Ishay and Sadeh 1975, 1978). This has long prompted attempts to elucidate the background for such directional building. While building a new cell, the building worker embeds in the ceiling at least one crystal—the so called 'keystone' (Stokroos et al. 2001), fastening it with polymeric saliva (Ganor and Ishay 1992).

In the present study, we investigated nests of *Vespa orientalis*, which are usually subterranean and contain a sizeable amount of minerals, being built mainly of red loam and from other soils in the vicinity of the nest and glued by their own saliva (Ishay 1967).

It is usually accepted that insects are able to respond continuously to deformation of their body and to various forces by proprio-receptors. These receptors provide the organism with information on posture and position (Chapman 1998; Gullan and Cranston 2000).

Over the years, Ishay et al. (1983, 1986) have reported the presence of statocysts and statoliths on the frons plate of hornets and wasps, along with silicon and calcium aggregates, and also the presence of large ciliary patches on the head of these insects, below the cuticle (Ishay et al. 2005a). In the latter instance, some of the cilia were connected to neighboring cilia either by side- or top-links, but many were interconnected by nerve fibers, on which a knob was attached. Earlier, we reported the presence of a new organ behind the frons plate of various species of Vespinae (Ishay et al. 1996). We named this organ 'the Ishay organ'. It consists of nerve fibers that are located in the space extending behind the frons plate and connected to the forebrain. It now seems that: (1) the Ishay organ encompasses the fibers behind the frons plate, the ciliated areas extending throughout the upper front part of the head, and also the statocysts and statoliths present on the frons and antennae; and (2) that the organ is a gravity organ. It should be mentioned that some of the fibers in the Ishay organ also bear knobs, which apparently are very sensitive to spatial acceleration. Hornets usually build combs in the direction of gravity, but when some of the fibers in their Ishay organ are damaged mechanically, the comb-building by such hornets becomes asymmetric and not precisely gravity-directed as before. It appears that the Ishay organ is especially contributory to vespan building in the direction of gravity and is present in all species of Vespinae examined by us (Ishay et al. 1996). For other activities like walking or flying, various proprio-receptors are probably the effective sensory organs.

Many representatives of the Hymenoptera, including Vespinae, have been deemed unable to see red light (Schremmer 1941; Menzel 1971; Beier and Menzel 1972). This has been a dominating opinion for quite a long time (Spradbery 1973; Edwards 1980; Matsuura and Yamane 1990). Recently, however, it was claimed that bees can see red light (Chittka and Waser 1997). This interesting finding now raises the question as to whether other Hymenoptera are also able to see longer wavelengths at the IR region.

Some beetles are known to have receptors for IR light (Schmitz et al. 2000; Evans 2005). As for Hymenoptera, although some species can sense temperature differences (Richerson and Borden 1972; Dyer et al. 2006), no one has yet proven that hornets can see IR light, and it appears that their nests are built in a manner that prevents sunlight from penetrating them. Hence, for hornets to see IR light, an IR source must be available, and there is the need also for IR reception capability. With respect to this possible source, it has already been reported that bees, bumblebees, and hornets are emitting IR light (Stabentheiner 2001; Seeley et al. 2003; Plotkin et al. 2005; Ishay et al. 2006a,b; Nieh et al. 2006).

The aim of the present study was to identify and characterize the 'keystones' that exist in the ceiling and walls of the social wasp cells in an attempt to better understand vespan-sensing mechanism/s. Bio-ferrography (Desjardins et al. 2001; Parkansky et al. 2007) was used to 'capture' the magnetic particles embedded in the cells. This technique is a modified version of conventional ferrography —a method of particle separation on a glass slide based upon the interaction between an external magnetic field and the magnetic moments of the particles suspended in a flow stream (Seifert and Westcott 1972).

Materials and methods

Collection of hornet nests

Nests of *Vespa orientalis* hornets were located in the field during the vespan active season and were ether-anesthetized and transported to the laboratory (Ishay 1964). Samples of hornet cell walls and ceilings were then selected randomly for bio-ferrography and related environmental scanning electron microscopy (ESEM) analyses.

