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RESEARCH ARTICLE

Organic linings in nests of the fire ants *Solenopsis electra* Forel and *Solenopsis* nr. *macdonaghi* Santschi from Argentina

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Abstract Although fire ants have been extensively studied, not much has been published about the structure and building material of their nests and even less on the lining of chamber walls. Nests built in unconsolidated sandy soils of *Solenopsis electra* and *Solenopsis* nr. *macdonaghi*, studied in La Pampa and Chubut (Argentina), respectively, show organic linings, which are reported herein for the first time. It is hypothesized that these organic linings may be of fecal origin, since there is no organic rich horizon in those soils. Apart from its significance as regards ant architecture and nest function, the presence of organic linings in ant nests is important for interpreting fossil nests, which have been often assigned to termites based on the presence of organic linings.

Keywords Fire ants · Nests · Sandy soils · Organic linings · Fossil nests

Introduction

Not much is known on the use of organic matter as building and lining material by ants nesting in soils, which, in contrast, is extensively used by the other main group of eusocial soil nesting insects: the termites (Noirot, 1970; Grassé, 1984; Genise, 1997; Cosarinsky, 2006). On the other hand, inorganic linings have been recorded in soil nests of different ants (Bruch, 1916; Déjean and Lachaud, 1994; Wang et al., 1995; Green et al., 1999; Halfen and Hasiotis, 2010; Cosarinsky and Roces, 2011).

Despite being one of the most recognized ants, not much has been published on fire ant nests (Tschinkel, 2003, 2006), and even less on their wall linings. Green et al. (1999) found no organic linings in nests of *Solenopsis invicta* and *Solenopsis richteri* Forel in the USA, but an inorganic one produced by illuviation. Cosarinsky (2006) found no organic lining in nests of species of *Solenopsis* sp. from Entre Ríos (Argentina). Similarly, one of us (FC) checked several nests of *Solenopsis saevissima* (Smith) from Tucumán (Argentina) for organic linings with negative results.

However, we will show herein that at least some species of this genus, namely *Solenopsis electra* Forel and *Solenopsis* near *macdonaghi* Santschi, nesting in single grained sandy soils from La Pampa and Chubut (Argentina), respectively, line the walls with organic matter, probably of fecal origin. Both species belong to the "fire ant" group or "*Solenopsis saevissima* species group" (Pitts et al., 2005), which includes only mound-building species, in contrast to the "thief ants" group of *Solenopsis*. The latter are characterized by the formation of small colonies, frequently displaying a lestobiotic lifestyle, occupying the nest walls of other ants.

Materials and methods

Ant's identification were made by comparison with specimens previously identified and deposited in the Kusnezov's

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Collection, Instituto-Fundación Miguel Lillo, Tucumán (IFML), Argentina and following keys and characters proposed by Trager (1991) and Pitts et al. (2005). Voucher specimens of identified ants for this study were deposited also in the Instituto-Fundación Miguel Lillo: *S. electra* (IFML#12655), *S.* nr. *macdonaghi* (IFML#12656), and *S. saevissima* (IFML#12657).

Thin sections of nests were prepared using blue epoxy resin to easily recognize the porosity. They were observed and photographed with a petrographic microscope Nikon Optiphot using plane polarised light (PPL) and cross polarised light (XPL). Nomenclature for micromorphological descriptions was taken from the Handbook of Soil Thin Section description by Bullock et al. (1985).

Results

Solenopsis electra nests

Two nests of *S. electra*, one abandoned and one active, were the only ones found at Gran Salitral, La Pampa province, Argentina (37°24′31″S, 67°12′54″W). This locality is dominated by dunes and interdunes, showing mostly bare sandy soils with sparse halophyte shrubs, surrounding a saline depression (Fig. 1a). The active nest was located beside a dune, close to the saline depression. It was composed of a conical mound 30 cm high and 35 cm in diameter (Fig. 1b), which continued below surface with a cylindrical area 30 cm deep (Fig. 1c). Both the mound and the hypogeous part of the nest were composed of an alveolar structure of interconnected, horizontal to inclined chambers, about 0.5 cm high, which most noticeable feature was a dark lining contrasting with the light soil matrix (Fig. 1d).

