Biometals (2017) 30:541–548
DOI 10.1007/s10534-017-0024-z

Titanium and iron titanium oxide nanoparticles in antennae of the migratory ant *Pachycondyla marginata*: an alternative magnetic sensor for magnetoreception?

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Received: 26 May 2017 / Accepted: 29 May 2017 / Published online: 12 June 2017

Abstract The most accepted hypothesis of magnetoreception for social insects is the ferromagnetic hypothesis which assumes the presence of magnetic material as a sensor coupled to sensitive structures that transmit the geomagnetic field information to the nervous system. As magnetite is the most common magnetic material observed in living beings, it has been suggested as basic constituent of the magnetoreception system. Antennae and head have been pointed as possible magnetosensor organs in social insects as ants, bees and termites. Samples of three antenna joints: head-scape, scape-pedicel and pedicel-third segment joints were embedded in epoxi resin, ultrathin sectioned and analyzed by transmission electron microscopy. Selected area electron diffraction patterns and X-ray energy dispersive spectroscopy were obtained to identify the nanoparticle compound. Besides iron oxides, for the first time, nanoparticles containing titanium have been identified surrounded by tissue in the antennae of ants. Given their dimension and related magnetic characteristics, these nanoparticles are discussed as being part of the magnetosensor system.

Electronic supplementary material The online version of this article (doi:10.1007/s10534-017-0024-z) contains supplementary material, which is available to authorized users.

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Keywords Magnetic nanoparticles · Magnetosensor · Social insects · Electron microscopy

Introduction

Magnetoreception is the ability to sense the magnetic field of the Earth and use it as a cue for orientation. Although several behavioral experiments suggested that many animals use the magnetic field as a source for guiding movements over long and short distances (Wiltschko and Wiltschko 1995; Lohmann et al. 2007), the mechanisms and structures underlying the process of acquisition, transduction and transference of this information to the nervous system remain unclear. Currently there are three main hypotheses of magnetic field perception, based on electromagnetic induction, biogenic magnetite and chemical reactions modulated by weak magnetic fields. The most accepted hypothesis of magnetoreception for social insects, including ants, is the ferromagnetic hypothesis (Wajnberg et al. 2010) which assumes the presence of magnetic material as a magnetic sensor coupled to sensitive structures that transmit the geomagnetic field information to the nervous system (Kirschvink and Gould 1981; Davila et al. 2003; Winklhofer and Kirschvink 2010).

Behavioural studies with social insects such as bees and ants have shown orientational and navigational responses to the geomagnetic field, and a magnetoreceptor system based on magnetite nanoparticles has been proposed (Riveros and Srygley 2008; Válková and Vácha 2012). In particular, it was suggested that the *Pachycondyla marginata* migratory ant may use the geomagnetic field as an orientation cue for the significantly oriented migrations in the dry/cold season (Acosta-Avalos et al. 2001).

In *P. marginata* and *Solenopsis interrupta* ants, and *S. quadripunctata* bees (Wajnberg et al. 2004; Lucano et al. 2006; Abraçado et al. 2009), consistent observations of the highest amount of magnetic material in the head and antennae, that are free of recently ingested material, have indicated them as magnetic sensor organs. Although ingested material passes through the insect mouth the amount of ingested material in the head would be negligible, and there should be none of it inside the antenna. As antenna is a tactile, olfactory and gravity sensor, it is also an interesting candidate for a magnetic sensor organ (Wajnberg et al. 2010).