Capturing of magnetic particles by bio-ferrography

The Bio-ferrograph 2100 (Guilfoyle) used in this work is a benchtop laboratory instrument that utilizes a magnetic field that has a maximum field strength across an interpolar gap, where the collection of magnetically susceptible particles occurs. The maximum magnetic field strength across the gap is 1.8 T. However, the gradient of that field is at a maximum at the edges of the gap, thereby concentrating deposition at the gap edges. Ceilings and walls from the same comb were crushed separately in clean glass beakers using non-metallic tools. Suspensions were prepared from each fine powder by adding deionized water. Neither magnetizing agents nor any other chemicals or reagents were added to the suspensions during the capturing process. The suspensions were mixed and then predetermined with equal volumes run through the sterile cassettes of the ferrograph. Several cycles of capturing were carried out to statistically ensure that many representative particles would be captured. At the end of the capturing cycles, the ferrogram (i.e., the slide deposited with magnetic particles) was separated from the cassette by means of a vacuum hold-down unit. After drying, the ferrograms were imaged by means of a digital camera and then inspected under an optical microscope (Olympus model IX 71) with a bichromatic illumination. In this illumination scheme, inverted and reflected illuminations are applied simultaneously. The matter through which light is transmitted can be easily distinguished from the matter that merely reflects light, and this is by their green and red colors, respectively, which result from the use of two different filters. Next, the ferrograms were delivered for characterization by ESEM and by electron-dispersive spectroscopy (EDS). The number of particles captured on the slide by bio-ferrography was higher than in previous publications. However, not all of them were eventually analyzed, and even for those that were analyzed, not all data are included in the present paper.

ESEM analysis

The ferrograms and original cells were investigated in a Quanta 200 FEG-ESEM (Field-Emission Gun Environmental Scanning Electron Microscope) from FEI. The ESEM analysis in the low-vacuum mode included: secondary electrons (SE) and backscattered electrons (BSE) imaging, EDS (Goldstein et al. 1992) and electron backscattered diffraction (EBSD; Randle and Engler 2000). The low-vacuum mode at 50 Pa provided sample analysis without the need for conductive coating, which is required in high-vacuum mode SEM. SE imaging was performed with the large field detector for surface topography, while the solid-state BSE detector was used for identification of particles of relatively high atomic number *Z*. After identification of the high-*Z* particles by BSE imaging, the chemical element analysis of each particle was performed by EDS relative to the background taken from adjacent regions. In addition, X-ray mapping of the constituent elements was performed. The EDS system was nitrogen-cooled (Oxford INCA), with 133-eV resolution. The analysis was carried out with INCA software, taking oxygen by stoichiometry (considering the oxidation state as −2) and normalizing total concentration to 100%. EBSD analysis was done at 70° tilt position of the sample, by means of an HKL Channel 5 detector. The EBSD signal was limited to a few nanometers at each inspection point, while EDS analysis was of sub-micron resolution under the working conditions.

Infrared photography

Hornet workers were imaged using an infrared (IR) digital video camera model Thermovision A20. The image was processed using ThermaCAM Researcher Pro 2.8.

Results

A combined BSE-EDS analysis revealed particles composed of elements of high atomic number, which had been used in the construction of the hornet comb. Inspection of these heavy-element particles at the SE mode, at either zero tilt or high-angle 70° tilt, enabled to reveal the intrinsic nature of these particles, i.e., that they were well embedded in the comb structure, possibly covered by an organic layer, which prevented the detection of EBSD signals from most regions of the particles. The relative percentage of each of the elements in the mineral has been previously presented in detail (Stokroos et al. 2001; Ishay et al. 2005b). In the present study, however, we focused on and sought mainly

