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Subterranean ant nests: trace fossils past and future?

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Abstract

Many species of ants excavate complex, species-typical nests in soil. The basic structural units of many nests are descending tunnels connecting flattened, generally horizontal chambers of oval to lobed outline. The species-typical structure of many nests results from variation in the size, shape, number and arrangement of these basic elements. Nest architecture can be rendered by filling subterranean nests with a thin slurry of orthodontal plaster, then excavating and reconstructing the hardened cast. Photographs of such nest casts of nine species of ants from northern Florida show the range and type of variation of architecture. Preservation conditions under which ant nests could form complex trace fossils are discussed, and reports of such traces reviewed. The images presented in this paper will help to alert trace fossil specialists to the potential range of appearance of such nest fossils.

Keywords: Formicidae; nest structure; trace fossils; burrows; ants; recent

1. Introduction

The conspicuous, often spectacular constructions of social wasps, bees and termites have received much attention (Wilson, 1971). By contrast, the subterranean nests of ants are hidden from view, and are fundamentally different because they are made by the removal of soil, not by construction. As a result, these nests are more difficult to study and are largely terra incognita. Reports beyond casual descriptions are rare and most are simply verbal descriptions or drawings (McCook, 1879; Wheeler, 1910; Talbot and Kennedy, 1940; Autuori, 1942; Scherba, 1961; Ettershank, 1968, 1971; Lavigne, 1969; Nielsen and Jensen, 1975; Dlussky, 1981; MacKay, 1981; Conway, 1983; Kugler and Hincapie, 1983; McCahon and Lockwood, 1990; Bristow et al., 1992; Antonialli-Junior and Giannotti, 1997). By and large, information on ant nest architecture is collected incidentally, rather than as a primary goal of research. Exceptionally, Tschinkel (1987) determined chamber area and shape in relation to depth and colony size. However, in spite of the lack of quantitative data, it is clear that ant nests are highly structured and species-typical in both size and 'morphology'.

With the recognition that the insect colony is a functional unit in the same sense that an organism is, the concept of the superorganism has re-emerged (Lumsden, 1982; Wilson and Sober,

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1989). This concept suggests that the social insect colony is organized on several levels, each subject to natural selection. Just as mechanisms evolved to integrate the parts of the individual ant into a whole functioning organism, so have mechanisms evolved to integrate the individual ants into a functioning superorganism, capable of drawing resources from the environment, regulating internal (colony) functions and responding to stresses (Wilson and Sober, 1989).

In this light, the nest and its architecture are almost certainly not simply shelter, but are such a mechanism of integration. To modify the ideas of Turner (2000) slightly, the nest is part of the extended superorganism. The natural nest architecture probably structures the colony within it, and organizes its functions, much as the architecture of a factory building organizes the labor force within it. The generally centrifugal movement of aging workers away from the brood creates an association of age, location and task, and therefore structures the colony spatially, even in laboratory colonies (Chew, 1960; Golley and Gentry, 1964; Lavigne, 1969; MacKay, 1981; Porter and Jorgensen, 1981; Tschinkel, 1987; Hölldobler and Wilson, 1990; Sendova Franks and Franks, 1995; Tschinkel, 1998, 1999a,b). Most significantly, when the social structure is disrupted experimentally or by a move to a new nest, workers resume the same positions they occupied in the previous nest (Sendova Franks and Franks, 1995). The pay-off returned by the nest, although currently unknown, must be considerable, for the large amounts of energy invested in nest excavation (up to 10% of daily energy intake; Sudd, 1969) could have been invested in other fitness-enhancing functions instead.

Trace fossils of what appear to be ant nests have been reported (Laza, 1982; Bown et al., 1995; Hasiotis and Demko, 1996; Laza, 1997). The great age of these fossils suggests that ants have been excavating nests for most of their evolutionary history. A deeper knowledge of the structure, function and mechanism of formation of modern ant nests would be helpful for detecting and understanding ant nest trace fossils. Study of such fossils might shed light on the evolution of sociality and ant behavior, as well as the paleoecological conditions under which ants evolved. The purpose of this short paper is to share what I have learned in the early stages of a long-term comparative study of ant nest architecture. Although no broad generalizations can yet be made across the family Formicidae, the information I have accumulated so far should be useful and interesting to those who pursue trace fossils.