As magnetite is the most common magnetic material observed in living beings, the majority of studies focus only on it as the possible magnetoreceptor sensor. Transmission Electron Microscopy (TEM) investigation of magnetically extracted materials from *P. marginata* head with antennae, thorax and abdomen has identified magnetite and/or maghemite particles (Acosta-Avalos et al. 1999). While the size distribution of particles in the abdomen corresponded to a single distribution, there was a bimodal splitting of distribution in thorax and head, suggesting the existence of two size populations of nanoparticles with iron and oxygen. The mean values for length and width of the particles were however, approximately the same in the three body segments (Acosta-Avalos et al. 1999). Magnetic measurements performed on different regions of this migratory ant showed that the strongest magnetic signal comes from the antennae suggesting that they might contain magnetic sensor organ or organs (Wajnberg et al. 2004). More recently pure Fe/O particles were found together with Al/Si/O particles, with the latter forming the major part in magnetic extracts of *P. marginata* body parts (Oliveira et al. 2010). TEM measurements of ultrathin sections were made in the third segment-pedicel, pedicel-scape and scape-head joints of the antennae. Nanoparticles of magnetite/maghaemite (Fe_3O_4/γ-Fe_2O_3), haematite (α-Fe_2O_3), goethite (α-FeOOH), besides (alumo)silicates and Fe/Ti/O compounds were identified within the tissues. As the particles were observed within the tissue, they do not represent contamination. It was proposed that ants incorporate particles from the soil and they act as magnetic sensor being able to detect the geomagnetic field (Oliveira et al. 2010).

In this paper, ultrathin slices of those three joints of the antenna of *P. marginata* were analyzed by TEM, to identify the Fe/Ti/O compounds as another magnetic sensor candidate.

Materials and methods

Pachycondyla marginata (Roger) ants were collected in the Santa Genebra Forest, Campinas, São Paulo, Brazil.

TEM

Magnetic contaminants are frequently present within laboratory environment where magnetic nanoparticles are produced. However, the analyzed samples of the antennae were prepared in biophysical laboratories in which this contamination is unlikely. Even so, care was taken to avoid it using only stainless or ceramic and other nonmagnetic tools.

TEM analysis of ultrathin sections, ant collection and sample preparation were as in Oliveira et al. 2010. Before ultrathin sectioning, the flagellum was aligned with the scape providing only one serial cutting direction, through the whole antenna. They were sequentially examined by TEM. Selected area electron diffraction (SAED) patterns and bright field images were obtained at 200 kV with a Jeol 2000 FX equipped with an EDAX Genesis system for X-ray energy dispersive spectroscopy (EDX).

SAED patterns were used to calculate the crystal planes from crystalline particles. Miller indices indexed in the electron diffraction patterns were used to describe the orientation (particular directions [hkl], particular planes (hkl), general plane {hkl} or diffracting plane hkl) of crystallites relative to the electron beam (Williams and Carter 2009).

Results

A crystalline region (black arrow) close to a sensorial sensilla (white arrow) composed of Ti, Fe and O was observed in a very well preserved ultrathin section of the scape-pedicel (Fig. 1a). This structure was present in eight subsequent ultrathin sections. Ti (8.5%) and Fe (12%) atomic fractions were obtained from EDX (Fig. 1b). SAED (Fig. 1c) identified 0.27, 0.22 and 0.18 nm planes that can be associated to different Fe/Ti oxides.

In the scape-pedicel joint, in the scape region, another crystalline particle was observed surrounded by tissue (Fig. 2a–c). Close to the particle, a cell-like biological structure (bottom in Fig. 2c) was observed continuously over approximately 35 μm in serial ultrathin sections. The Ti and Fe atomic fractions were similar, as shown in Fig. 2d. Selected area electron diffraction from the 500 nm crystallite (Fig. 2e) indicates a single crystal pattern and revealed plane distances of d = 0.38 and 0.27 nm that suggests an ilmenite crystal.