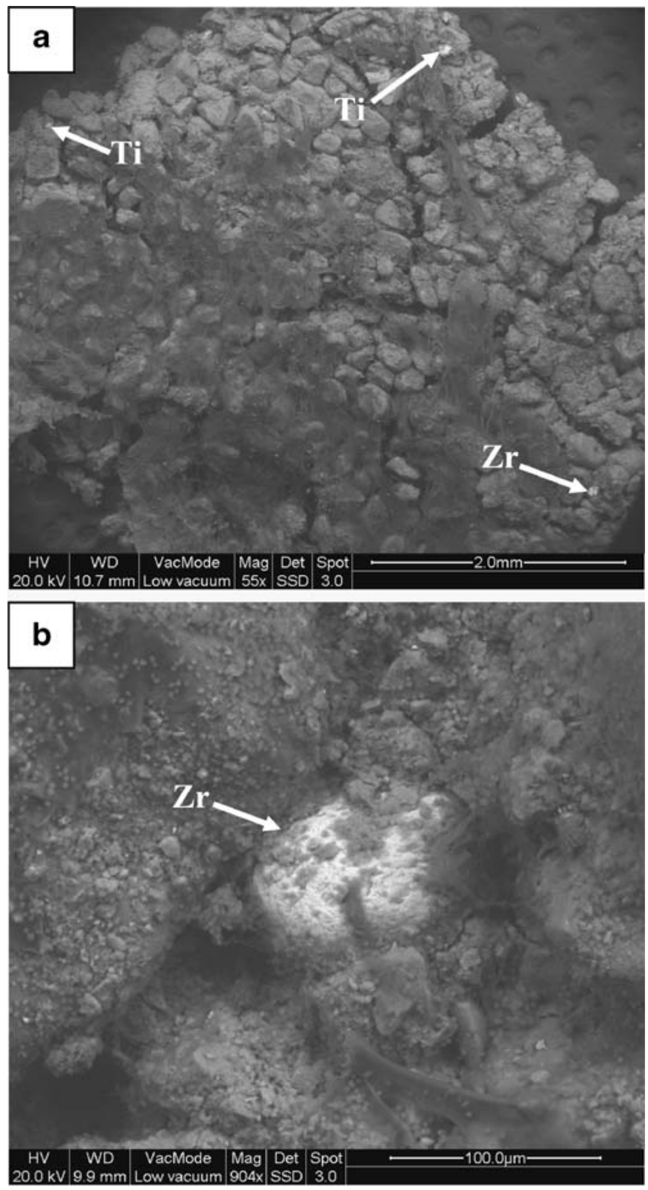

Fig. 1 The presence of particles composed of heavy elements in the Oriental hornet comb. **a** ESEM BSE image of the cell roof demonstrating the presence of two Ti-rich particles and one Zr-rich particle (*bar*=2 mm). **b** ESEM BSE image at higher magnification of the Zr-rich particle from **a** (*bar*=100 μm)