Thin sections of the mound showed mainly a single grained microstructure and a subordinate bridged grain microstructure, the latter due to the presence of grains coated with dark fine matter (25–30 %). High porosity (30 %) is represented by equant to elongated voids, single or interconnected among grains. The coarse fraction is composed of single mineral grains and some rock fragments moderately sorted (50–500 μm), mostly ranging from silt to very fine sand. The coarse fraction is composed mostly of lithic fragments of volcanic and sedimentary rocks, whereas twining plagioclase and volcanic glass shards are less common, and quartz, altered feldspar and heavy minerals are scarce. The fine fraction, only represented by grain coatings, had no clay minerals. The lining of walls is composed mainly by grains coated with a dark fine matter (Fig. 1e), which observed with XPL is opaque, crossed by abundant fungus hyphae, and consequently organic in origin (Fig. 1f). Coated grains are also included in the matrix. The organic matter produced in several cases bridges among grains. Beneath the organic lining, there is a layer, 0.5–1 mm thick, showing less porosity than the matrix.

Solenopsis near *macdonaghi* nests

Two nests of *S.* nr. *macdonaghi*, 25–30 cm wide and 20–40 cm high, were studied in the Punta Peligro area at southern Chubut Province (45°30′34″S, 67°13′02″W). This is the southernmost record of *S.* nr. *macdonaghi* known and reported herein for the first time. The study site is characterized by fluvial and aeolian sandy deposits, and shrubby vegetation. Two excavated nests, ellipsoid-shaped, were active, and occurred in sandy soils deprived of an organic horizon (Fig. 2a). As in the nests of *S. electra*, the internal architecture of the hypogeous part was alveolar, with chambers about 0.5 cm high and 0.5–1 cm long. Chambers show a preferential horizontal elongation and tiered arrangement (Fig. 2a–c).

Thin sections show mainly a single grained microstructure and a subordinate bridged grain microstructure, the latter due to the presence of grains coated with dark fine matter (10 %). High porosity (30 %) is represented by single packing voids, symmetric to elongated, interconnected among grains. The coarse fraction is composed of single mineral grains and poorly sorted rock fragments (50–1000 μm), mostly ranging from medium to coarse sand. The coarse fraction is mostly composed of twining and zoned plagioclase and lithic fragments of volcanic, granitic, and sedimentary rocks, whereas quartz, altered feldspar, volcanic glass shards, and heavy minerals are scarce. The fine fraction, only represented by grain coatings, has no clay minerals. The lining of walls is composed mainly by a layer of dark fine matter (Fig. 2d), which observed with XPL is opaque, crossed by abundant fungus hyphae, and consequently organic in origin. This organic lining coats grains included in the matrix (Fig. 2f), in many cases producing bridges among them (Fig. 2e). Some galleries, which preserve old linings, are filled with more oriented, packed, and sorted (about 150 μm) grains than the matrix (Fig. 2f).

Discussion

The use of organic material as lining material in ant nests in soils is poorly known and most recorded cases correspond to mound building species. Cowan et al. (1985) found a dark, “macerated fine organic matter (leaves, rootlets)” coating the walls of galleries in the mound of *Camponotus intrepidus* (Kirby) (Formicinae) nests. In addition, they observed that coarse organic debris (leaves, twigs, charcoal) were used as a thatch to protect the mound against rainsplash erosion. Mounds of *Iridomyrmex purpureus* (F. Smith) (Dolichoderinae) were also covered with coarse organic