More crystalline materials were identified in ultrahin sections from the head-scape junction. Electron-dense regions of approximately 12 μm diameter were observed surrounded by cuticule (k) (Fig. 3a) and biological tissue (Fig. 3a, black arrow). Plate-like crystallites (Fig. 3a, dashed square) were observed and analyzed by EDX and SAED. Detailed images of these plate-like particles are shown in Fig. 3b. The diamond knife probably caused fractures and loss of crystalline material during ultramicrotomy. The crystallites in this section present about 1 × 0.5 μm (length × width). EDX from 16 individual plate crystals were performed showing similar atomic fractions of Ti and Fe of 18 ± 3%. As an example, the EDX of the crystal indicated by a white arrow in Fig. 3c is shown in Fig. 3d. Oxygen is also observed in these crystals and most of them reveal a minor fraction of Mn, Si and Al. The interplanar distances of 12 of these plate-like crystals were determined from SAED patterns and compared to ilmenite, pseudobrookite, pseudorutile and ulvospinel data. The SAED (Fig. 3d) from the crystal indicated by a white arrow (Fig. 3b) is typical of a single crystal with interplanar distances of d = 0.45, 0.20 and 0.18 nm (open circles in the SAED). Ulvospinel can be discarded because the expected Mn peak is not present in the corresponding

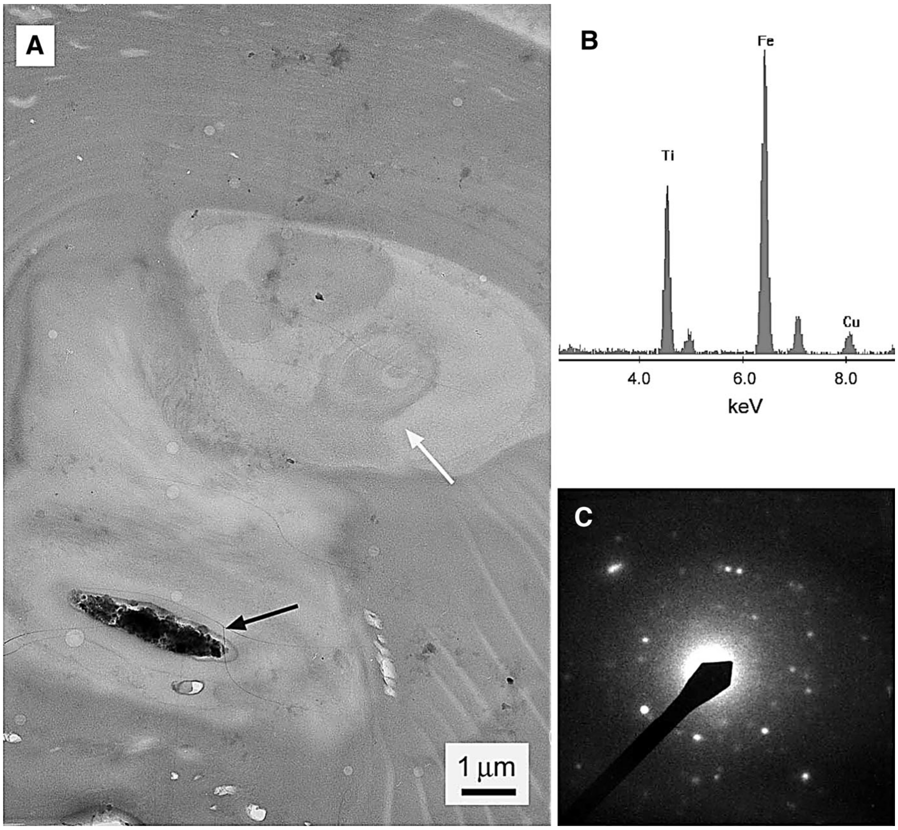

Fig. 1 **A** TEM of an ultrathin section of the scape-pedicel connection, *black arrow* points to crystalline region close to a sensorial sensilla indicated by *white arrow*, **B**, **C** EDX and SAED, respectively of the particles indicated by *black arrow* in (**A**)