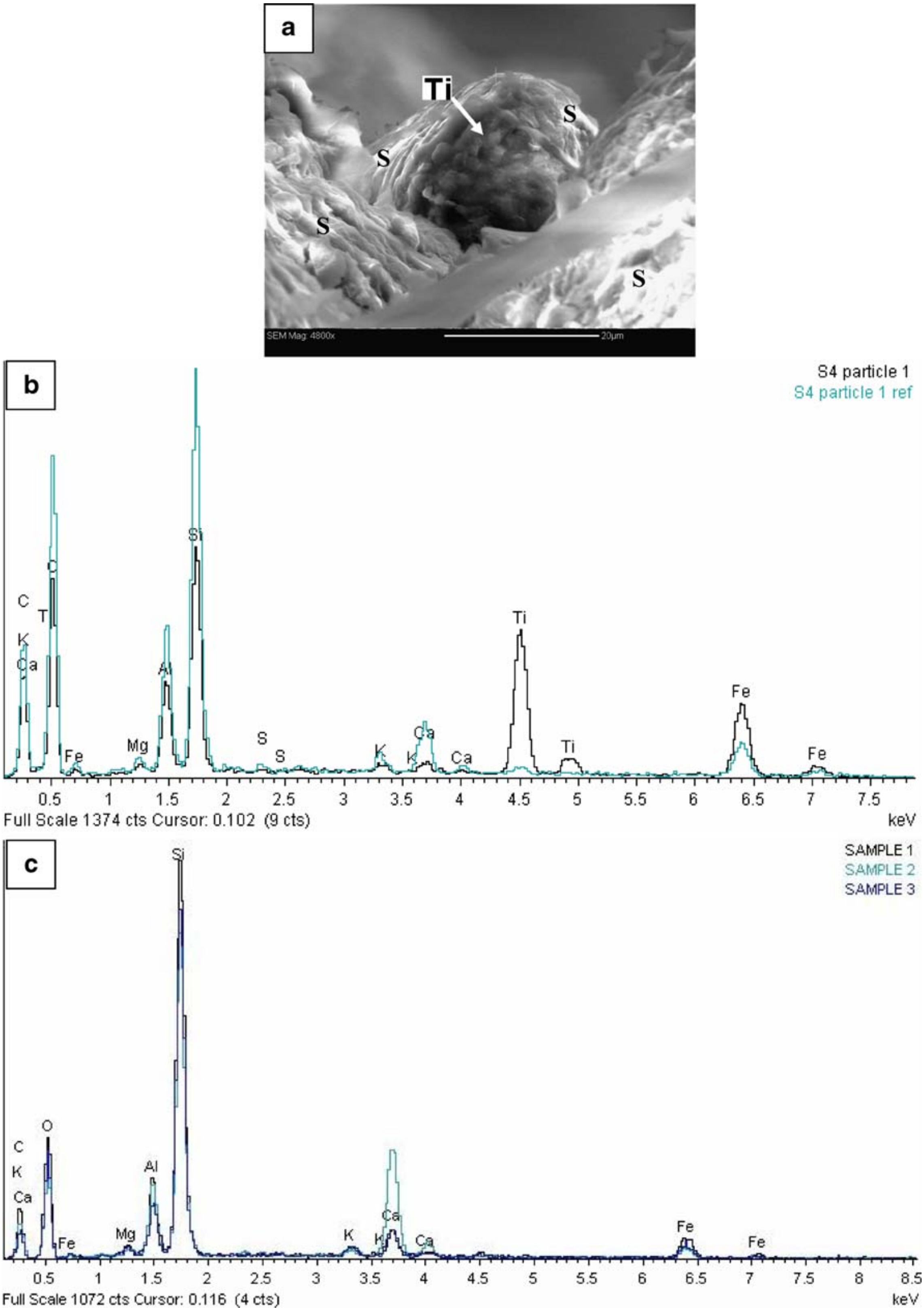

Fig. 2 A titanium particle from the roof of a hornet's comb cell: its composition compared to three soil types surrounding the nest. **a** ESEM SE image of Ti-rich particle (*arrow*) at 70° tilt. "*S*" marks the saliva fibers (*bar*=20 µm). **b** EDS spectra from a Ti-rich particle (sample S4, particle 1; see Table 1, *black line*) and from its surroundings (designated as *ref*, *cyan line*). **c** EDS spectra from three soil types in the vicinity of the nest: Sand (sample 1), Red loam (sample 2), and Garden soil (sample 3). As can be seen, the soil around the nest contains C, K, Ca, Fe, Mg, Al, Si, but not the specific elements that were found glued to the ceilings or walls of the comb cells, like Ti and Zr

ferromagnetic regions, in which the Si constituent is scarcer than the metallic components.

ESEM imaging of original, whole cells revealed keystones with some degree of freedom that were embedded in the ceilings. Mineral particles that contained titanium (Ti) were fastened to the roof by means of a layer of enwrapping saliva gum. Iron-base particles that contained Ti were so fixed to the ceiling as to allow their surfaces containing Ti to protrude from the inner aspect of the cell, facing down into the cell. Titanium and zirconium (Zr), with a spattering of hafnium (Hf), were detected in the center of the dome-shaped cell roof (Fig. 1a). Bio-ferrography revealed that such crystals exist also on the cell walls. At both sites, these two types of mineral crystals were endowed with either luminescence (Ti) or clarity and transparency (Zr; Fig. 1b).

Figure 2 demonstrates certain characteristics of the Ti-rich particles. A Ti crystal (arrow) on a cell ceiling and the EDS spectrum of elements that constitute the particle are shown in Fig. 2a and b, respectively. The analysis (Fig. 2c) of three typical soil types in the vicinity of the nest, namely, (1) sand, (2) red loam, and (3) garden soil, showed, upon analysis (Fig. 2c), high compositional similarity to the soil surrounding the Ti particle (Fig. 2b). Also performed was an EDS analysis of element concentrations in the heavy particles (taken from either the ceilings or the walls) relative to their surrounding, deemed herein as reference regions, and this is shown in Table 1. For such comparison between different particles and material collected from reference regions, four major elements were selected, namely, Fe, Ti (or Zr), Si, and O. Carbon and elements in relatively low concentrations such as K, S, and Ca were not included in the analysis. The particles were composed mainly of Fe, Si, O, and Ti, with traces of Ca, K, Al, and Mg, as can be seen in the EDS spectra, pertaining to the surroundings of the particle (Fig. 2b). From Table 1, one can learn that: (1) Fe is found in the particles, which could account for their magnetic properties; (2) there is some variance in the Ti-to-Fe atomic ratio; (3) in the Ti-rich particles, Ti enhancement is observed toward one of their facets, which suggests that these particles might not be of a single phase; (4) similarity is observed in terms of particle composition for wall particles and particles in comb roof (also after ferrography); and (5) Zr-based particles have low Fe concentrations.

Four samples obtained from the ceiling of four different comb cells (designated as S1, S2, S3, and S4) were assessed in the present study. BSE imaging combined with EDS analysis revealed that two of them (S1 and S2) contained one Zr particle (Fig. 3a), while one of these (S1) was also Ti-rich (Fig. 3b). The presence of the heavy Zr-based particles is evident from the 30-kV EDS spectrum, which shows both the Zr K-line (at 15.75 keV) and the Zr L-line (at 2.04 keV) and also by X-ray mapping (see Fig. 4b), which showed the location of the Zr element and its restriction to the particle region. Another of the four samples (S3, not included in Table 1) contained neither Ti nor Zr (Fig. 3c), whereas sample S4 contained a few Ti-based particles.

After bio-ferrography, minerals originally embedded either in the ceilings or in the walls were analyzed while being separated from their polymeric glue. This investigation established that fixated iron particles were ubiquitous both on the walls and on the ceilings of the comb cells. Figure 4a and c show ferrites isolated from the roof dome by ferrography. X-ray mapping further confirmed the location of Zr (compare Fig. 4a and b). Corresponding EDS analysis showed that mainly three types of particles were embedded in the walls containing different relative amounts of iron and titanium (see "Fe particle," "Ti–Fe," and "Ti particle" in Fig. 4d). Hafnium has been recently proven to have a capability as a catalyst to advance N_2 and C–H activation reaction (Marschner 2007).

