Asociación Paleontológica Argentina. Publicación Especial 9. Buenos Aires, 30-10-2003 ISSN 0328-347X
IV Reunión Argentina de Icnología y II Reunión de Icnología del Mercosur: 53-64.

Micromorphology of the mound of *Cornitermes cumulans* (Kollar) (Isoptera: Termitidae)

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Abstract. The micromorphology of the nest of *Cornitermes cumulans* (Isoptera: Termitidae) is described and interpreted using thin sections of its different parts, following the methodology for studying soil micromorphology. Workers employ soil, fecal, regurgitated and plant material for nesting, and the constructions show a microstructure remarkably different from that of the surrounding soil. Additionally, each part of the nest (peripheral wall, middle region, hive and hipogeous region) shows a different type of microstructure, probably in relation to its particular function. Workers basically construct the nest with "bricks" of different composition according to the soil composition where the colony inhabits. When the prevailing soil material is fine (clayish soils) the bricks are small pellets of clay moulded in their bucal cavity, whereas in sandy soils the bricks may be coarse grains of quartz or moulded pellets of fine, organic material (humus) including fine sand grains. Studies on termite nests applying micromorphological analysis of soils are very few and deal with African and Australian species. This is the first report for the nest of a Neotropical species, which is compared with the known ones.

Resumen. MICROMORFOLOGÍA DEL NIDO DE *CORNITERMES CUMULANS* (KOLLAR) (ISOPTERA: TERMITIDAE). Se presenta la descripción y el análisis de la micromorfología del nido de *Cornitermes cumulans* (Isoptera, Termitidae) a través de la observación de cortes delgados de cada una de sus partes y empleando la misma metodología utilizada en estudios micromorfológicos de suelos. Los obreros utilizan materiales del suelo, excrementos, material regurgitado y fragmentos vegetales para la construcción de sus nidos. La microestructura de sus construcciones es notablemente diferente a la del suelo circundante, lo cual permite reconocerlas aún en ausencia de sus constructores, inclusive en material fósil. Cada parte del nido (muralla exterior, región media, habitáculo y región hipogea) presenta un tipo diferente de microestructura, posiblemente en relación con su función. Los obreros construyen básicamente con "ladrillos" cuya composición difiere según el tipo de suelo que habita la colonia. En suelos predominantemente arcillosos, los ladrillos son pequeñas bolitas de arcilla moldeadas en su cavidad bucal, mientras que en suelos arenosos, los ladrillos pueden ser granos gruesos de cuarzo o bolitas moldeadas de materia orgánica fina (humus) que incluyen pequeños granos de arena. La aplicación de la micromorfología de suelos al estudio micromorfológico de nidos de termitas ha sido escasamente utilizada y sólo en termitas de Australia y África. Éste es el primer estudio micromorfológico del nido de una termita Neotropical, que incluye comparaciones con estudios anteriores de nidos de otras termitas.

Key words. Termite nests. Micromorphology. Neotropical. *Cornitermes.*

Palabras clave. Nidos de termitas. Micromorfología. Neotropical. *Cornitermes.*

Introduction

This paper describes the micromorphology of the nest of one of the most conspicuous species of Neotropical termites from Southern South America. The new data presented are useful for studies on termite behavior, soil and agricultural practices, and insect palaeoichnology.

Studies on micromorphology of termite nests are scarce. Stoops (1964) described nests of the African species *Macrotermes bellicosus* Smeathman, *Cubitermes sankurensis* Wasman and *Cubitermes* sp., and Mermut *et al.* (1984) compared the micromorphology of nests built by three *Macrotermes* species (*M. michaelseni* Sjöstedt, *M. subhyalinus* Rambur, and *M. herus* Sjöstedt) from different ecoclimatic regions of Kenya. Eschenbrenner (1986) showed important micromorphological features of nests of the African *Crenetermes* sp., *Cubitermes* sp., *Nasutitermes* sp., *Thoracotermes* sp. and *Sphaerotermes* sp. Lee and Wood (1971) and Sleeman and Brewer (1972) described nests of several Australian termites. These studies show a great diversity of micromorphological fabrics, suggesting that the building behavior differs among species.

On the other hand, many trace fossils of supposed termite origin from several paleosols have been described in the last 20 years (Bown and Laza, 1990; Genise, 1997; Genise and Bown, 1994; Hasiotis

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 0328-347X/03$00.00+.50

Figure 1. Mound of *Cornitermes cumulans*. **A,** External view (hammer size: 26 cm). **B,** Middle part of the mound exposed after removal of the outer wall. Arrow points to a recent construction. / *Nido de* Cornitermes cumulans. ***A,*** *Vista exterior (longitud del martillo: 26 cm).* ***B,*** *Vista de una porción interior del nido, luego de remover la pared externa. La flecha señala una construcción reciente.*

and Dubiel, 1995; Smith and Kitching, 1997). However, only three studies confirmed the termite origin of the materials, through micromorphological analyses (Machado, 1983a, 1983b; Sands, 1987). Micromorphology of fossil insect nests is one of the most powerful tools for the recognition of the trace-makers, and also for ichnotaxonomical purposes (Genise and Hazeldine, 1998), particularly in some diffuse nests constructed by termites (Genise and Poire, 2000).

Cornitermes cumulans (Kollar, 1832) is a common and conspicuous mound-building termite that inhabits the NE region of Argentina, particularly northern Corrientes and southern Misiones provinces (Torales *et al.*, 1997). The mounds of reworked soil are free of vegetation, irregularly conical in shape, and commonly 1 m high and 1 m in basal diameter (Silvestri, 1903; Emerson, 1952; Grassé, 1958, 1984; Howse, 1970; Mathews, 1977; Coles de Negret and Redford, 1982; Torales, 1984). They are showy constructions, reddish, grayish or brown depending on the surrounding soil, common in fields and other open vegetation, mostly pastures in floodplains, and also house gardens, parks and squares in towns (figure 1.A).