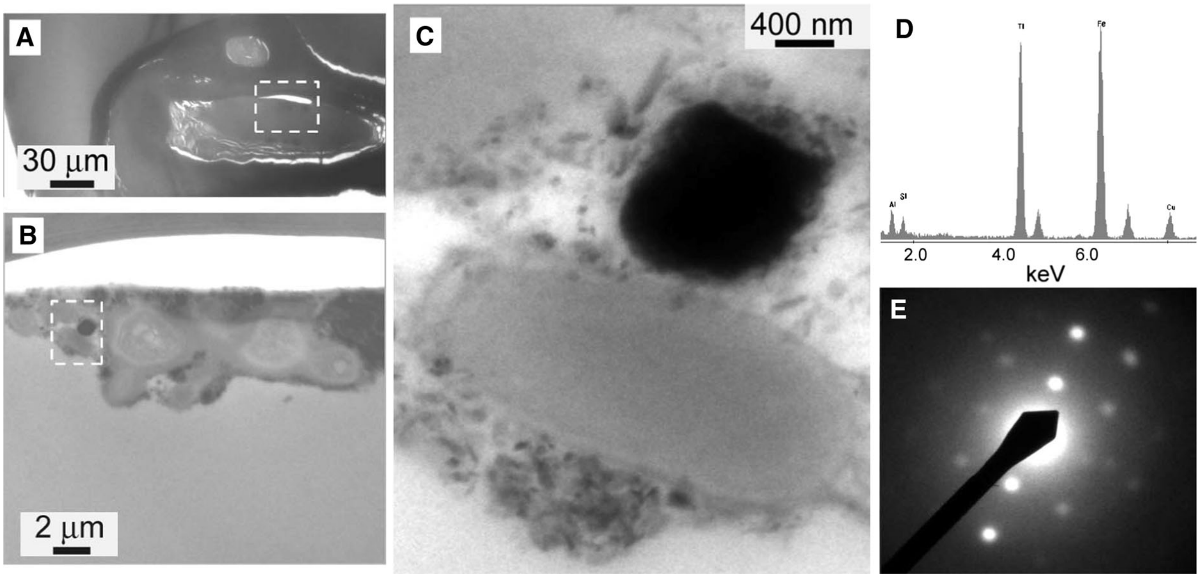

Fig. 2 **A** Low magnification TEM of an ultrathin section of the scape region. **B** Higher magnification image of the region inside the *dashed square* in (**A**) showing a biological structure inside the scape. The *dashed square* shows a Fe/Ti/O crystal close to a cell-like structure. **C** Higher magnification of the *dashed square* in (**B**) showing the nanoparticle and the cell-like structure, **D**, **E** EDX and SAED, respectively, of the Fe/Ti/O crystal