Because Ti- and Zr-base surfaces were found not only in the roof domes but also in the walls of the comb cells, we

Table 1 Mineral composition of inspected hornet cell ceilings and walls (at.%)

Sample	Analysis particle	Si	Ti	Fe	O
S4	1	15.5	11.4	9.6	63.5
	ref of 1	28.9	0.7	5.6	64.8
	2	6.5	18.4	12.7	62.4
	3	11.6	20.9	1.2	66.3
S1	1	7.4	18.7	10.9	63.0
	2	4.5	15.2	20.5	59.8
		Si	Zr	Fe	O
S1	3	20.2	12.4	1.1	66.3
	ref of 3	31.7	0.3	2.0	66.0
S2	1	16.6	16.4	0.5	66.5
Wall 1	TiFe particle	14.5	8.7	15.2	61.6
Wall 2	Fe particle	14.0	1.2	27.2	57.6

Sample S3 (obtained from the ceiling) did not contain any crystals.

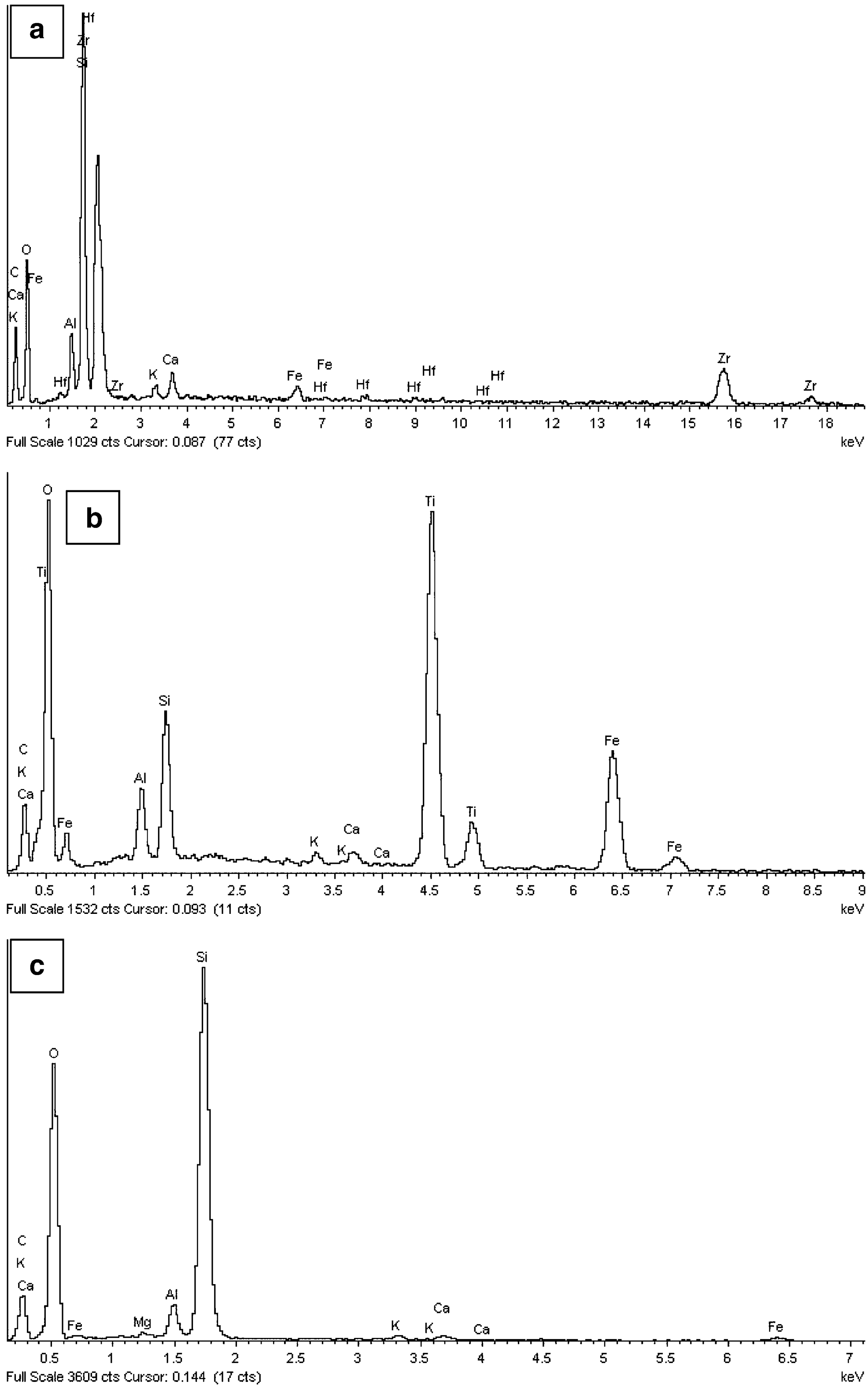

Fig. 3 Typical EDS spectra from particles embedded in the hornet comb. **a** Zr-rich particle. **b** Ti-rich particle. **c** Containing neither Ti nor Zr