The mound consists of three distinct parts (Silvestri, 1903; Grassé, 1958): (1) the peripheral wall, a very tough and compact external structure, (2) a middle region composed of an intricate net of irregular, interconnected galleries (figure 1.B), and (3) the innermost region, which has been called hive (Bouillon, 1970), nursery (Hill, 1942) or habitacle (Noirot, 1970), composed of a foliated structure of thin, carton, sinuous walls delimiting broad chambers. There are numerous, lenticular crusts, 3 to 5 mm in diameter, adhered to the walls of the hive and the inner galleries of the middle region. These crusts are quite distinct and light red in color. The mound continues underground, without any macroscopic difference between the inner chambers and galleries of the epigeous and the hipogeous parts. The hipogeous part is commonly separated from the soil by an empty space and there are many large tunnels connecting the construction to the surrounding soil. The empty space is connected to the outside by rounded openings at the base of the mound, which are about 5 cm in diameter at the ground level (Silvestri, 1903; Emerson, 1952). Subterranean peripheral galleries extend downwards and laterally from the nest to a very long distance (Grassé, 1958; Fontes, 1998). The mound grows by the sudden addition of new rounded blocks of earth material to the mound surface.

These blocks look like broad patches of damp, loose soil material that soon become dry and hard at sunlight and gradually thickened by workers. The complex architecture of the mound is accompanied by a complex micromorphology. Mound micromorphology and its surrounding soil, the mandible opening and the hindgut content of the workers reveal important behavioral aspects of the termite.

Material and methods

The micromorphology of two mounds of *Cornitermes cumulans* (Kollar) from Argentina was studied. Mound 1 was located in Ituzaingó (27º 33´S, 56º 42´W), Corrientes Province and mound 2 in Posadas (27º 22´S, 58º 55´W), Misiones Province (figure 2). Mound 1 occurred in an alluvial, sandy molisol and mound 2 was in a ferruginous ultisol (S.E.A.G. and P- I.N.T.A, 1990).

The samples collected in the field were: 1) each macroscopically recognizable part of the mound, namely, the peripheral wall, the middle region, the hive and the hipogeous region, 2) each visually distinct horizon of the surrounding soil, 3) alates, workers and soldiers, to confirm the identification of the constructors and to accomplish other studies at the laboratory.

The micromorphology of each sample was qualitatively studied and documented by means of thin sections analyzed under a petrographic microscope Nikon HFX-DX Optiphot-Pol. Thin sections were prepared from undisturbed, vacuumed samples impregnated with stained polyester resin (Murphy, 1986). The thin section methodology commonly used to describe the micromorphology of soils is applied herein successfully to describe the micromorphology of mounds of *Cornitermes cumulans* and to interpret its building behavior.

The terminology of micromorphological descriptions is taken from Bullock *et al.* (1985). The specific terminology of soil micromorphology may be interpreted under the light of termite behavior. Mounds are built with coarse and fine mineral materials such as quartz grains or hematites, larger than silt size in the former case and than clay in the latter. There are also coarse and fine organic materials, such as fragments of plants and insect cuticle, fecal and regurgitated, fine, organic material. Clay and fine organic material are also present in pellets moulded by workers to be utilized as "bricks". The type of microstructure explains how the termites arrange these materials, in order to adequate each part of the nest to its function. Bullock *et al.* (1985) assigned names and definitions to the most common soil microstructure types. Almost all the mound microstructures can be compared with a known soil type. However, it was impossible to assign the microstructure of the peripheral and hipogeous walls of mound 1 to any known types, and therefore the new type was named herein "intergrain cemented microstructure". There is also some micromorphological terminology to describe the related distribution of coarse and fine materials, the frequency of coarse particles that can be visually estimated and the different spatial arrangements or fabrics of fine material (b-fabric) that can be observed with polarized light. Pedofeatures describe discrete micromorphological units present in soil materials recognisable from adjacent material by a difference in concentration or distribution in one or more components. Particularly in mounds, pedofeatures describe some micromorphological features resulting from particular behaviors such as coatings around coarse grains, organic linings of galleries and organic bands crossing the walls.

Some samples of a hive were disintegrated to identify the presence and origin of coarse organic material and how it was reworked by termites. To accomplish the disintegration, the samples were submerged in water with detergent during two days. The loose material obtained was washed and filtered through a sieve, 0.5 mm in aperture. The retained material (larger than 0.5 mm) was included in glycerine and observed under the microscope.

To elucidate the origin of the quartz grains present in the nests, 60 grains were randomly selected in thin sections of the peripheral wall, middle region, hive and horizons of the surrounding soil of each nest, and their major and minor axes were measured. Within the hive, 60 quartz grains of the lenticular crusts were measured also. The values of those taken from the nest were then compared with those taken from the soil, and also with the maximum mandible opening and grain size found in the hindgut content of the workers.

The hindgut contents of 20 workers were analyzed. The major and minor axes of 120 quartz grains were measured to determine the largest grains that workers can swallow and incorporate as fecal material to their constructions. In addition, the maximum spontaneous mandible opening of 10 workers was measured to check the maximum grain size that workers can transport with their mandibles.

Results

Micromorphological descriptions

Micromorphological features are summarized in tables 1 to 6.