2. Rendering nest architecture in three dimensions

Subterranean ant nests consist of shaped voids in a soil matrix. Although a researcher can readily excavate nests from at least some soils, this is not very effective in making these voids visible. I have used two methods for studying nest architecture. In the first, a pit is dug next to the nest and the chambers are exposed one at a time, starting from the top. As each is exposed, its depth and orientation are recorded, its contents are collected for later counting and measuring, and its outlines are traced on transparent acetate sheets. Using this method, I completed detailed excavations and complete census of 35 Florida harvester ant nests (*Pogonomyrmex badius*), ranging from 2 to 3.5 m deep and consisting of five to 150 chambers (Tschinkel, 1998, 1999a,b). This method resulted in a reasonable rendering of the two-dimensional outlines and spatial distribution of the horizontal chambers, but did not record the vertical tunnels connecting them. On the other hand, the method produced a complete record of how the colony members are distributed within the nest.

The second method begins with filling ant nests with a thin slurry of orthodontal plaster (Williams and Lofgren, 1988) to produce a potentially perfect three-dimensional rendering of the nest's voids. The hardened cast is excavated and then reassembled to produce the finished cast. For reassembly, chambers are supported with steel rods driven into holes in a backboard. When the tunnels are large in diameter, the thin slurry may completely fill a 3-m-deep nest, but when they are narrower, the plaster slurry may stop flowing at an intermediate level. In such cases, it may

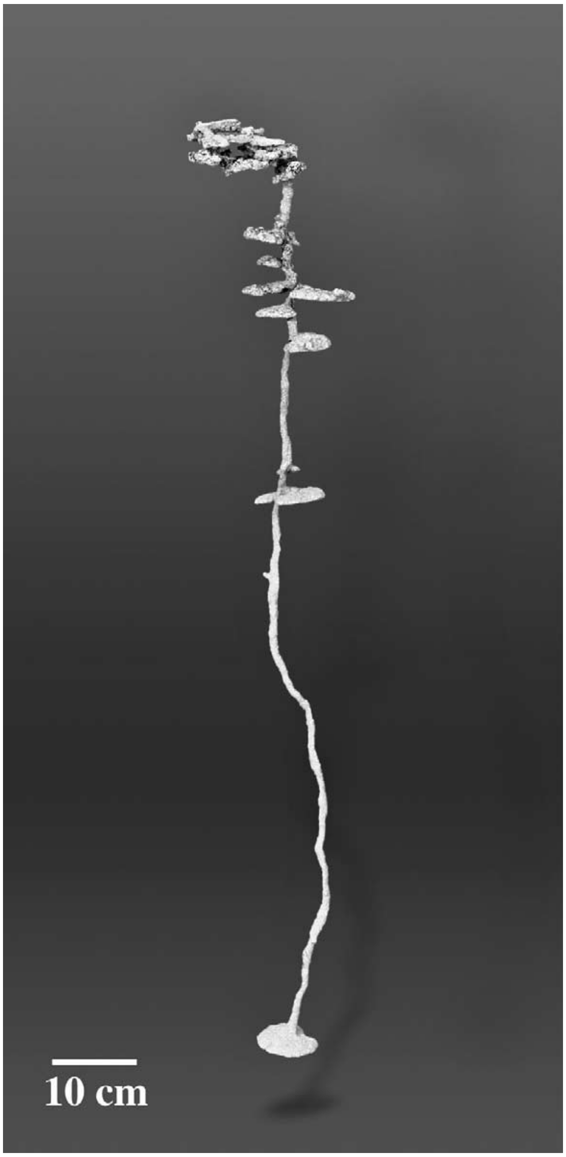

Fig. 1. *Odontomachus brunneus*, the trap-jawed ant. A relatively primitive ant with colonies of up to 300 workers. Common in mixed woodlands in north Florida. Nest structure is a single vertical tunnel connecting chambers that increase in spacing toward the nest bottom. $N = 3$ plaster casts.

require multiple cycles of pouring followed by excavation to make a complete cast. Casting works best in very sandy soils. Heavy clay soils do not allow air to be displaced from chambers, and therefore produce incomplete casts and voids within the plaster.

