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# Fluidization in Insect Constructions in Soils

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Fluidization, a special case of liquefaction, is a physical process occurring in unconsolidated, water-saturated, sediments that can be verified in insect constructions in soils. Behavioral analysis of the bees *Ptilothrix relata* and *Diadasina distincta* shows that the fine-grained material of the soil pellets, utilized to construct the chimneys and cells of the nest, have been subjected to fluidization. The increment of pore pressure transmited by the bee's appendages to the moulded soil pellets, produces the outward escape of water, which drags the fine-grained material. Micromorphologically, the fluidization is reflected in the thin layers of clay and organic matter deposited on those surfaces of the constructions exposed to direct contact with the bee's appendages and in the higher content of fine-grained material close to these layers. Along with the reorientation of the coarser grains of the soil, produced also by the moulding behavior of the bee, these micromorphological features, having high preservational potential, constitute important ichnotaxobases and valuable clues to aid in the recognition of insect trace fossils in paleosols.

*Keywords:* Insect constructions, fluidization, micromorphology

## INTRODUCTION

Although seldom employed, micromorphology of fossil insect nests is probably one of the most powerful tools in the recognition of trace maker identity and it is important in erecting a healthy ichnotaxonomy (Genise and Hazeldine, 1998). In addition, the architecture of some insect traces in paleosols is so diffuse that only by undertaking micromorphological studies is it possible to recognize them accurately.

Genise and Hazeldine (1998) found in the microstructure of modern and fossil bee cells, the presence of thin, dark, layers of fine-grained soil material covering the inner smoothed surfaces of cells and inserted between the different pellets of material used to construct their walls. In this paper we are proposing an explanation for these micromorphological features, namely that the soil pellets used by bees to construct different parts of their nests are subjected to fluidization, a physical processes commonly studied by sedimentologists in relation to the deformation of unconsolidated sediments (Pettijohn et al., 1973; Friedman and Sanders, 1978; Leeder, 1982; Allen, 1985; Collinson and Thompson, 1989).

Many insects that construct nests with soil material prepare pellets from pre-existing water-saturated material, or from dry soil mixed with water and/or secretions from the constructor itself. The soil pellets, while being moulded or applied to the construction, are exposed to external forces, made by the insect, that are sufficient to trigger fluidization. It is our view that the micromorphological features described herein are probably more common in insect con-

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structions than is currently known, and consequently they have great potential in the wider recognition of not only fossil bee cells, but probably other insect trace fossils in paleosols (cf. Johnston et al., 1996).

## MATERIAL AND METHODS

This paper is based on observations of the nests and behavior of the solitary bees *Ptilothrix relata* and *Diadasina distincta* (Apidae: Emphorini), whose behavior and nests were studied in detail in a shared nesting site by Hazeldine (1997 a, b). The reasons for the choice of these bees are that: they construct chimneys and cells with soil material; a detailed behavioral study exists; and video records of their behavior as well as the chimneys and cells for the micromorphological studies were available to us, being deposited in the Laboratorio de Icnología (Museo Argentino de Ciencias Naturales).

*P. relata* and *D. distincta,* as well as other Emphorini, excavate the nest using water to moisten the dry soil. The water is transportated in the bees crop from nearby ponds or streams (Fig. 1a). The excavation mechanism involves pouring out the water inside the tunnel to moisten soil material, which is then moulded with the mandibles, legs and abdomen to form a pellet that is then removed. Each pellet represents the maximum amount of material that a given bee is capable of work at any one time. In the first instance of the tunnel construction the pellets are used to construct a chimney, which extends upwards around the entrance of the nest (Fig. 1b, c). Pellets measure 0.4 cm – 0.5 cm (*P. relata*) (Fig. 1c) and 0.2 cm – 0.35 cm (*D. distincta*) and in both species the studied chimneys were composed of rings of nine pellets each. After the chimney is completed, the pellets that result from excavation of the tunnel are discarded by ejecting them from the nest with the hind legs. The cell construction was not seen directly but examination of cells at different stages of construction demonstrates that after digging a cavity, the bees construct the cell wall by the sucessive addition of pellets (Hazeldine, 1997a).

The described behavior was originally recorded with a close-up lens and then analyzed by computer, from where the behavioral images presented herein were taken (Fig. 3). Chimneys and cells of *Diadasina distincta* and *Ptilothrix relata* collected for the original study (Hazeldine, 1997 a, b) were impregnated and sectioned to study micromorphology under a petrographic microscope (Fig. 2 a-h). A thin section of a cell of an unrelated bee, *Protoxaea gloriosa* (Oxaeinae), was also examined for comparison.