Analysis of the workers

Table 1. Micromorphology of the peripheral wall / *Micromorfología de la pared periférica.*

	Mound 1 (figure 2A)	Mound 2 (figures 3A, B, C, D and E)
Microstructure	In new construction: Spongy structure. Many large, interconnected, complex packing voids. Rounded masses, 0.40 to 0.85 mm of axis size, partially welded, composed of mineral grains cemented with fine organic material	In new construction: Spongy structure. Many large, mammilated, interconnected, complex packing voids. Rounded masses, 0.25 to 2 mm of axis size, partially welded, composed of reddish clay with mineral grains smaller than 0.1 mm included
	In old construction: Intergrain cemented structure. Common thin and short planar voids and very small, complex packing voids	In old construction: Crack structure. Rounded masses, 0.25 to 2 mm in diameter, separated by short and curved planar voids, resembling a mosaic
Coarse mineral material	Mostly quartz grains, silt to medium sand size. Scattered hematites grains, silt to fine sand size Maximum grain size: 0.37mm x 0.36 mm in diameter	Similar proportion of quartz grains, silt to coarse sand size, and hematite grains, silt to fine sand size. Maximum grain size: 0.75 mm x 0.33 mm in diameter
Abundance of coarse constituents	Common (30-50%)	Few (10%) in most areas Common (40%) in minor areas
Coarse organic material	Cell walls or other unrecognizable plant structures. Fragments of insect cuticle.	Fragments of insect cuticle
Fine material	Cementing mass composed of fine, amorphous, organic material and clay in variable concentrations	Ultrafine granules of clay with iron oxides, densely welded together forming rounded masses
Birefringence fabric of fine material (b-fabric)	Mostly stipple-speckled, granostriated surrounding scattered grains	Undifferentiated b-fabric
Related distribution of coarse and fine material	Single and double spaced porphyric	Mostly open porphyric. Coarser grains are located among the rounded clayish masses, but in some areas they are nearly in contact forming compact groups (Single and double spaced porphyric)
Pedofeatures	Simple organic intercalations: dark brown strands composed of amorphous and fine organic material with quartz grains included (mostly of fine and very fine sand size), rather parallel, slightly arched in shape	Absent

The mandibles of the worker can be opened spontaneously up to 0.55 mm ± 0.05 mm. The worker hindgut content is semi-liquid and consists of fine and amorphous organic material mixed with partially digested plant remains, clay, some coarse quartz granis and very fine mineral particles. Quartz grains are silt size to medium sand size. Maximum size of coarse quartz grains is 0.40 mm x 0.30 mm (maximum and minimum particle axes). Plant remains are well digested, too altered to be identifiable, and measure less than 0.15 mm.

Discussion

The study of nests of *Cornitermes cumulans* revealed important micromorphological differences among: (1) the different regions of the nests: peripheral wall, inner walls, hive and hipogeous region, (2) the nests and the surrounding soil and (3) nests of this species and termites from other regions.

Different nest parts have distinct microstructures, probably related to different functions. Crack and intergrain cemented structure present in the hard peripheral walls are probably related to their role in mechanical protection and environmental isolation. The walls in the middle region show airy pellicular or spongy microstructures probably related to thermal isolation. The hives display a constant platy microstructure made of superposed layers of fecal material laid down in fluid state and reinforced with fragments of leaves. The material of the hive is more hygroscopic than that of the periphery, and plays an important role in the maintenance of a high humidity level, which is required by the young larvae (Noirot, 1970). Hipogeous walls show dense microstructures (intergrain cemented or compact grain structure) probably related with their basal position.

The coarse mineral components of the nests are

Table 2. Micromorphology of the middle region / *Morfología de la región media.*

	Mound 1 (figure 2B)	Mound 2 (figures 3 F and G)
Microstructure	Pellicular grain structure. Abundant simple packing voids	In the interior of the walls: Complex structure: - Spongy structure. Many large, mammilated compound packing voids and channels - Crack structure. Short and curved planar voids - Compact grain structure In the surface of the walls: - Massive structure. Scattered thin planar voids
Coarse mineral material	Mostly quartz grains, silt to coarse sand size. Scattered hematite grains, silt to medium sand size. Maximum grain size: 1mm x 0.45 mm in diameter	In the interior of the walls: similar proportion of quartz grains, silt to coarse sand size, and hematite grains, very fine to medium sand size. Maximum grain size: 0.9 mm x 0.4 mm in diameter In the surface of the walls: grains of silt to very fine sand size
Abundance of coarse constituents	Common (40-50%)	Few (10%) in some areas, common (40%) in others
Coarse organic material	Absent	Absent
Fine material	Cementing mass dominatly composed of clay, mixed with amorphous and fine organic material in some areas	In areas of spongy and crack structure: ultrafine granules of clay with iron oxides, densely welded together forming rounded masses In areas of compact grain structure: cementing clay mass pasting the coarse grains In areas of massive structure: homogeneous clay mass
Birefringence of fabric of fine material (b-fabric)	Mostly granostriated, minor areas undifferentiated	Undifferentiated
Pedofeatures	-Typical clay coatings on coarse quartz grains -Typical organic coatings lining the galleries composed of dark brown, amorphous and fine organic material - Simple organic intercalations: dark brown strands, straight or bow-like in shape, composed of amorphous and fine organic material	Absent

the same present in the soil. Torales (1984) observed workers of *C. cumulans*, under laboratory conditions, transporting grains of sand between the mandibles from the soil to the nest. In general, soil material may be transported in two ways: between the mandibles or in the crop (Eschenbrenner, 1996). The size of the particles carried between the mandibles is equal or smaller than the maximum opening of the worker mandibles, which is 0.6 mm for *C. cumulans*. Accordingly, quartz grains found in all nest regions measured less than 0.6 mm in at least one of its axes, whereas numerous larger grains were found in the surrounding soils of the two nests, suggesting grain selection. Conversely, the size of the particles ingested and subsequently regurgitated or defecated depends on the geometry of the cibarium (regurgitation) or gut (defecation) (Eschenbrenner, 1996). Mineral particles present in the alimentary canal of the workers probably result from the accidental ingest of soil particles (Lee and Wood, 1971; Machado, 1983a). The maximum size of quartz grains found in the hindgut of workers of *C. cumulans* was 0.40 mm x 0.30 mm. This indicates that particles measuring from 0.40 to 0.60 mm were certainly transported between the mandibles, whereas particles smaller than 0.4 mm may be ingested. Hive and linings of galleries show mostly particles smaller than 0.4 mm, suggesting that they were built with organic material of fecal origin. Occasionally, scattered grains of larger sizes can be found in fecal wall linings.