3. Examples of ant nest architecture

Using this plaster-casting method, I have made and reconstructed the mature subterranean nests of nine species of ants (Figs. 1–9[1]) from the Apalachicola National Forest in northern Florida. Although only one example is shown for each species, I have made multiple casts and/or excavations of all species, and confirmed that the architecture is species-typical. The sample size is given in each figure caption, along with a summary of each nest's key features. These nests vary greatly in total size, from 20–30 cm deep (Figs. 3 and 6) to huge underground fortresses extending to depths of almost 4 m (Figs. 7 and 9). Although each of the species builds a species-typical nest, there are elements that are common to most or all. The most obvious such elements are more or less vertical tunnels connecting more or less horizontal chambers. These can be distinguished in most casts in spite of variations in their expression. Most of this variation can be ascribed to differences in the element parameters. Thus, tunnels may vary in diameter, chambers may vary in horizontal area, perimeter and outline, spacing between chambers may differ, total depth may vary, and so on. The sum of this variation gives rise to distinct, species-typical architectures, as the accompanying photographs show (Figs. 1–9). In most cases, the basic unit – the combination of tunnels and chambers – remains recognizable. In addition to interspecific variation, elements may also vary within the nest of a species, for example, from the soil surface to the bottom of the nest, or among nests of different size.

Some examples of patterns follow. A very common type of nest structure is one in which a single vertical tunnel connects a series of flattened horizontal chambers, which serve as living space for

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[1] For Figs. 1–9 plaster casts of the subterranean nests of several ant species. All casts were made by filling the nest with a thin slurry of orthodontal plaster, allowing this to harden, excavating the cast and reconstructing it with support. In these images, the backboard and steel rods supporting the casts have been digitally removed. Scale is provided by a scale bar. The number of casts or excavations is given as N in each figure caption.