wondered whether an IR light source exists inside the nests and whether the minerals possibly have an optical role—that of reflectors. Recently, we have ascertained that in the case of either hornets or bees, there is a region (or site) in the back of the prothorax that produces IR light. This is demonstrated in Fig. 5a. The emitted IR light is not constant even for the same individual hornet; it apparently increases or decreases in accordance with the effort invested in a given activity, such as building (see Fig. 5b) or other activities like brood warming or flying.

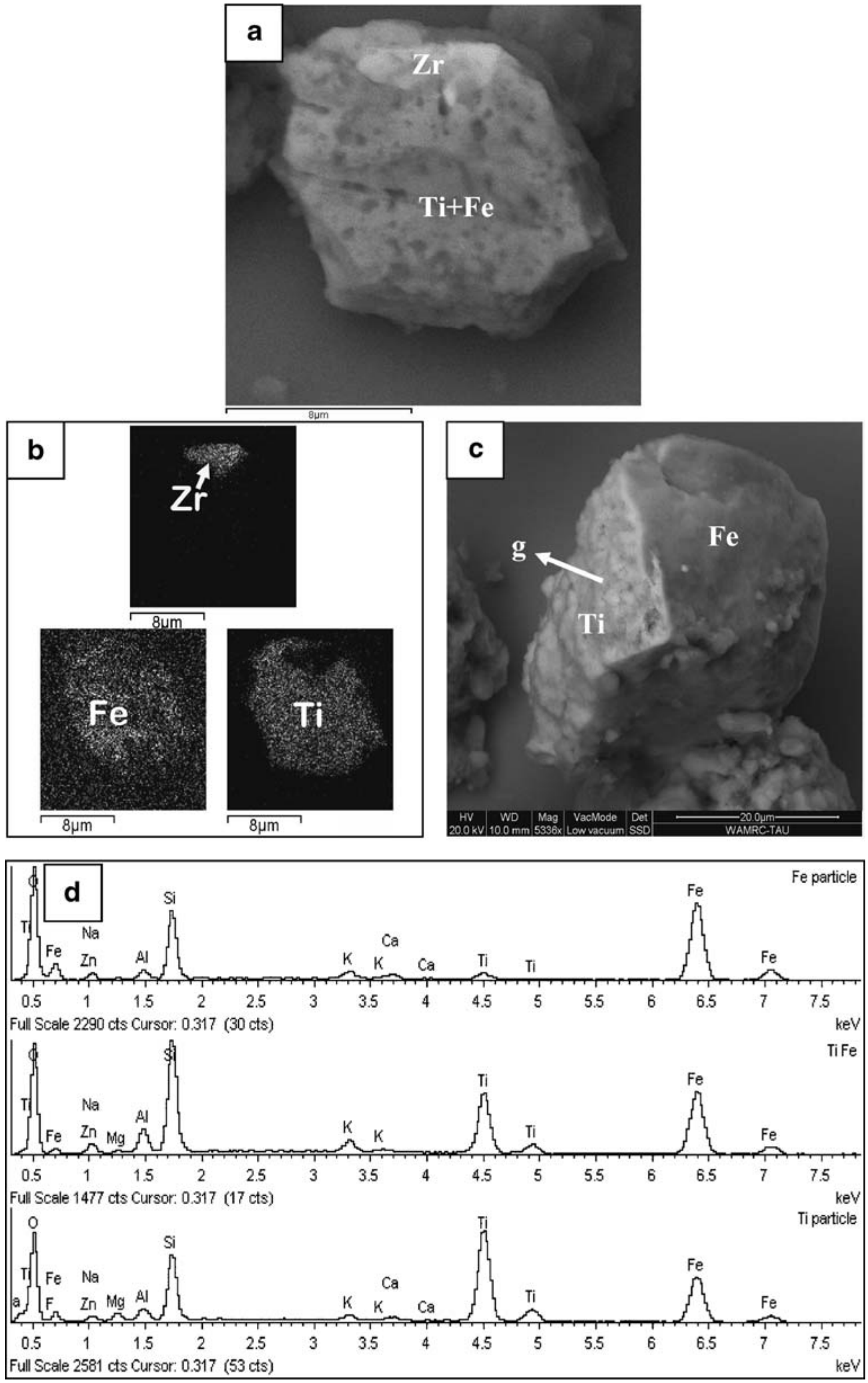

Fig. 4 Particles captured on slide by bio-ferrography. **a** ESEM image zooming-in on a particle on a slide that is rich in Zr in one area and in Ti + Fe in another area (*bar*=8 μm). **b** X-ray mapping of Zr, Ti, and Fe particles (cf. with Fig. 4a). **c** ESEM image zooming-in on another ferrogram bearing an Fe-based particle whose one facet is covered by a thin Ti layer, arrow pointing to gravity direction (*g*; *bar*=20 μm). **d** EDS spectra revealing three types of particles embedded in the walls of the comb. These particles contain different relative amounts of titanium and iron