The peripheral walls of mound 1 were built with soil pellets micromorphologically described as rounded soil masses composed of mineral grains cemented with fine organic material. Torales (1984) observed that building soil materials collected and transported by workers of *C. cumulans* are moulded by the palp and head movements against the wall, before applying them to the substrate. Grassé (1984) stated that the hypopharynx can modify, by pressure, the shape of pasty materials carried in the bucal

Table 3. Micromorphology of the hipogeus region (based wall) / *Micromorfología de la región hipogea (pared basal)*

	Mound 1	Mound 2 (figure 3H)
Microstructure	Intergrain cemented structure. Abundant simple packing voids.	In the interior of the wall: compact grain structure. In the surface of the wall: massive structure. Scattered planar voids.
Coarse mineral material	Mostly quartz grains, silt to coarse sand size. Scattered hematite grains, very fine to fine sand size. Maximum grain size: 0.57 mm x 0.57 mm in diameter.	In the interior of the wall: similar proportion of quartz grains, silt to coarse sand size, and hematite grains, very fine to coarse sand size. Maximum grain size: 0.60 mm x 0.53 mm in diameter. In the surface of the wall: silt to very fine sand size grains
Abundance of coarse constituents	Common (40-50%)	Dominant (50-70%), in the interior of the wall.
Coarse organic material	Well preserved cross-sectioned leaves of living grasses. Fragments of insect cuticle.	Absent.
Fine material	Cementing mass composed of amorphous and fine organic material mixed with clay.	In the interior of the wall: cementing clay mass pasting the coarse grains. In the surface of the wall: homogeneous clay mass.
Birefringence fabric of fine material (b-fabric)	Undifferentiated	Undifferentiated
Related distribution of coarse and fine materials	Single and double spaced porphyric	Close porphyric and single spaced porphyric in the interior of the wall.
Pedofeatures	Absent	Absent

cavity, and also that it is used as a smoothing tool. After that, the pasty pellets are regurgitated and placed exerting pressure on the nest site. The presence of very thin fissures in older constructions and of mammillated voids in recent buildings point the limit of the pellets. Sleemann and Brewer (1972) and Eschenbrenner (1986) observed similar features in nests of many Australian and African termite species respectively. Mineral grains in the pellets are embedded into a homogeneous organic mass probably because of the process of moulding of soil organic microaggregates with saliva. In the middle region of mound 1 the pellets are not discernible, the walls are very porous and composed of coarse mineral grains cemented with a thin, birefringent layer of clay. This birefringence indicates the presence of a parallel arrangement of clay particles of similar size, reflecting that the origin of the cement is regurgitated clay with saliva (Scasso and Limarino, 1997). Accordingly, Harris (1956) observed that workers of *Macrotermes bellicosus* ingest clay from the subsoil and carry it inside the crop. At the same time, they carry sand grains, held firmly in the mandibles. When they reach the nest, the sand grain is placed in position and the clay in the crop is regurgitated along with saliva around the grain as a mortar. In *C. cumu-*

Table 4. Micromorphology of the hive of mound 1 and 2 (figures 2.C and D). / *Micromorfología de los nidos 1 y 2 (figuras 2.C y D).*

Microstructure	Platy structure.
Coarse mineral material	Mostly quartz grains, very fine size, oriented in parallel lines respect to the surface of the wall. Maximum grain size: 0.18 mm x 0.08 mm in diameter. Abundance of coarse constituents: Very few (2.5-5.0 %).
Coarse organic material	Small pieces of leaves distributed without any orientation in the thicker walls, showing stomata, parallel nervation and many cytoplasmatic crystals.
Fine material	Parallel laminae of amorphous and fine organic material mixed with clay. Birefringence fabric of fine material (b-fabric): Parallel striated (very weak birefringent streaks).
Related distribution of coarse and fine materials	Open porphyric.
Pedofeatures	Small, lenticular crusts, 3 to 5 mm in diameter and 1.4 to 2 mm in thickness, lying on the surface of the walls, showing crack microstructure, composed of well-sorted quartz grains, mostly fine size, embedded into a limpid red, clayish material. Maximum grain size: 0.3 mm in diameter. Abundance of coarse constituents: common (30-40%). Related distribution of coarse and fine materials: close and single spaced porphyric.

Figure 2. Micromorphology of mound 1 and surrounding soil. **A,** Peripheral wall. Intergrain cemented structure. Arrows indicate an organic strand. **B,** Middle region. Pellicular grain structure. Arrows indicate the organic coating of a gallery. **C,** Hive. Arrows indicate fragments of leaves included in the wall. **D,** Hive. Platy structure. Arrow indicate to a lenticular crust. **E,** Surrounding soil 0 to 30 cm deep. Intergrain microaggregate structure. Cross-sectioned leave of grass. **F,** Surrounding soil 30 to 48 cm deep. Complex structure (bridge grain and intergrain microaggregate structure). Scale bars: 1 mm. / *Micromorfología del nido 1 y del suelo circundante.* ***A,*** *Pared externa. Estructura de granos cementados con materia orgánica fina. La flecha señala una banda de materia orgánica.* ***B,*** *Región media. Estructura de granos revestidos por una película de material fino. Las flechas señalan el revestimiento orgánico de la pared una galería.* ***C,*** *Habitáculo. Estructura laminar. La flecha señala una incrustación lenticular.* ***D,*** *Habitáculo. Estructura planar. La flecha señala una cubierta tentacular.* ***E,*** *Suelo circundante de 0 a 30 cm de profundidad. Estructura de microagregados de materia orgánica entre granos. Corte transversal de una gramínea.* ***F,*** *Suelo circundante de 30 a 48 cm de profundidad. Estructura compleja (estructura de granos conectados y de microagregados de materia orgánica entre granos). Escala: 1 mm.*

Table 5. Micromorphology of the surrounding soil, 0-30 cm deep. / *Micromorfología del suelo circundante, 0-30 cm de profundidad.*