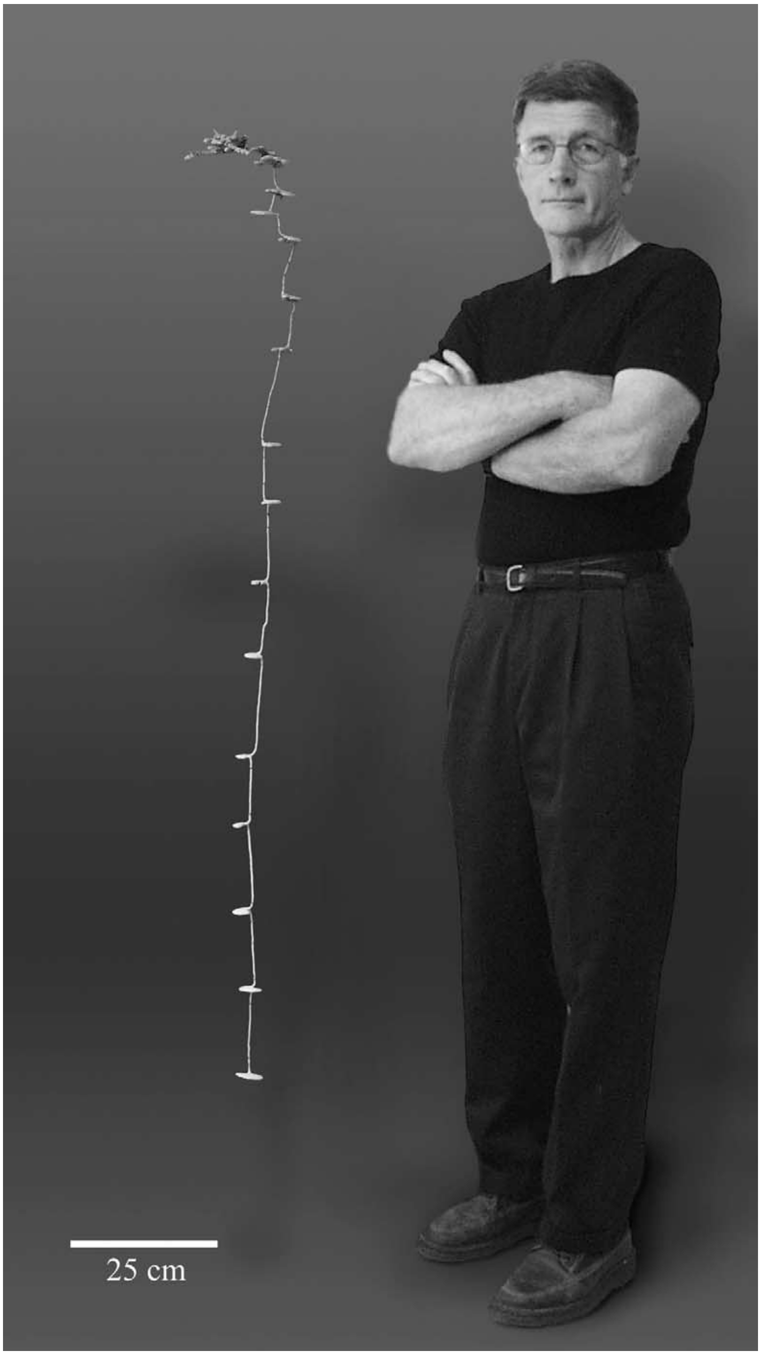

Fig. 2. *Conomyrma* sp. A common ant in very hot, barren sites. Colonies may contain up to 1000 or more workers. A simple vertical tunnel connects horizontal chambers in a ladder-like fashion. Chambers vary little in spacing or size except just below the surface, where they have a very different structure of complex, fused, elongated chambers. $N=2$ plaster casts and 1 excavation. Height of person is 1.78 m.

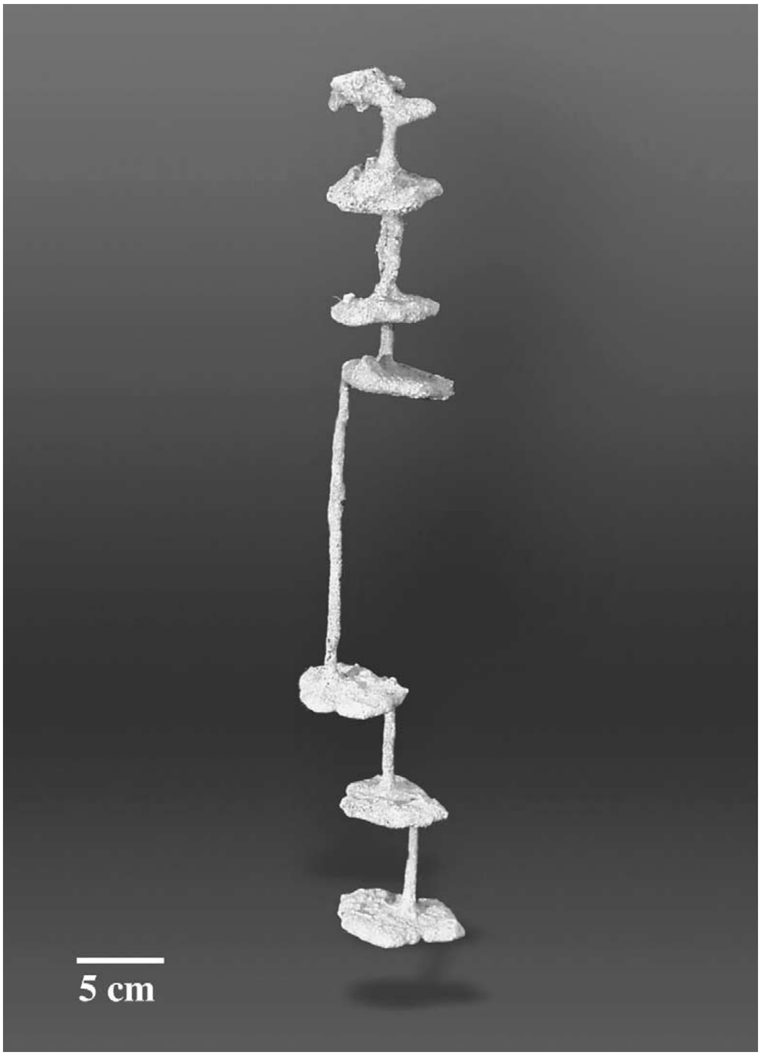

Fig. 3. *Aphaenogaster* sp. A common woodland ant. Colonies are small, up to 200 workers, and the nests are very shallow. Chambers vary little with depth, but the vertical connection usually enters the center of each chamber from above, but may emerge from close to the margin of the chamber below. $N = 3$ plaster casts.

the ants. We can refer to this as the 'shish-kebob' unit. Examples of this structure can be seen in Figs. 1–5 and 7. The chambers may be evenly spaced, as in Figs. 2, 3 and 5, concentrated near the top as in Figs. 1, 4 and 9, or irregularly spaced as in Fig. 7. The chambers may be all about the same size, as in Figs. 2, 3, 5 and 7, or they may decrease in size with depth, as in Figs. 1, 4 and 9. Because all these nests were formed in pure sandy soil, these differences are species differences, not differences imposed by soil variation.