## RESULTS

Detailed video records of the behavior of both species show distinct stages in the alteration of soft sediment as it is worked by the bees during pellet moulding. It was observed that originally the soil surface is dry and loose, but by releasing water, the bee obtains a water saturated paste from which a pellet is moulded (Fig. 3a, b). Each pellet is located in its final position in the chimney by means of the mandibles, legs and abdomen (Fig. 3c-i). While worked by the bee, water-saturated pellets are subjected to an external compression by the bee's appendages that causes the continuous escape of water to the surface of the pellet. This process is demonstrated by the presence of a brilliant water layer that covers the pellet during its moulding and that disappears shortly after the bee locates it in its definite position in the chimney (Fig. 3). Once it has dried, individual pellets exhibit irregular, "lumpy" surfaces (Fig. 1c).

Bees construct chimneys and cells from their interior outwards and as such they are not smoothed externally, the irregular outer surfaces being effectively produced by the aggregation of lumpy pellets (Fig. 1b, c). Internally, the chimneys show a smooth surface which is achieved by lateral movements of the abdomen. This is

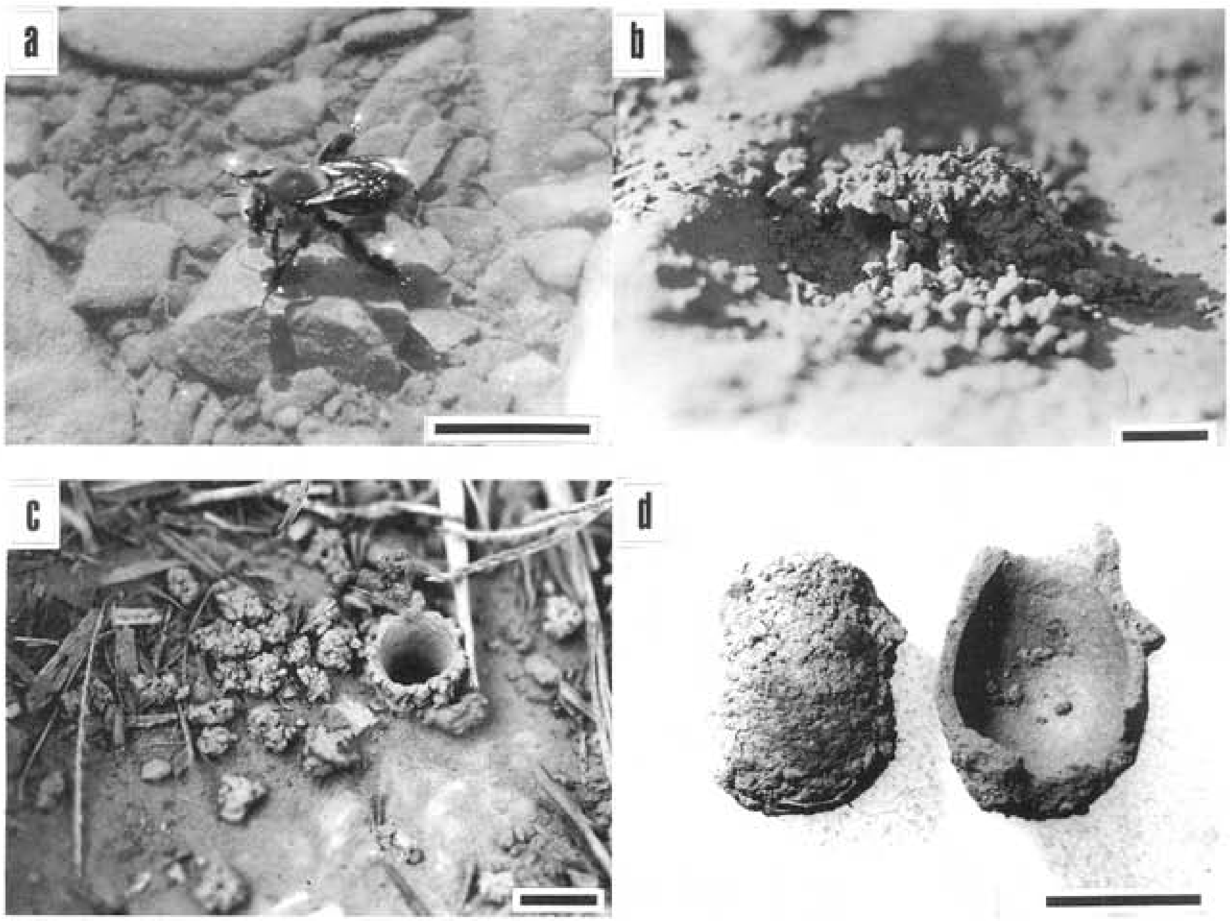


FIGURE 1 A, *Ptilothrix albidohirta* collecting water from a stream; B, chimney of *Diadasina distincta*; C, chimney and pellets of *Ptilothrix relata*. Chimney shows the smoothed inner surface and the "lumpy" external appearance. Note the soil pellets discarded by the bee after completion of the chimney showing a lumpy aspect; D, two cells of *P. relata* showing the irregular outer surface and the smoothed inner surface. Bars: 10mm

accomplished by a process of gradual smoothing caused by friction of the pygidial plate against the chimney wall each time the bee descends into the chimney (Hazeldine, 1997 a, b). The video records show that the water contained in each pellet escapes, particularly because of the abdominal movements, to the smoothed inner surface of the chimney, which dries shortly after the bee its movements (Fig. 3).

Thin sections of a chimney of *D. distincta* (Fig. 2a) showed that the soil material contained about 40% of sand, mainly very fine – (62μ-125μ) (125μ-250μm) The inner outline showed a thin dark layer (100μm-125μ) composed mostly of clays and mica laminae (Figs. 2a, b). The chimney wall also shows these dark layers surrounding portions of soil material which are interpreted as different pellet lumps (Fig. 2c), whereas in other parts of the same wall, pellet lumps can be distinguished by the presence of gaps between them (Fig. 2e). Additionally, it was possible to recognize, at least in some sections of the wall, that the inner part showed a higher content of fine-grained material and the longest