Discussion

In this study, it was found that both the ceiling and the walls of each comb cell bear minerals, which consist of ferrites and of Ti and Zr. It is not known that any other animals integrate these elements in their surrounding. Such elements were not found in a random sampling of soil around the nest (see Fig. 2c). Traces of Hf were also detected. Ti, Zr, and Hf belong to the same group (IVb) in the periodic table. Titanium belongs to the “minor

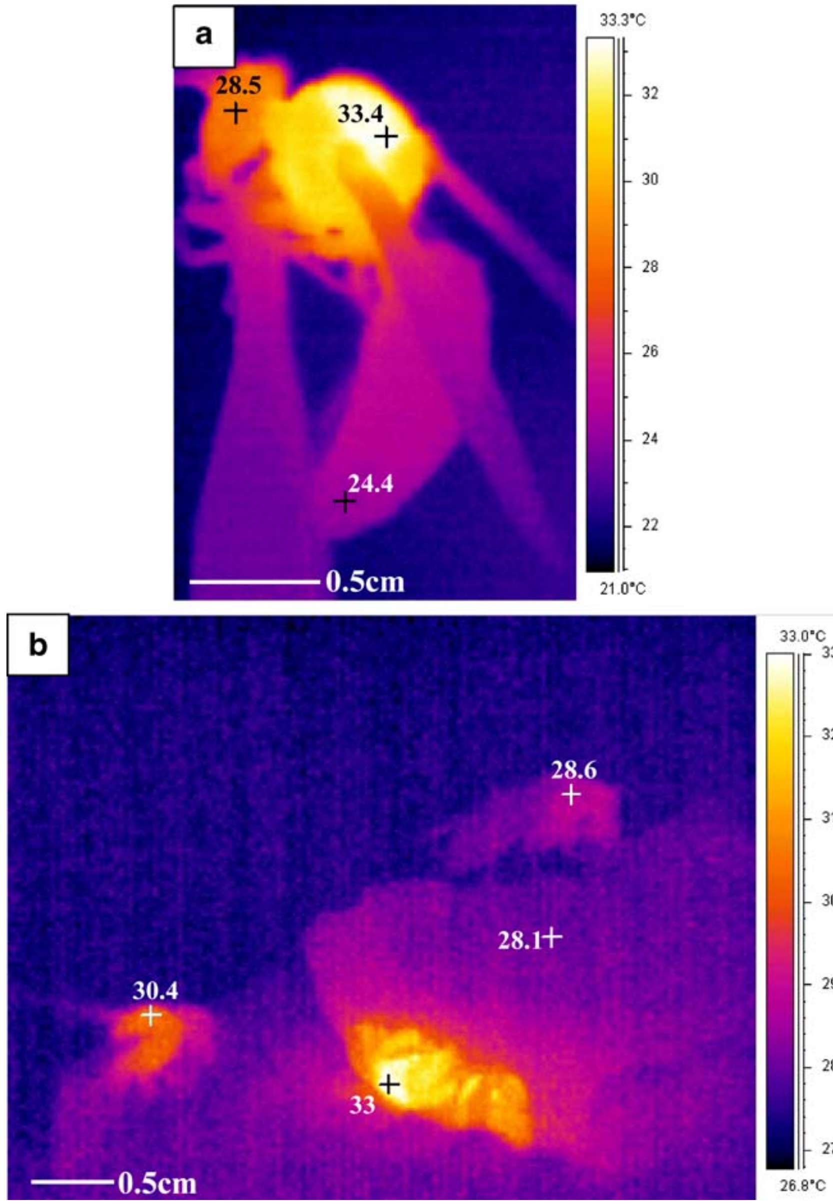

Fig. 5 Infrared images of the Oriental hornet. **a** Infrared image showing a thermoregulatory center in the dorsal thorax of an Oriental hornet. The temperature of the thorax is the highest (33.4°C), whereas those of the head and gaster are lower (28.5 and 24.4°C, respectively; *bar*= 0.5 cm). **b** Infrared image showing the silhouette of a comb with several hornets resting on it. Note that the hot spot in the uppermost hornet shows a temperature of 28.6°C while that of the one on the left is 30.4°C and that of a building hornet in the center is 33°C. The comb temperature is 28.1°C (*bar*= 0.5 cm)

elements," with an abundance of Ti/Si=16:1,000 (atom ratio) in the crust (Flexer 1992). Thus, a possible origin of Ti, Zr, and Hf in the comb should be suggested.