Combining multiple 'shish-kebob' units in close proximity can create much more complex nests, as for example in the nest of the fire ant, *Solenopsis invicta* (Fig. 8A). This nest is composed of many such units packed so closely together that many chambers merge with one another. The same structural unit that composes all the previous nests (Figs. 1–7) remains apparent.

The best-characterized nest is that of the Florida harvester ant, *Pogonomyrmex badius* (Fig. 9). These seed-harvesting ants are a characteristic

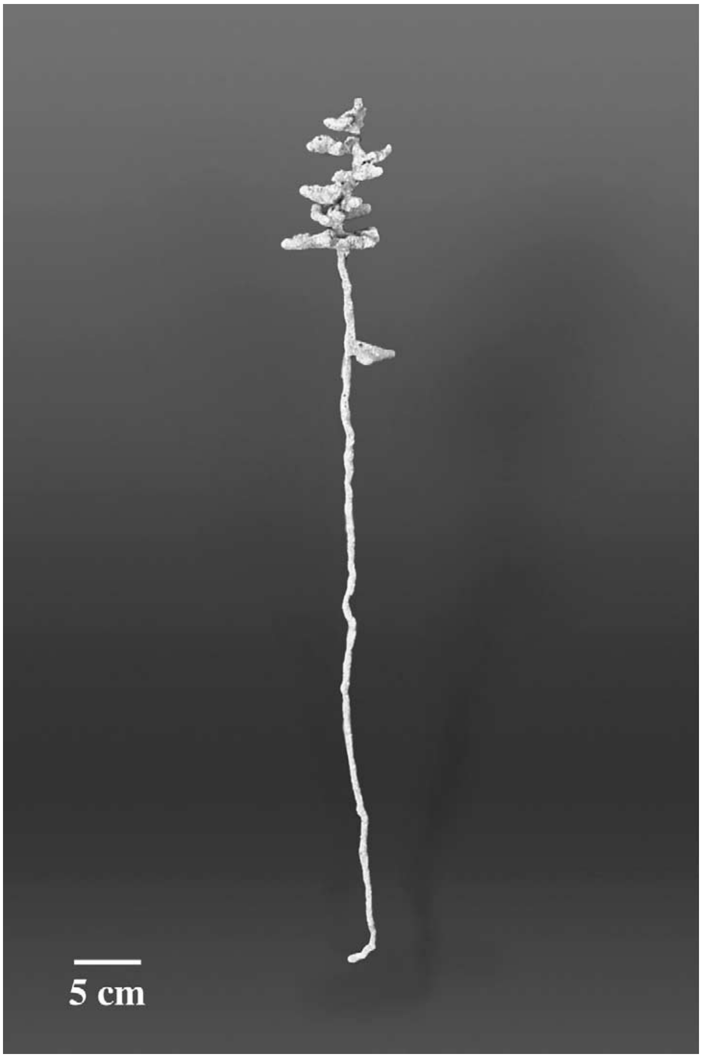

Fig. 4. A young nest of *Pheidole morrissi*. At maturity, colonies may contain up to 6000 workers, and the nest may consist of several vertical chamber series. Note the concentration of chambers near the surface. This feature is retained in mature nests. $N = 2$ plaster casts.

feature of the deep, sandy Gulf Coastal Plains soils. Colonies may contain up to 8000 workers, who dig these monumental nests in 4–5 days, and do this once or twice a year, just prior to moves (personal observation). The top-heavy shape of these nests is therefore not the consequence of a gradual downward enlargement of a small nest, but is the structure that the workers 'intend' to build. A newly founded nest consists of a single chamber at the end of a simple vertical tunnel 20 cm deep. During colony growth, the nest is enlarged more through nest deepening and chamber addition than through chamber enlargement (Tschinkel, 1999a,b). Nevertheless, the vertical distribution of chamber area does not change with nest size, remaining top-heavy at all sizes. A mature nest may contain 150 chambers in four to five vertical series connected by a total of 10 m of tunnels. More than half of the total chamber area occurs in the top quarter of the nest, giving it the top-heavy shape apparent in Fig. 9. Chambers near the surface are larger,