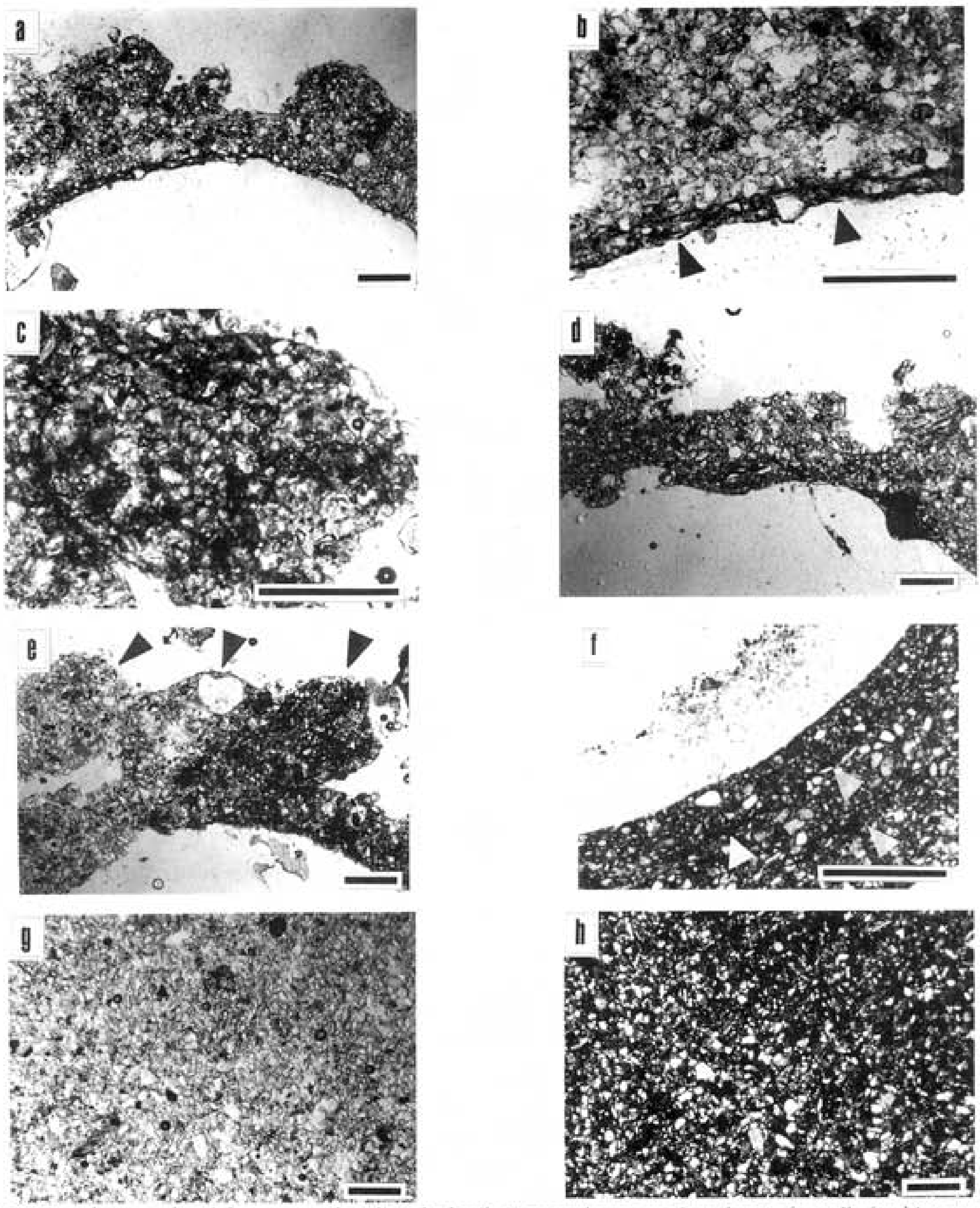


FIGURE 2 Microphotographs of chimneys and undisturbed soil. A, general cross-section of part of a wall of a chimney of a nest of *Diadasina distincta* showing lumpy outer layer and smooth inner surface; B, close up showing the darker inner wall of the chimney richer in clay material (arrows); C, close up of a lump of a pellet in the chimney of *D. distincta*; D, chimney of *D. distincta* showing the irregular, lighter and coarser-grained wall and the darker and finer-grained inner part; note a preferential orientation of the elongated grains (mainly feldspar and mica) in some parts of the dark layer; E, at least three lumps of pellets (arrows) forming the outer surface of the chimney; F, dark clay layers (arrows) in a cell wall of *Ptilothrix relata* with an oriented fabric of elongate grains parallel to the inner surface; G, disordered fabric of the undisturbed soil close to the nest of *D. distincta*; h, same view under crossed-nicols. Bars: 0.5 mm

grains oriented with their longitudinal axes parallel to the chimney wall (Fig. 2d). The packing of grains is variable in different parts of the wall but indistinguishable from that of the undisturbed soil.

In thin sections, the soil (Fig. 2g, h) shows a compact grain microstructure, with close packing and few intergranular voids. The coarse mineral fraction is of fine- to very fine-grained sand size, moderatly sorted and it is composed of quartz, plagioclase, feldespar, mica (biotite and muscovite) and, to a lesser extent, opaques, heavy minerals (epidote and basaltic hornblende) and lithic fragments (250µ-1500µ) of volcanic origin. The quartz grains are mostly subangular to angular, with few rounded individuals (250µ). The fine-grained fraction is composed of clays very impregnated with organic matter, without a preferential orientation, distributed in patches or around coarse grains. Recognizable pedofeatures include rootlets, incipient nodules and clay coatings.