	Mound 1 (figure 2E)	Mound 2 (figura 3F)
Microstructure	Intergrain microaggregate structure. Simple and complex packing voids and many irregular vughs	Complex structure: mostly spongy structure but compact grain structure in some minor areas. Many irregular, interconnected vughs and curved channels
Coarse mineral material	Mostly composed of quartz grains, silt to very coarse sand size. Scattered hematite grains, silt to fine sand size. Maximum grain size: 1.12 mm x 0.30 mm	Similar proportion of quartz grains, silt to coarse sand size, and hematite grains, silt to fine sand size. Maximum grain size: 0.67 mm x 0.28 mm
Abundance of coarse constituents	Mainly common (50%), but occasional (20%) in some areas	Mainly common to dominant (50%), but occasional (20%) in some areas
Coarse organic material	Abundant well preserved remains of roots, leaves and stems of grasses, decreasing downwards. Fragments of insect cuticle	Strongly deformed remains of small cell groups or cell walls, lignified tissues and rootlets. Fragments of insect cuticle
Fine material	Microaggregates of amorphous and fine organic material	Welded and rounded clay microaggregates, 0.5 to 0.8 mm in diameter with iron oxides
Birefringence fabric of fine material (b-fabric)	Undifferentiated	Undifferentiated
Related distribution of coarse and fine materials	Mainly enaulic, but open porphyric in some areas	Mainly close porphyric, but open porphyric in some areas
Pedofeatures	Absent	Absent

lans mounds the presence of a thick cement with finer organic material in the peripheral wall would improve the isolation and strenghthening of the nest, whereas a lighter suspension of saliva and clay would be enough to cement the airy walls of the middle region. The fine organic materials and mineral grains present in the hive are similar to the hindgut content, suggesting a fecal origin. Lee and Wood (1971) stated that the components of the hive of *Coptotermes lacteus* and *Nasutitermes exitiosus* Hill are of fecal origin too.

The peripheral and interior walls of mound 2 were constructed with rounded pellets moulded with soil clay microaggregates. They are also recognized by the presence of curved fissures and rounded or mammilated voids. Coarser grains located between the pellets and in compact groups must have been transported by the mandibles and located when the pellets were still moist. Some sectors of the walls and the pillars show a close structure of coarse grains cemented with clay. The origin of this cement is probably moulded clayish soil adhered to the grains, because its opacity looks like the flocculated clay present in the soil.

Many authors noted the presence of pellets in termite nests showing a different composition and origin. Sleeman and Brewer (1972) named pellets the constructional units of regurgitated or fecal origin. They observed both types in nests of 12 Australian species and described them as spheroidal or ovoid bodies composed by organic material, mineral soil or various combinations of both materials that may occur as single units, welded or somewhat flattened. Stoops (1964) observed a loose arrangement of parcels of soil carried by individual workers in new constructions of *Macrotermes natalensis* (Haviland) nests and named it pellet-structure. Such pellets were composed of soil repacked quartz grains cemented

Table 6. Micromorphology of mound 1 surrounding soil, 30 cm deep to water table (figure 2.F). / *Micromorfología del suelo circundante al montículo 1, 30 cm de profundidad hasta nivel freático.*

Microstructure	Complex, showing areas with bridge grain structure and others with intergrain microaggregate structure. Simple and complex packing voids. Numerous circular, unconnected voids, 0.20 to 0.45 mm in diameter
Coarse mineral material	Mostly quartz grains, silt to coarse sand size. Scattered hematite grains, silt to very fine sand Frequency of coarse constituents: dominant (more than 70%)
Coarse organic material	Very few, decomposed, lignified tissue remains
Fine material	Microaggregates of amorphous and fine organic material Birefringence fabric of fine material (b-fabric): undifferentiated
Related distribution of coarse and fine materials	Chitonic in some areas, enaulic in others
Pedofeatures	Absent

with clay and saliva and were considered as prefabricated constructive elements utilized in rapid building. Lee and Wood (1971) observed similar pellets composed of packs of soil grains in new constructions of *Coptotermes lacteus* (Froggatt), *Nasutitermes exitiosus* (Froggatt) and *N. triodidae*, and lenticular parcels of transported soil coated by a thin layer of fecal material in nests of *Amitermes laurensis* Mjöberg, *Microcerotermes nervosus* Hill and *Tumulitermes pastinator* Hill. They also found fecal pellets composed of fine organic matter and comminuted fragments of wood in nests of *Mastotermes darwiniensis* Froggatt. Another type of pellet was described by these authors in *Coptotermes acinaciformis* Froggatt nests, entirely composed of fragments of wood and too large to have a fecal origin, which probably could have been moulded with masticated wood. The two last types of pellets were coated by a thin layer of fecal material. Eschenbrenner (1986, 1996) described mineral, organic and organo-mineral pellets as the elementary building units in nests of *Sphaerotermes sphaerothorax* Sjöstedt, *Thoracotermes* sp., and *Crenetermes* sp. and Mermut *et al.* (1984) found pellets composed of sand and clay in nests of three *Macrotermes* species: *M. michaelseni*, *M. subhyalinus* and *M. herus*. Machado (1983a, 1983b) and Fontes and Vulcano (1998) described clay pellets in fossil termite constructions found in lateritic paleosols.

Many types of organic remains are included within the structure of different parts of the nests. The walls of the hive include many fragments of leaves distributed without any orientation. The presence of parallel nervation and many cytoplasmatic crystals suggests that they belong to halophyte gramineae (Esan, 1959), whereas large sized fragments with rectangular shape and sharp contours suggest that they were cut from living plants, carried between the mandibles and placed directly in the nest site in a