Fig. 5. *Trachymyrmex septentrionalis*, a fungus-gardening ant with up to 1500 workers. Each of the ovate chambers contained a fungus garden constructed of caterpillar droppings and plant parts. Basic structure is still vertical tunnels connecting chambers, although chamber shape is not flattened as in most ant nests. In life, the chambers are simple voids without internal structure. Mature colonies typically consist of two chambers, but can contain as many as five. $N = 4$ plaster casts.

have more lobes and are more closely spaced than deeper chambers. Circumstantial evidence suggests that workers dig more under the low carbon dioxide concentrations found near the soil surface. In the bottom of the nest, concentrations of carbon dioxide are five times as high as at the surface (unpublished data). This non-linear carbon dioxide gradient may provide ants with information on their location within the soil column. It is possible that the observed depth-related arrangement of workers by age and of chambers by size and shape is based on information derived from this gradient. The tunnels are helical (Fig. 10A), with pitch increasing from 45° to about 60° in the first 50 cm of depth, and then remaining constant. They may spiral either clockwise or counter-clockwise, and sometimes change directions at a chamber base. All chambers are initiated on the outside of the helical tunnels and are enlarged in an outward direction (Fig. 10C), becoming more lobed as they become larger (Fig. 10B). The homogeneity of soil texture from the surface to the bottom of these nests makes it unlikely that these patterns are in response to changing physical characteristics of the soil.

4. Trace fossils from ant nests

There are several reports of trace fossils pre-

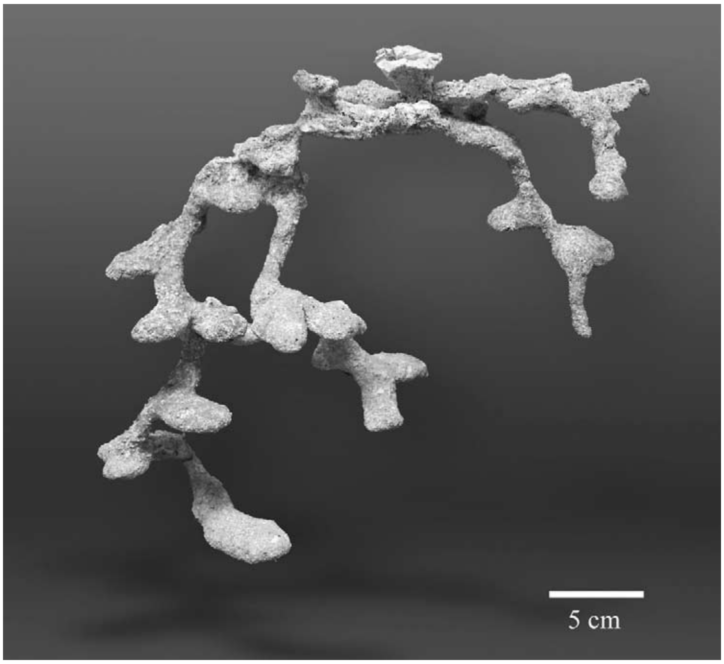

Fig. 6. *Formica pallidifulva*. Colonies are small and nests are very shallow. The tunnels are variable in cross-section and orientation, and the chambers more irregular and thicker than most other species. In addition, multiple branching gives the nest greater complexity. $N = 17$ plaster casts (thanks to my graduate student, Alexander Mikheyev, who made 16 of these casts as part of the research for the M.S. degree).

sumed to be fossilized ant nests (I am grateful to Stephen T. Hasiotis and Robert B. MacNaughton for making me aware of these). The presumed chambers of the majority of these are large and sub-globular, rather than flattened, suggesting that they were constructed by species of attine ants (*Atta*, *Acromyrmex*, *Trachymyrmex*) to contain their fungus gardens (Laza, 1982; Bown et al., 1995; Hasiotis and Demko, 1996; Laza, 1997). An ichnofossil described by Bown et al. (1995) has much smaller, more flattened, chambers arranged in tiers and connected by galleries, suggesting a non-attine species of ants (Hasiotis and Demko, 1996). However, resemblance to known ant nest architectures was insufficient to attribute this fossil to any particular modern ant genus. The ages of these fossils range from Jurassic and Tertiary to Late Pleistocene. Some therefore predate body fossils of ants by 100 million years, suggesting that their identity as fossil ant nests should be subjected to rigorous test.