Similarly, thin sections of a cell of *P. relata* (Fig. 2f) showed that the soil material contained about 50% of coarse-grained silt (31µ – 62µ) and very fine-grained sand (62µ – 125µ). The inner surface showed a thin dark layer, higher content of fine-grained material and the longest grains oriented with their longitudinal axes parallel to the cell wall. However, it was possible to recognize in the cells up to three beds of material in the wall, each one separated by the same dark layers composed of fine-grained soil material, but in this case a mixture of clays and organic matter. The packing of grains is indistinguishable from that of the undisturbed soil. The dark layers of *Protoxaea gloriosa* cell walls (Genise and Hazeldine, 1998) also show a high organic matter content.

## DISCUSSION

Liquefaction and fluidization are common processes known at a planetary scale, produced by gravity, earthquakes, landslides, tsunamis and water waves among other factors (Allen, 1985). Different definitions are given by authors for these and allied processes producing the deformation of soft sediments. For example, Friedman and Sanders (1978) defined liquefaction as any process that causes a body of particles to change their behavior from that of a solid to that of a liquid, and fluidization as a special case of liquefaction created by the upward flow of fluids within the pores of the body of particles. Leeder (1982) emphasized that in the liquefaction process the grains attempt to find the closest possible packing and define another process, thixotropy, for many natural, freshly deposited muds and man-made substances that show a pattern of reversible liquefaction. Collinson and Thompson (1989) defined liquefaction as a condition where sediment and water behave as a liquid, deforming very readily until the pore-water pressure falls, due to escape of excess water and the sediment takes on a closer packing and grains make frictional contact with one another. Further, they stated that fluidization took place when the excess of pore-fluid pressure is dissipated by a vigorous escape of fluid along restricted pathways, allowing the upward removal of fine-grained sediment.