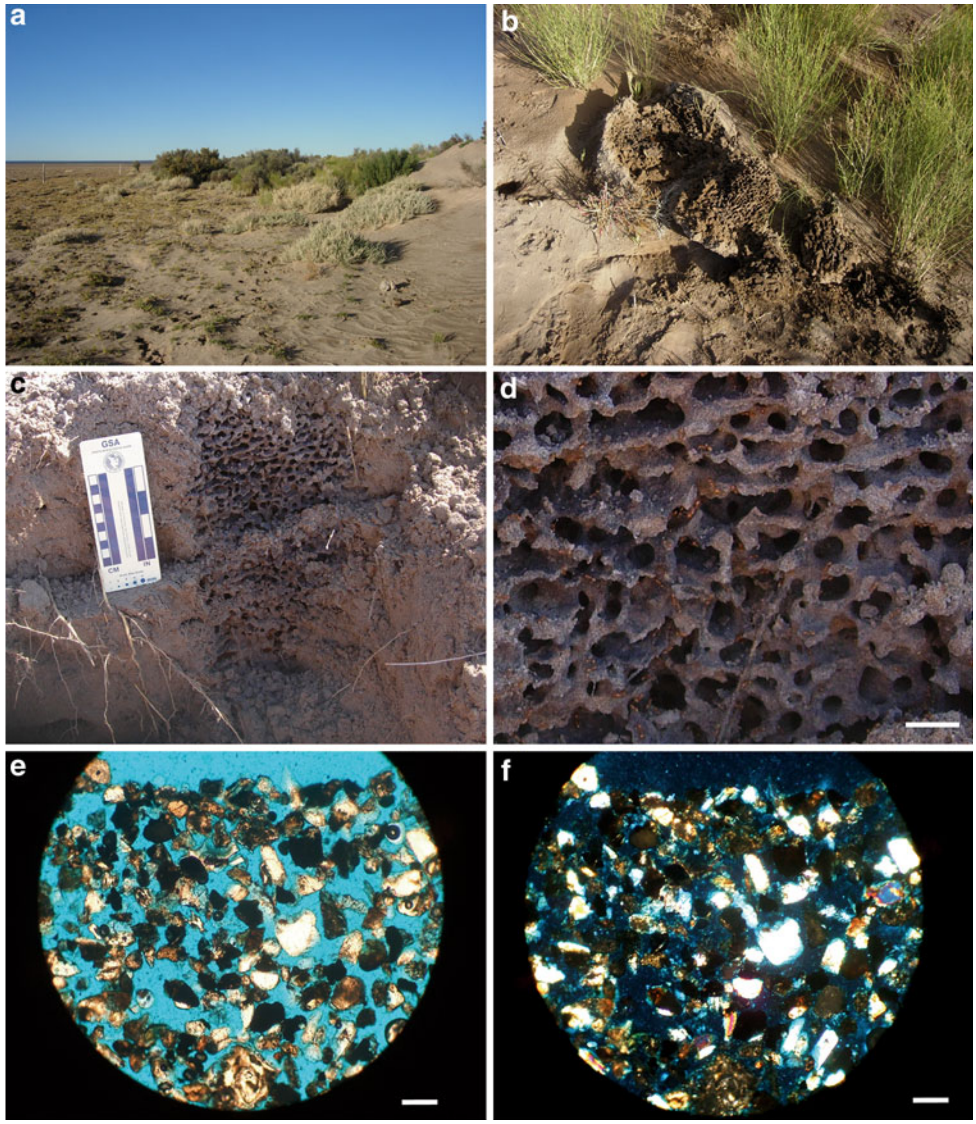

Fig. 1 *Solenopsis electra*. **a** Low relief sandy area, where the nest was located, bordering a dune and close to the saline depression (*left and bottom*) at Gran Salitral, **b** broken mound showing the internal structure composed of a boxwork of interconnected galleries. Mound diameter: 35 cm, **c** hypogeous part of the nest, **d** detail of the structure showing the *dark lining* contrasting with the *light* soil matrix. *Bar* 1 cm, **e** thin section observed with PPL showing the matrix composed of single grains, some of them coated with dark fine matter. The lining is composed mostly of coated grains. *Bar* 200 µm, **f** the same section observed with XPL showing that the dark fine matter is opaque. *Bar* 200 µm

debris and miscellaneous materials. Organic materials were present in the A soil horizon of that site. Peeters et al. (1994) observed that pieces of cocoons were used to deposit a "wallpaper lining" in soil nests of *Harpegnathos saltator* Jerdon (Ponerinae). Wang et al. (1995) found that nest walls of *Lasius niger* (L.) (Formicinae) had dark infillings resembling fused spheres between sand grains. These authors proposed no origin for this material, apart from pointing out that it was not observed in the soil matrix and that it was unknown from the activities of other ants. Old World *Lasius* ants of the subgenera *Dendrolasius* and *Chthonolasius* cultivate fungus with honeydew to reinforce carton nests built in tree and soil cavities (Mueller et al., 2001; Schlick-Steiner et al., 2008). Cosarinsky (2006) described linings of walls in *Camponotus punctulatus* Mayr (Formicinae) nests as composed of silt particles densely embedded in a dark, yellowish or reddish brown mass of clay, and fine, organic matter.