Figure 3. Micromorphology of mound 2 and surrounding soil. **A,** Peripheral wall. Crack structure. Arrows indicate clay pellets. **B,** Peripheral wall. Detail of pellets. **C,** New peripheral construction. Spongy structure. **D,** New peripheral construction. Detail of pellets. **E,** Peripheral wall. Upper left: old construction. Down right: new construction. **F,** Middle region, gallery's wall. Spongy structure. **G,** Middle region, gallery´s surface. Massive structure. **H,** Hipogeous region. Compact grain structure. **I,** Surrounding soil 0 to 35 cm deep. Spongy structure. Scale bars: 1 mm (A, C and E); 0.25 mm (B, D, F, G, H and I). / *Micromorfología del nido 2 y del suelo circundante.* ***A,*** *Pared externa. Estructura agrietada. Las flechas señalan pellets arcillosos.* ***B,*** *Pared externa. Detalle de pellets.* ***C,*** *Construcción reciente de la pared externa. Estructura esponjosa.* ***D,*** *Construcción reciente de la pared externa. Detalle de pellets.* ***E,*** *Pared externa. Arriba, izquierda: construcción antigua. Abajo, derecha: construcción reciente.* ***F,*** *Región media, pared de una galería. Estructura esponjosa.* ***G,*** *Región media, superficie de la pared de una galería. Estructura masiva.* ***H,*** *Región hipogea. Estructura de granos cementados.* ***I,*** *Suelo circundante de 0 a 35 cm de profundidad. Estructura esponjosa. Escalas: 1 mm (A, C y E); 0.25 mm (B, D, F, G, H e I).*

fresh condition, without previous digestion. Lee and Wood (1971) described a similar platy microstructure for the hive of *Coptotermes lacteus*, but the hive of *C. cumulans* differs in having these accumulations of fragments of leaves in the thicker walls. Some insect remains were also found within the walls of the two mounds studied here: entire mandibles of termite soldiers and sectioned appendices of unidentified insects. Previous authors noted the presence of plant remains and fragments of insect cuticle in termite constructions. Machado (1983a, 1983b) observed strongly sclerotized anisotropic fragments corresponding to broken termite mandibles and plant remains of variable degree of decomposition in tubulo-alveolar laterites and bauxites, originated in fossil termite nests. Torales (1984) documented entire or fragmented bodies of workers and soldiers in buildings of *C. cumulans* pasted together with sand grains and fecal cement.

Distinct dark brown, elongate strands were found crossing the peripheral wall and middle region of mound 1. Their fine organic composition suggests a fecal origin. Excrement was probably laid down in a fluid state without being reworked in any way. Larger mineral grains must have been transported with the mandibles and inserted in the fresh and moist excrement. These strands probably would strengthen the walls. Lee and Wood (1971) observed similar organic strands in nests of *Nasutitermes exitiosus*, *Amitermes laurensis* and *Amitermes meridionalis* (Froggatt) and attributed them to the outline of the walls of old galleries. The bow-like structure described by Stoops (1964) in nests of *Macrotermes* sp. resembles in some aspects the organic strands observed herein, and are arranged in alternated lines of dark, bow-like layers rich in humus and light, essentially mineral layers. In *C. cumulans*, the distribution of the organic strands is not so regular; in some cases they are parallel distributed and in others they show no recognizable orientation. Additionally, their appearance is not so regular; they are simple or branching bands and straight or bow-like in shape.

The organic coatings lining the galleries of mound 1 have the same organic components of the strands, suggesting a fecal origin too. This organic plaster of variable thickness smooths and strengthens the surface of the galleries. No organic lining was found in the galleries of mound 2, whose surface was densely plastered with clay pellets keeping the same function. The thick organic linings of the gallery walls of *Nasutitermes exitiosus* described by Lee and Wood (1971) have the same laminar structure than those of galleries of mound 1. The same authors decribed similar thick linings in *Microcerotermes nervosus* and thin ones in the outer walls of mounds of *Nasutitermes triodiae*, *N. magnus* (Froggatt), *Amitermes laurensis*, *A. meridionalis*, *A. vitiosus* Hill, *Tumiletermes pastinator* and *T. hastilis* Froggatt.

Lenticular crusts of sand grains cemented with a rather limpid red clayish material were adhered to the walls of the hive and to the inner galleries of the middle region in mound 1. This seems to reflect some kind of particle selection because the size of the sand grains was rather homogeneous (well sorted) and less than 0.3 mm. The small size of the particles and the presence of almost pure clay as cement suggest that these crusts are composed of regurgitated materials. Machado (1983a) observed similar small lenticular accumulations of clayey-quartzose mortar in the chamber walls of some laterites.

Important micromorphological differences were also noted between the mounds and the surrounding soil, indicating that the building behavior of the termites modified the soil micromorphology. The soil surrounding mound 1 shows intergrain microaggregate and bridge grain structures, whereas the soil surrounding mound 2 shows spongy structure. No part of any mound displays the same microstructure of the soil. Only in newly repaired parts a spongy structure similar to the soil was observed, but arranged in pellets. The two mounds have the same mineral grains present in the surrounding soil, such as quartz and hematite grains. However, their sizes differ. In soils, the particle size ranges from clay to very coarse sand size, whereas in the nests the maximum size scarcely exceeds the limit between medium and coarse sand. Fine components of soils and nests are remarkably different also. The soil surrounding mound 1 has loose organic microaggregates filling the intergranular space and the soil surrounding mound 2 has crumbs of clay microaggregates. In contrast, the fine components of the mounds (clay and fine organic matter) form a homogeneous cement-like material surrounding coarse grains or forming rounded masses of clay. Other distinct micromorphological features are present in mound 1, such as typical clay and organic coatings, intercalations and crusts, which are absent in the surrounding soil.

In laboratory experiments Jouquet *et al.* (2002) demonstrated that *Odontotermes pauperans* Silvestri (Termitidae, Macrotermitinae) utilizes soil particles selectively, favoring finer particles and making constructions which match ecological, physiological and behavioral needs. They studied the selection of building materials offering soil of two contrasting horizons: superficial soil (15-20 cm) and a deeper layer (70-80 cm). They did not find any evidence of particle selection where only top-soil was available; however, when deeper soil was offered, the constructions contained less coarse sands and fine particles. Termites exhibited no preference when establishing vertical foraging galleries, but preferentially utilized the deepest soil for building their fungus-comb chamber walls where they found finer material which has greater water-holding capacity. Thus, these authors stated that particle selection by termites depends on the soil inhabited. Workers of *C. cumulans* also utilize the available soil materials at different types of soil, but the soil particle selection only depends on the quantity of soil particles they can carry in their bucal cavity. In constrast, they adapt the microstructure of their constructions to their different functions. The same study states that *O. pauperans* can modulate the incorporation of supplementary organic matter according to the type of construction and the nature of the soil used. Accordingly, *C. cumulans* utilizes organic matter of fecal origin to plaster the galleries in nests built in sandy soils, whereas no organic linings have been observed in the galleries of nests built in clayish soils.