Ilmenite ($FeTiO_3$) is a weakly magnetic mineral found in metamorphic and igneous rocks. Rutile (TiO_2) is another Ti-containing mineral endowed with a tetragonal structure, a density of 4.2–4.3 g/cm^3 and a refractive index of 2.616–2.903 (Schumann 1999). The principal source of Zr is the zirconium silicate mineral, zircon ($ZrSiO_4$), which has a density of 3.93–4.73 g/cm^3 and refractive index of 1.810–2.024 (Schumann 1999). Zirconium and hafnium are contained in zircon at a ratio of about 50:1 and are difficult to separate. It is of interest to mention that the reaction of di hafnocene–N_2 complex with CO_2 leads to a double insertion of CO_2 into the Hf–N bonds to form a N_2–CO_2 core (Bernskoetter et al. 2007; Hustad et al. 2007). This reaction may be important for a multi-member colony that is producing high levels of CO_2. Thus, it seems that Hf is a potential supercatalyst.

Previously, it was suggested that a perovskite phase may be the origin of the titanium-containing particles (Stokroos et al. 2001; Ishay et al. 2005b). Although main emphasis was given to the ilmenite, likewise identified by X-ray diffraction, the $FeSiO_3$ phase was also considered. It should be pointed out that the Ti-rich oxides and titanomagnetites [$Fe^{2+}(Fe^{3+},Ti)_2O_4$] (Tarling and Turner 1991) pertain not only to ilmenite but also to a larger family of $Ti_xFe_{1-x}O_3$ crystals. Additionally, it is possible that different crystals may agglomerate to a single particle.

As shown in Fig. 5, the social wasps possess a warm area in the back of their prothorax, in which an infrared radiation source is identifiable. Interestingly, titanium (and zirconium) oxides have been found to reflect IR light (Pauling 1958). Hence, taking into account the limited abundance of these elements in the Earth's crust on the one hand and their presence both in the ceilings and in the walls of the vespan comb, one could speculate that they are intentionally incorporated in the comb during its construction. As reported in "Results," the minerals are glued by saliva and are oriented in such a way that their Ti-rich zones face the cell interior. IR light reflected from these keystones could possibly aid the hornets in building cells more accurately, and probably faster, if they indeed can sense this light. In this regard, it is important to point out that comb building in the laboratory, i.e., with no ferrites available to the hornet workers, is somewhat slower, and the number of comb cells is lower (Ishay et al. 1995). Infrared sensing could provide information on what transpires inside, either in the comb cells or in the nest cavity. This information would encompass the daily routine activities such as inspection of the comb and larvae and their constant nursing, with the customary food exchange (trophallaxis) between the workers and the larvae (Wheeler 1928; Ishay and Ikan 1968). As the larva develops and grows in size, it might block the nursing worker from seeing some but not all of the reflected light.

A sudden opening of the nest envelope will induce a change in the microclimate of the nest that the hornets are quick to repair: temperature, relative humidity, CO_2 concentration, and probably also other gases and volatile pheromones are all subjected to a change, and beside them a burst of sunlight is introduced providing supersaturating of short and medium wavelengths inside the nest instead of the darkness that prevailed beforehand.

In summary, two issues have been addressed herein concerning wasps and hornets, namely: (1) the difficulty of building in the dark sizeable symmetric combs, whose hexagonal cells are all oriented towards gravity (Ishay and Sadeh 1975) and (2) nursing the brood in the dark, from egg to adult. These two challenges could be resolved with the aid of 'the Ishay organ' or the hornet's proprio-mechanoreceptors. However, we now offer herein a new hypothetical sensing mechanism, utilizing Ti- and Zr-containing ferrites to reflect long-wave IR light emitted by the Oriental hornet. This latter mechanism has yet to be proven, and IR receptors, such as those found in the jewel beetles of the genera Melanophila and Merimna, have yet to be identified in social wasps. In short, one needs to prove that the social wasps indeed sense the IR light reflected from these keystones and use it as a guiding cue during two independent tasks, namely, the construction of cells and brood nursing. The IR vision of wasps could perhaps be ascertained by: (1) behavioral experiments in which any heat convection from the thermal source is carefully excluded or (2) verification of an IR receptor by morphological and physiological investigation. The present study should hopefully trigger ongoing investigations that could ultimately prove conclusively the presence of a sensory mechanism of IR vision in wasps.

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