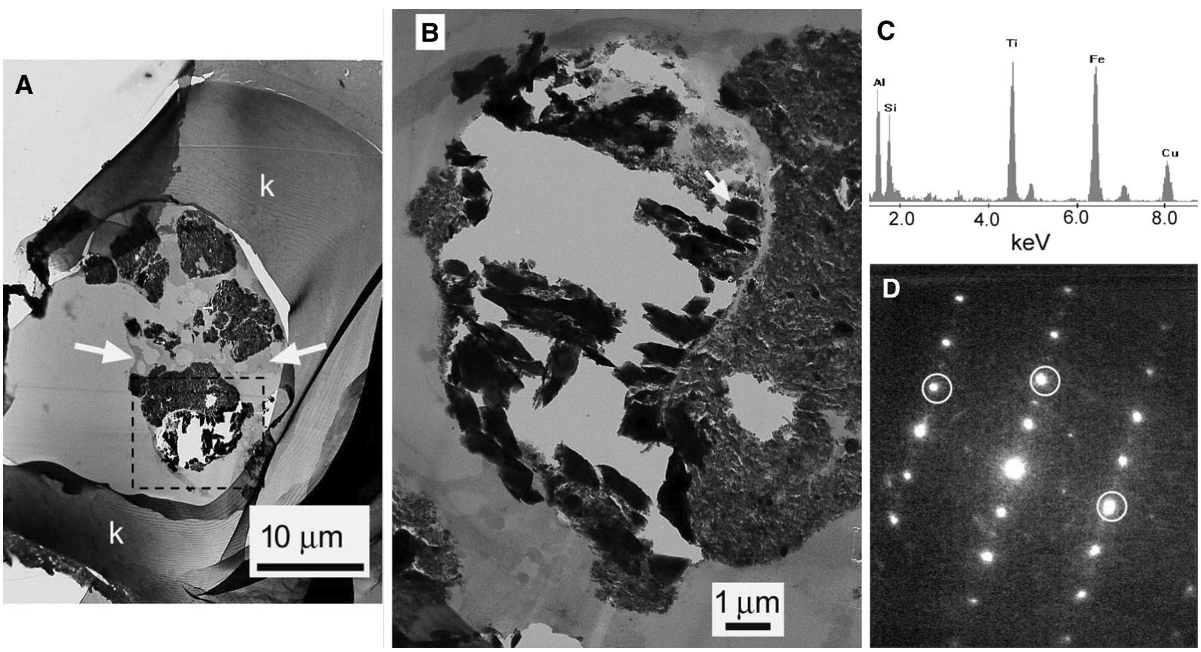

Fig. 3 **A** TEM of an ultrathin section of the head-scape connection. *Dashed square* indicates a region of plate crystals surrounded by biological material (*white arrow*) and the presence of cuticule (k); **B** amplified image of this structure, inside the *dashed region* **C**, **D** EDX and SAED, respectively, of the crystal indicated by an *arrow*. *Open circles* in the SAED correspond to 0.45, 0.20 and 0.18 nm interplanar distances

EDX spectrum (Fig. 3c). Distances and angles between planes obtained from the diffraction pattern were in accordance with ilmenite crystal and were indexed in the [871] zone axis. Interplanar distances of 0.45, 0.20 and 0.18 nm correspond to {-111}, {0-17} and {10-8} from ilmenite, respectively. Interplanar distances of three other crystals could be associated to pseudorutile. The diffraction patterns of the other plate-like particles could be associated to pseudobrookite, pseudorutile or landauite.

More Fe/Ti/O particles were observed in two other ultrathin sections of the head-scape junction from where biological tissue could be observed in one of them (Figure SI in Online Resource ESM1.pdf, black arrow). Figures SI and SII (in Online Resource ESM1.pdf) show TEM images of crystals observed in these sections that are of similar composition and size (~1 μm) than those in Fig. 3. EDX and SAED, (Figure SI in Online Resource ESM1.pdf) showed Ti/Fe/O and Ti/O particles. In a third ultrathin section of head-scape junction, in the scape region, a Ti/O single crystal of ~60 nm was observed (Figure SIII in Online Resource ESM1.pdf). Anatase, one of the mineral forms of TiO_2, is suggested as the constituent.

In the pedicel-third segment joint crystalline regions containing Fe/Ti/O particles were also observed from EDX. Data are condensed in Table 1 that shows atomic fractions, interplanar distances and the probable compound from Figs. 1, 2, 3 and SI–SIII (Online Resource ESM1.pdf).

Discussion

This paper investigates the magnetic particles in the antennae of the *P. marginata* ant that might be part of a magnetoreceptor system. Despite the increasing interest in the subject in the last decades, the magnetoreceptor identification, localization, the signal transduction and neural response are still an open question.