It is possible to reproduce these processes at a smaller scale, such as in the examples of quicksand reproduced inside a glass jar, or that of a man jumping up and down on a sandy beach used by Allen (1985) and Collinson and Thompson (1989) respectively. At an even smaller scale, such as insect constructions, behavioral and micromorphological evidence shows that the soil pellets worked by *Ptilothrix relata* and *Diadasina distincta*, also undergo processes indicative of fluidization.

The addition of water to the dry soil produces a change of soil state from solid to more or less fluid-like. This process, which allows the bee to obtain a plastic material to mould, would be compatible with liquefaction (Friedman and Sanders, 1978). However, the process of liquefac-

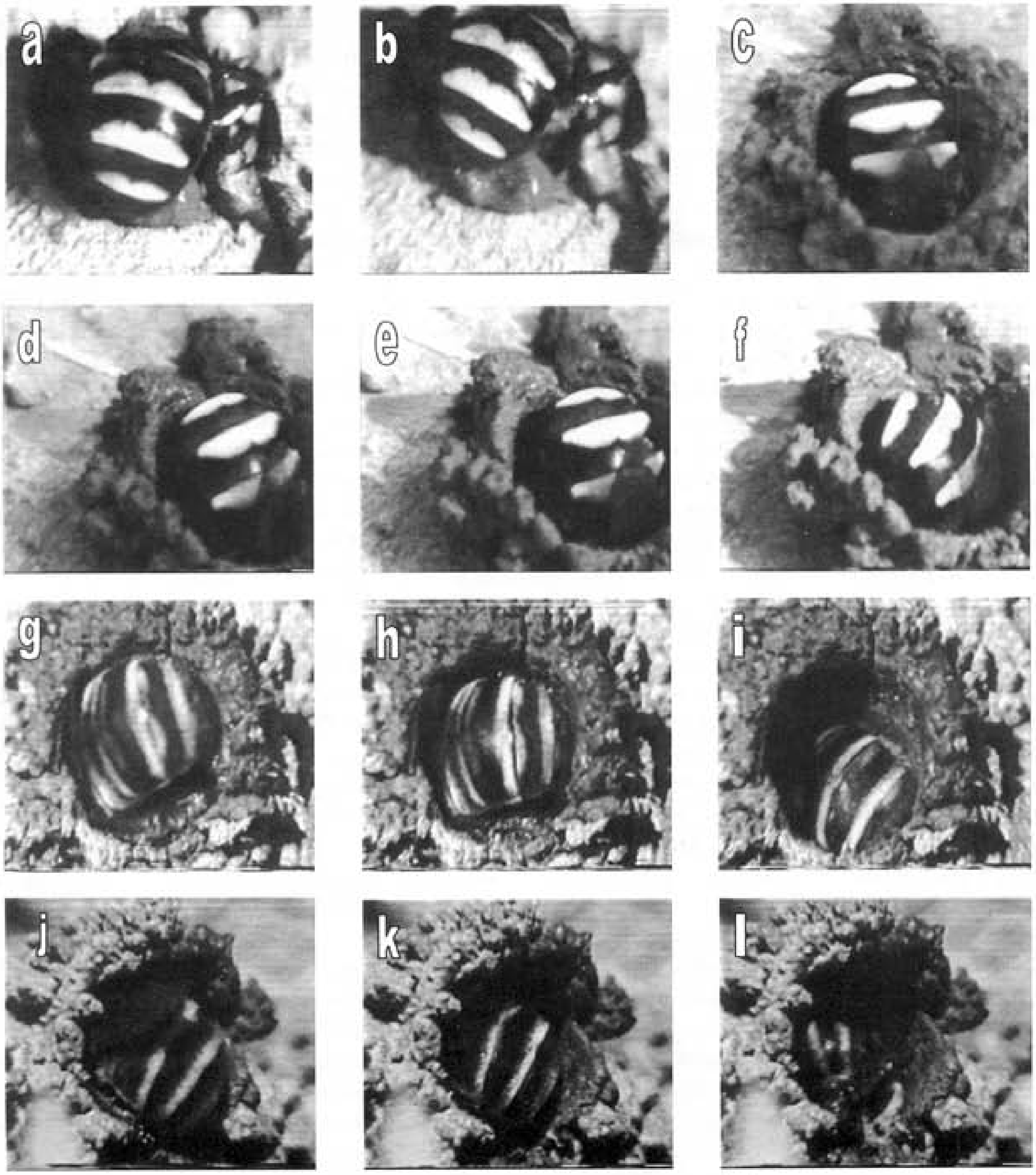


FIGURE 3 Sequences of pictures taken from a video record showing different stages of the chimney construction in Emphorini. A and B, *Ptilothrix relata* moulding a water saturated soil pellet; note the external wet surface of the pellet caused by the outward expulsion of fluids; C, D, E, and F, same effect observed in the construction of a chimney by *Ptilothrix relata*; G, H, I, J, K, and L, *Diadasina distincta* smoothing the inner surface of the chimney; note the water brilliant layer produced by the friction of the abdomen (See Color Plate I at the back of this issue)

tion should necessarily involve the repacking of sand particles (Leeder, 1982; Collinson and Thompson, 1989), a fact that could not be confirmed micromorphologically, being the packing of the undisturbed soil similar to that of the bee constructions (Fig. 2g). During the moulding, the increment of pore pressure that the insect appendages transfer to the sandy pellet (compare the size of the bee with that of the pellet) causes the fluidization of the fine-grained material: the water escapes outwards, producing the removal of the fine-grained material (Leeder, 1982; Collinson and Thompson, 1989). Fluidization can be checked behaviorally by the outward expulsion of water observed during moulding and application of pellets to the chimney (Fig. 3). Micromorphologically, the effects of fluidization can be recognized by the presence of layers of dark, fine-grained, material covering the part of the constructions more exposed to the contact with the bee appendages and abdomen: the inner smoothed surface of cells and chimneys and the outer surface of pellets. Similarly, it can be recognized by the higher concentration of fine material close to these dark layers.