Conclusions

The micromorphology of nests differs from that of the surrounding soil. Such differences allow the recognition of termite nests even in the absence of the constructors as is the case of fossil structures.

Workers utilize basically “bricks” to construct the different parts of the nests. Depending on the available soil material and the region of the nest, bricks are pellets moulded in the bucal cavity of the workers with clay or sand mixed with humus, or singly coarse grains of quartz carried between their mandibles. The maximum size of the quartz grains is relatively constant and corresponds to the mandibular opening of the workers, whereas the pellets may reach larger sizes (not exceeding 2 mm), because they are composed of plastic material. Pellets are placed in site without any kind of cement. Coarser quartz grains are fastened among pellets or are cemented with regurgitated clay.

The microstructure is closely related to the function of each part of the nest. Hard peripheral walls show very compact microstructures (crack and intergrain cemented structures) probably in response to their function of protection and environmental isolation. Porous microstructures (pellicular and spongy structures) predominate in the middle region, where the airy structure of the walls can enhance the thermic isolation. Hives show platy structure composed of fine organic matter of fecal origin to maintain the high level of moisture necessary for rearing immatures. Hipogeus walls show different types of microstructure (compact grain or intergrain cemented to pellicular structure) related to its basal position.

Some micromorphological features observed in the mound of *C. cumulans* can be compared with those described for other species of termites. For example, similar organic linings are also seen in many species of *Nasutitermes* and in some species of Termitinae and Macrotermitinae. Pellets and organic strands were also described in other Nasutermitinae, Termitinae, Macrotermitinae and Rhinotermitidae, but with differences in composition, shape or distribution. The variety of microstructures observed in the different parts of the mounds of *C. cumulans* was not reported for other termites.

Acknowledgments

I am deeply grateful to Dr. Axel Bachmann, my teacher of Entomology and to Dr. Daniel Roccattagliata, who encouraged me to study termites. A special thank to Dr. Jorge Genise for his patient help in all steps of this work and for his contagious enthusiasm, and to the reviewers, Charles Noirot and Luiz R. Fontes, who carefully read the manuscript and gave helpful comments. I also wish to thank Carmen Godoy and her daughter for doing my stays in Ituzaingó so nice.

References

Bouillon, A. 1970. Termites of the Ethiopian Region. In: K. Krishna and F. M. Weesner (eds.), *Biology of termites*, Academic Press, New York and London, vol. 2: 643 p.

Bown,T. M. and Laza, J. H. 1990. A Miocene termite nest from southern Argentina and its paleoclimatological implications. *Ichnos* 1: 73-79.

Brewer, R. 1964. Fabric and mineral analysis of soils. John Wiley and sons (eds.), New York, 470 pp.

Bullock, P., Fedoroff, N., Jongerius, A., Stoops, G. and Tursina, T. 1985. *Handbook for Soil Thin Section Description*. Waine Research Publications, England, 150 p.

Coles de Negret, H. R. and Redford, K.H. 1982. The biology of nine termite species (Isoptera: Termitidae) from the Cerrado of Central Brasil. *Psyche* 5: 81-106.

Emerson, A. E. 1952. The neotropical genera *Procornitermes* and *Cornitermes* (Isoptera: Termitidae). *Bulletin of the American Museum of Natural History* 99: 477-539.

Esan, K. 1959. *Anatomía Vegetal*. Ediciones Omega, Barcelona, 779 p.

Eschenbrenner, V. 1986. Contribution des termites a la micro-agregation des sols tropicaux. *Cahier ORSTOM, Série Pedologie* 22: 397-408.

Eschenbrenner, V. 1996. Termite activity and soil morphology in tropical areas. *Congresso Latino-americano de Ciência do Solo*, 13 (Águas de Lindóia, 1996). *Solo-suelo* 96, (Piracicaba). SBCS / SLCS (CD-room).

Fontes, L. R. 1998. Cupins nas pastagens do Brasil: algumas indicações de controle. In: L. R. Fontes and E. Berti Filho (eds.), *Cupins. O desafío do Conhecimento*, FEALQ, Piracicaba, Brasil, p. 211-225.

Fontes, L.R. and Vulcano, M.A. 1998. Cupins fósseis do Novo Mundo. Atividade sub-recente de cupins no solo. In: L. R. Fontes and E. Berti Filho (eds.), *Cupins. O desafío do Conhecimento*, FEALQ, Piracicaba, Brasil, pp. 285-295.

Genise, J.F. 1997. A fossil termite nest from the Marplatan stage (late Pliocene) of Argentina: palaeoclimatic indicator. *Palaeogeography, Palaeoclimatology, Palaeoecology* 136: 139-144.

Genise, J. F. and Bown, T.M. 1994. New trace fossils of termites (Insecta: Isoptera) from the late Eocene- early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. *Ichnos* 3: 155-183.