Numerous difficulties arise when attempts are made to find deposits of magnetic material in insects. To find small amounts of nanoparticles inside a large volume of cells and tissues is a challenge. During TEM sample preparations the resin does not completely penetrate the cuticle of the ants and it was difficult to obtain complete slices from each of the three joints of the antenna that we studied. In some slices there was no evidence of tissue, in others the cuticle was visible but internal tissue could not be clearly identified. However after exhaustive preparations and analyses crystalline nanoparticles were identified inside intact tissue. Care was taken to minimized contamination by chemicals reagents and manipulation tools. Extensive rinsing under ultrasound vibration were performed to reduce

Table 1 Parameters obtained from EDX, Ti and Fe atomic fractions, and from SAED, interplanar distance d, and most probable compounds of particles observed in ultrathin sections of the head-scape, scape-pedicel and pedicel-3rd junctions

Figure	Antenna junction/part	Ti atomic %	Fe atomic %	D (nm)	Probable compound
1	Scape-pedicel	8.5	12	0.27, 0.22, 0.18	Fe/Ti oxides
2	Scape			0.38, 0.27	Ilmenite
3	Head-scape	16	14	0.45, 0.20, 0.18	Ilmenite
SI	Head-scape	17	13	0,28, 0.26, 0.16	Ilmenite or pseudobrookite or pseudorutile
		13	14	0.37	
		1.3	32	0.24, 0.22	Titanomagnetite or iron oxide
SII	Head-scape	11	1.1	–	Ti/O
		16	17	–	–
		9	14	0.28, 0.17	Pseudorutile
SIII	Head-scape			0.37	Anatase
—	Pedicel-3rd segment	8.5	7.3		
		23	1.7		
		0.3	9.3		

(Figures SI–SIII in Online Resource ESM1.pdf) soil magnetic particles externally adhered to the ant body.

Although magnetic particles used for magnetoreception are likely to be biologically produced, an organism might ingest or incorporate the precursors that comprise more complex, biogenic magnetic particles or they might ingest other organisms that possess the precursors or even more complex mineral/protein complexes. Particles composed of Fe/O, Si/Al/O, Ti/O and Fe/Ti/O, were previously identified in antenna extracts of *P. marginata ant* by TEM. As soil contaminants as Fe/O, Si/Al/O, Ti/O and Fe/Ti/O can be present in magnetic extracts of animal tissues, the biological relevance of magnetic crystals can only be considered by observation in ultrathin sections within well-preserved embedded tissue. Different iron oxides nanoparticles were observed in the tissue of three junctions of antennae of *P. marginata* ant by TEM, which were suggested to be incorporated from the soil and as a good magnetic sensor candidate (Oliveira et al. 2010).

Incorporation from the soil is supported by the behavioral and Ferromagnetic Resonance (FMR) experiments which showed that another ant species, *Atta colombica* requires contact with soil to incorporate magnetic particles that can be used as a magnetic compass; though, it was also shown that they can biosynthesize magnetic particles (Riveros et al. 2014). The presence of magnetite/maghemite as the magnetic sensor is widely suggested in animals (Wiltschko and Wiltschko 1995) and, in particular, in social insects (Hsu et al. 2007; Jandacka et al. 2015) based in the ferromagnetic hypothesis, originated on the observation of this oxide in bacteria, yet other magnetic oxides can play this role. Hematite, in an ellipsoid arrangement, was shown to be sensitive enough for detecting the geomagnetic field, so it was suggested as another magnetosensor candidate (Oliveira et al. 2010). This study takes a step further in the subject by looking at Ti containing particles in three antennae junctions as another magnetosensor candidate.

The use of a magnetoscope coupled to a single-cell correlative light and electron microscopy has been applied to study magnetic cells from various tissues of pigeon and trout. These methods revealed that a small percentage of cells appear to have large magnetic moments with the presence of extracellular structures composed of iron, titanium, and chromium accounting for their magnetic properties (Edelman et al. 2015). These particles were considered, by the authors, as contaminants primarily due to their extracellular location and properties that differed from those expected for biogenic magnetite. Nevertheless, other cells with lower magnetic moments than those analyzed, could be present as a magnetite-based receptor.