Additionally, the same moulding behavior would be responsible for the orientation of elongated grains parallel to the wall described herein in *D. distincta* chimneys and in some bee cells described by Genise and Hazeldine (1998). These authors postulated that the movements performed by the pygidial plate were probably those responsible for this orientation. Consequently, by means of this single behavior the bee orientates the elongated grains and causes the finer-grained material to concentrate on the inner surfaces of cells and chimneys. In most cases the lining of cells is completed by the addition of impervious secretions.

Incidentally, fluidization occurs in the same kind of unconsolidated sediment in which bees commonly nest, that of sandy substrates. Bees nest in soils containing 33% to 94% sand, and avoid soils with more than 20% clay (Cane, 1992). Whereas, liquefaction and fluidization are common in fine- grained sands and silts (Pettijohn et al., 1973). Thixotropy, a reversible kind of liquefaction, is the equivalent process that takes place in some clay substrates (Leeder, 1982).

Evidence presented herein, involving two bee species, demonstrates that a physical process, fluidization, may be triggered each time water saturated soft sediment is moulded with the necessary strenght by any insect constructing a nest. Regrettably, micromorphology of nests is a rarely studied subject for any group of insects. Johnston et al. (1996) described the micromorphology of coleopteran pupal chambers (*Fictovichnus*) from the Upper Cretaceous of the Gobi Desert and from the Quaternary of Australia. In both cases, these authors found a clayrich zone in the inner part of the cocoons, very similar to that described herein They interpreted it as "a mechanical artifact of the process of pupal chamber excavation" (Johnston et al., 1996, p. 519) proposing that during excavation the larvae pushed the coarser grains outwards, whereas, clay and silt became densely packed into the open pore spaces of the inner zone. Similarly, Retallack (1984) described a clayey rind covering the pupal chambers of Scarabaeidae (*Pallichnus*) from the Oligocene of Dakota (U.S.A.). Lee and Wood (1971) presented good examples of micromorphology of termite nests. The re-packing of soil particles is well-known in several termite nests; however, in the studied cases it seems that the re-packing is the result of an active behavior of the termites, which select the grains and locate them in specific positions of their nests. In other thin sections it is possible to recognize layers of fine-grained material covering soil and carton pellets; however, Lee and Wood (1971) postulated that the pellets were covered actively by the termites using excreted organic matter.

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