The nests of both species of *Solenopsis* studied herein, *S. electra* and *S.* nr. *macdonaghi*, occurring in single grained sandy soils show the same fine dark matter as wall linings, grain coatings, and bridges among grains. The coated and bridged grains found inside the matrix are probably the product of repetitive infilling, reworking of galleries and linings (Fig. 2f), and mixture of materials within the nests as observed in other ants (i.e., Halfen and Hasiotis, 2010). Thin sections demonstrate that the lining is composed of organic matter crossed by fungus hyphae. These linings, grain coatings, and bridges are probably responsible for the stability of the nests in these single grained sandy soils. Figure 2b shows that even in a weathered section of a soil composed exclusively of sand, the nest of *S.* nr. *macdonaghi*, remains as a cohesive, resistant structure. This organic matter is probably of fecal origin because of (1) its black colour similar to fecal material of other *Solenopsis* (Howard and Tschinkel, 1976), and (2) the lack of organic-rich layers

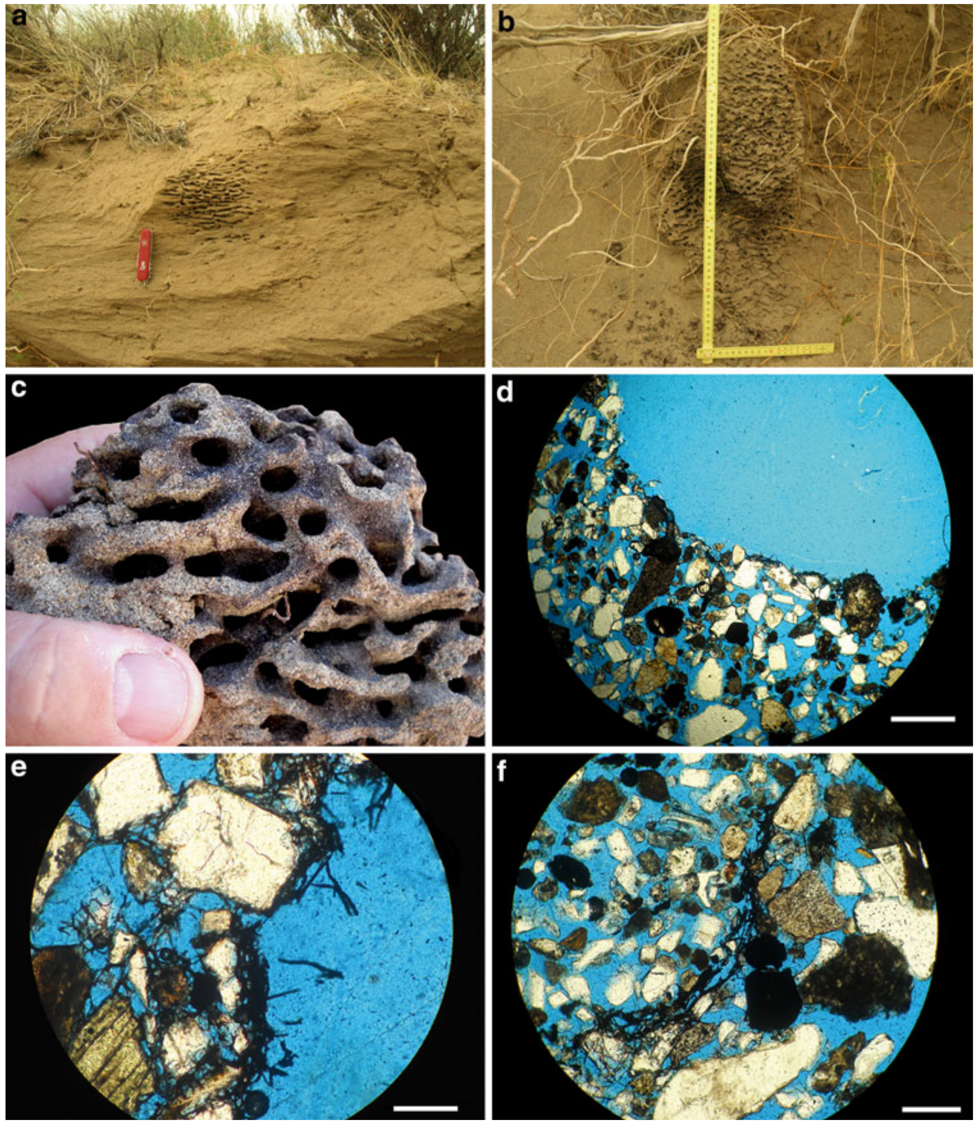

Fig. 2 *Solenopsis* nr. *macdonaghi*. **a**, **b** Nests located in a sandy soil with sparse vegetation from Punta Peligro, **c** detail of the boxwork showing the *dark lining* contrasting with the *light* soil matrix, **d** thin section showing the matrix composed of single grains, some of them coated with dark fine matter. The lining is composed of a layer of organic matter. *Bar* 700 µm, **e** detail showing organic matter crossed by fungus hyphae forming the lining, and coating and forming bridges among grains. *Bar* 150 µm, **f** detail of the lining of an old chamber filled with well-sorted smaller grains in contrast with unsorted, larger ones of the matrix. Note also the grains coated with organic matter. *Bar* 250 µm

in the sandy soils, where they occur (Figs. 1a, 2a). Organic coatings on grains (organans) are developed in soils from humid climates and thick plant litter, such as Spodosols and Andosols (Duchaufour, 1978; Shoji et al., 1993), very different from the cases of the pure sand Entisols, where the nests occur.