The present work is the first observation of intracellular Titanium and Iron Titanium oxides in antenna tissues of this migratory ant. We are not aware of any report of these materials in any other animal, but it was shown that the fungi *Fusarium oxysporum* is able to synthesize extra cellular Titanium oxide crystals by stimulating it with TiS_6 solution at room temperature (Bansal et al. 2005).

In the plate region of the head-scape junction (Fig. 3), the diffraction pattern of some of the Iron Titanium oxide crystals observed indicates different oxide phases as ilmenite, pseudobrookite and pseudorutile. For other crystals the Fe and Ti atomic fractions, obtained from the EDX, do not fit the expected Ti/Fe ratio of known compounds. Some others cannot even be addressed to a known material as the d-spacing (not shown) are not listed in any Iron Titanium oxide tables. These controversial data suggest that this region can contain a superposition of different Iron Titanium oxide crystals or of Fe oxide and Ti oxide crystals. Titanium oxide and Iron Titanium oxide nanoparticles could have a magnetic property due to their dimension, as discussed bellow.

Natural TiO_2 bulk particles are known as diamagnetic, and could not act as a magnetic sensor, however remarkable room-temperature ferromagnetism was observed in TiO_2 200 nm-thick films (Hong et al. 2006). Rutile cluster films revealed a size dependence of the magnetization for average sizes from about 15 to 40 nm (Wei et al. 2009). It was recently shown that synthesized reduced rutile nanoparticles ($TiO_{2-\delta}$), 10–50 nm, exhibit room-temperature ferromagnetism (Parras et al. 2013). Similarly, nanosized ilmenite (approximately 20–60 nm) exhibits a very weak ferromagnetism (Chen 2011), a magnetic behavior different from the bulk ilmenite (antiferromagnetism). Furthermore, solid solutions of ilmenite-hematite series, $xFeTiO_3(1-x)FeO_3$ are ferromagnetic for $x > 0.55$, ilmenite rich (Nagata and Akimoto 1956).

The presence of Ti was observed previously in extract of the ant body parts, but the crystal phase was not addressed as the diffraction pattern was not attainable. The first and unique observation of Ti in living beings was reported three decades ago, in grains isolated from magnetococcoid bacterial cells (Towe and Moench 1981). Electron microprobe analysis showed the magnetite to be slightly titanoferrous. The possibility that the Ti could be a clay contamination was discarded. Based on this result Ti or other trace element was suggested to be present in the magnetite nanoparticles of bee abdomens, to explain the shift of the Verwey transition temperature (T_v), that characterizes this material to lower values, observed through the line shape and intensity changes of the FMR spectra (El-Jaick et al. 2001). A similar change in the FMR parameters of *P. marginata* ant abdomens and a T_v shift were also observed (Wajnberg et al. 2000).

While magnetite is well accepted as magnetosensor because of its strong ferrimagnetism and wide spread occurrence among living beings, Iron Titanium oxide and Ti oxide particles were never considered except for the observation of bacterial magnetite with low concentration of Ti as Iron substitute (Towe and Moench 1981). As Titanium oxide and/or Iron Titanium oxide nanoparticle systems, observed in the antenna tissue of the *P. marginata* ant, can present ferromagnetic properties, we might hypothesize that they are part of a magnetic sensor system, as well as also be part of a gravimetric system or any other sensor system in which the antenna plays a role.

This paper points to new magnetic materials, besides magnetite or other iron oxides, as potential magnetosensors in ants under the ferromagnetic hypothesis. It stimulate more investigation of the magnetic properties of these Titanium and Iron Titanium oxides crystals, whether biomineralized or soil incorporated, and of their role in the magnetoreception mechanism.

Acknowledgements We thank Dr S. Weinkauf, Dr M. Hanzlik and Dr Jandira Ferreira de Oliveira for the support in the SAED patterns and bright field images in the Jeol 2000 FX equipped with an EDAX Genesis system in the F. G. Elektronenmikroskopie of the Technische Universitat Munchen, Garching, Germany.

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