Genise, J.F. and Hazeldine, P.L. 1998. The ichnogenus

Palmiraichnus Roselli for fossil bee cells. *Ichnos* 2: 1-16.
Genise, J.F. and Poire, D.G. 2000. Fluidization in insect constructions in soils. *Ichnos* 7: 127-134.
Grassé, P.P. 1958. Sur le nid et la biologie de *Cornitermes cumulans* (Kollar), termite brésilien. *Insectes Sociaux* 5: 189-199.
Grassé, P.P. 1984. *Termitologia. Fondation des sociétés, construction.* Masson, Paris vol. 2: 613 p.
Harris, W.V. 1956. Termite mound building. *Insectes Sociaux* 3: 261-268.
Hasiotis, S. T. and Dubiel, R. F. 1995. Termite (Insecta: Isoptera) nest ichnofossils from the upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos* 4: 119-130.
Hill, G.F. 1942. Termites (Isoptera) from the Australian Region (Including Australia, New Guinea and Islands South of the Equator between 140 E longitude and 170 W longitude). *C.S.I.R.O.*, Melbourne, Australia.
Howse, P.E. 1970. *Termites: A study in social behaviour.* Hutchinson University Library, London, 150 p.
Jouquet, P., Lepage, M. and Velde, B. 2002. Termite soil preferences and particle selections: strategies related to ecological requirements. *Insectes Sociaux* 49: 1-7.
Kollar, V. 1832. Braziliens vorzüglich lästige Insekten. In: J.B. E. Pohl (ed.), *Reise ins Innern von Brasilien*, Vienna, 1: 1.
Lee, K. E. and Wood, T. G. 1971. *Termites and Soils.* Academic Press, London, New York, 251 p.
Machado, A. B. 1983a. The contribution of termites to the formation of laterites. In: A.J. Melfi and A. Carvalho (eds.), *Laterisation Processes*. Proceedings, II International Seminar on Laterisation Processes (São Paulo, Brazil), p. 261-270.
Machado, A. B. 1983b. Termitic remains in some bauxites. In: A. J. Melfi and A. Carvalho (eds.), *Laterisation Processes.* Proceedings, II International Seminar on Laterisation Processes (São Paulo, Brazil), pp. 251-254.
Mathews, A. 1977. *Studies on termites from the Mato Grosso State, Brazil.* Academia Brasileira de Ciências, Rio de Janeiro, 267 p.
Mermut, A.R., Arshad, M.A. and St-Arnaud, R.J. 1984. Micropedological study of termite mounds of three species of *Macrotermes* in Kenya. *Journal of the American Soil Science Society* 48: 613-620.
Murphy, C. P. 1986. *Thin section preparation of soils and sediments.* A. B. Academic Publishers, 150 p.
Noirot, CH. 1970. The nests of termites. In: K. Krishna and F. M. Weesner (eds.), *Biology of Termites*, Academic Press, New York and London, vol. 2: 73-123.
Ruelle, J. E. 1964. L´architecture du nid de *Macrotermes natalensis* et son sens fonctionnel. In: A. Bouillon (eds.), *Études sur les Termites africains*, Éditions de l´Université, Leopoldville, pp 327-362
Sands, W. A. 1987. Fossil invertebrates. Ichnocoenoses of probable termite origin from Laetoli. In: M. D. Leakey and J. M. Harris (eds.) *Laetoli. A Pliocene site in northern Tanzania.* Oxford Science Publications. p.
S. E. A. G. and P - I. N. T. A. 1990. Secretaria de Agricultura, Ganadería y Pesca- Instituto Nacional de Tecnología Agropecuaria. Atlas de Suelos de la República Argentina.
Scasso, R. A. and Limarino, C. O. 1997. Petrología de las pelitas y minerales de arcilla. *Petrología y Diagénesis de Rocas Clásticas*. Asociación Argentina de Sedimentología Publicación especial N°1.
Silvestri, F. 1903. Contribuzione alla conoscenza dei Termitidi et Termitofili dell´ America meridionale. *Redia* 1: 1-234.
Sleemann, J. R. and Brewer, R. 1972. Microstructures of some Australian termite nests. *Pedobiology* 12: 347-373.
Smith, R. M. H. and Kitching, J. 1997. Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: A reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. *Palaeogeography Palaeoclimatology, Palaeoecology* 131: 29-50.
Stoops, G. 1964. Application of some pedological methods to the analysis of termite mounds. In: A. Bouillon (eds.), *Études sur les termites africains.* Edition de l´Université, University of Leopoldville, pp. 379-398.
Torales, G. J. 1984. Contribución al conocimiento de las termitas de Argentina (Pcia. de Corrientes). *Cornitermes cumulans*. (Isoptera: Termitidae). *FACENA* 5: 95-133.
Torales, G. J., Laffont, E. R., Arbino, M. O. and Godoy, M. C. 1997. Primera lista faunística de los isópteros de la Argentina. *Revista de la Sociedad Entomologica Argentina* 56: 47-53.

Recibido: 10 de enero de 2002.
Aceptado: 20 de enero de 2003.

Appendix

Glossary (Based on Brewer, 1964 and Bullock et al., 1985)

Microstructure

Spongy structure: Continuity of the solid material broken by numerous, often interconnected voids. Few, if any, separated aggregates.

Intergrain cemented structure: Coarse fraction wholly embedded into a dense mass of fine material.

Pellicular structure: Coarse grains completely or partly surrounded by fine material, which bridges and welds the grains together.

Platy structure: Elongate units or laminae separated by thin, straight, planar voids.

Types of voids

Simple packing void: Equant to elongate, interconnected, occuring between single grains.

Complex packing void: Voids occuring between single grains and small aggregates.

Planar void: Planar according to the ratio of main axes. Fissure.

Vugh: Relatively large void other than a packing void, spherical to elongate, irregular, not normally interconnected to voids of comparable size.

Birefringence fabric of fine material

Undifferentiated: Absence of interference colours in the fine mass due to being composed of isotropic or opaque materials or to masking by humus.

Granostriated: A birefringent halo is seen around the grains in polarized light.

Stipple-speckled: Slight individual and isolated birefringent speckles, randomly distributed throughout.

Parallel striated: Birefrigent streaks occur in parallel or subparallel sets.

Related distribution of coarse and fine materials

Single spaced porphyric: The distance between coarse grains is less than their mean diameters.

Double spaced porphyric: The distance between coarse grains is one or two times their mean diameters

Close porphyric: Coarse grains have points of contact.

Open porphyric: Coarse grains are embedded into a dense mass of fine material and their distance is more than twice the diameters.

Chitonic-gefuric: Coarse grains are wholly or partially coated by finer material. There are also traces of fine material linking the