Howard and Tschinkel (1976) described that *Solenopsis invicta* Buren produces black fecal material, which was thrown outside of the nest. In other cases, the excreta remain in the mounds, where it is considered to be a source of element enrichment (Green et al., 1999) favouring plant growth (Chen, 2007). When reared in laboratory gel nests, the workers of this species deposited fecal droplets along the edge of the artificial nests (Chen, 2005, 2007), which indicates that these ants can use actively fecal droplets as a building material. These observations suggested to Chen (2005, 2007) that organic acids, which are antimicrobial agents found in *Solenopsis* mounds, could be incorporated to the nests by the excreta, together with secretions. If so, fecal linings extended along the whole chamber system of *S. electra* and *S.* nr. *macdonaghi* would have an antimicrobial function besides stabilization. Zettler et al. (2002) found that *Solenopsis invicta* mounds contain greater fungal abundance and lower species richness than the surrounding soil because of the changes that ants produce in the physical and chemical components of soil. Accordingly, the abundant fungus hyphae found in the linings of *S. electra* and *S.* nr. *macdonaghi* nests probably results from organic enrichment, and in turn, the mass of hyphae probably aid in lining cohesiveness or in maintenance of colony microenvironment. Schlick-Steiner et al. (2008) found five ascomycete fungi contributing to the reinforcement of walls in nests of species of *Lasius* (*Dendrolasius*) and *Lasius* (*Chthonolasius*). The ants cultivate, manage, and transmit across generations these specific fungi, reflecting the importance that this mutualism has for nest architecture.

Apart from its significance for ant architecture and nest function, the presence of organic linings in ant nests is important for the interpretation of fossil nests (Genise, 2004). Organic linings in fossil nests in palaeosols attributed to social insects are usually considered to be a diagnostic character for termite origin. For example, *Krausichnus trompitus* from the Oligocene Jebel Qatrani Formation of Egypt was considered a termite nest (Genise and Bown, 1994) mostly based on the organic linings of its walls. The same was proposed for South American records of *Krausichnus* (Genise et al., 1998; Netto et al., 2007). These attributions may be revised under the light of the new evidence presented herein. More recently, Genise and Farina (2011) analysing Pleistocene nests with organic linings from Buenos Aires, Argentina, proposed tentatively ants as putative producers based on a preliminary observation of *Solenopsis electra* nests described herein.

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