Clearly, terrestrially deposited formations can retain trace fossils of ant nests. Several modern processes might form such fossils under the right conditions. Deep ant nests often penetrate through several soil horizons varying in color, grain size and other physical attributes. Sometimes the ants themselves fill existing chambers with soil excavated from elsewhere in the nest. I have seen *Prenolepis imparis* nests in which chambers in the white sands near the surface were filled with the deep red, clay-stained sands from much deeper chambers. Alternatively, water might fill chambers with finer, coarser, different colored or chemically different material than the surrounding soil matrix. Organic matter in chambers, such as the seeds of harvester ants, or the excreta or bodies of the ants themselves, might mark the inner chamber surfaces with a different color. If any of these contrasting fillings were later cemented into rock, they ought to show the 'ghosts' of nest chambers and tunnels. Such ghosts are

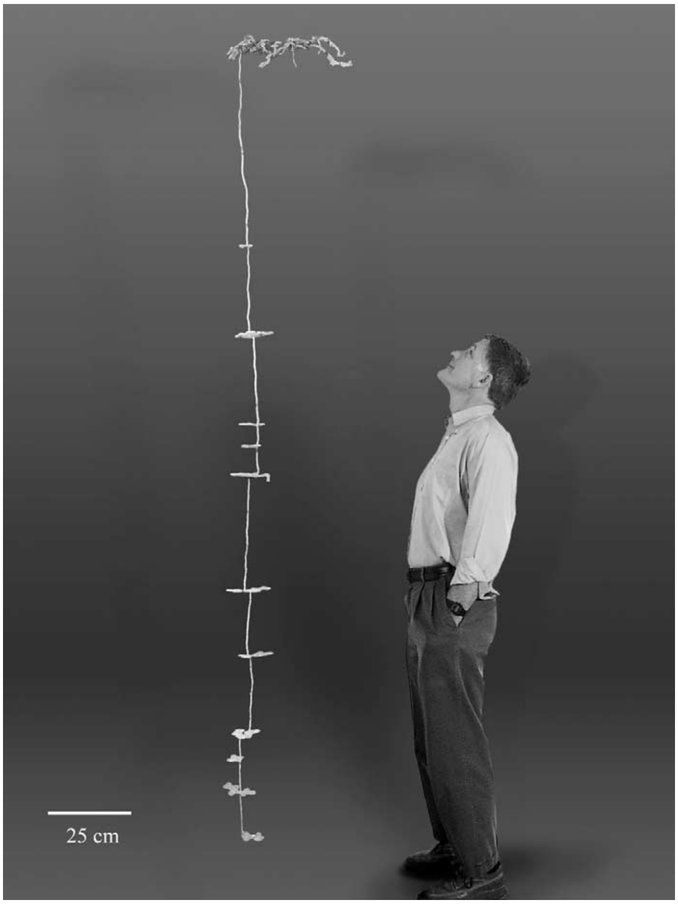

Fig. 7. *Prenolepis imparis*. Colonies of up to 11 000 workers make nests up to 4 m deep, with no chambers within 1 m of the surface. A single tunnel connects horizontal chambers whose outlines increase in complexity with size, but whose size does not change radically with depth. Connecting tunnels sometimes do not run straight through a chamber, but are offset, perhaps because they represent the next year's deepening. The structure just under the surface consists of complex, intersecting tunnels and chambers of irregular structure, often associated with roots. The function of this upper region is unknown. Height of person is 1.78 m. $N=2$ plaster casts and 11 excavations.

occasionally encountered during excavations. Finally, some types of soils might retain voids long enough to be consolidated into something rock-like with voids.

The photographs accompanying this article should help build an awareness of the structure of modern ant nests among ichnologists, and will help extend the search for further examples, as well as distinguish between true fossil ant nests and other traces. These images show that nests of many ant species are strongly patterned with respect to the arrangement and number of their subunits. The presence of similar organization in putative trace fossils should be part of the evidence that the trace was made by ants. Complete fossilization of many of the ant nests described in this paper would rival the marine burrow trace fossils described by Miller (2001) and Miller and Alberto (2001) in complexity.

As more examples of such fossils are discovered, they will help us to understand the evolution of ant nest-building behavior and the paleoecological conditions under which it evolved. Ants are believed to have descended from a tiphiid

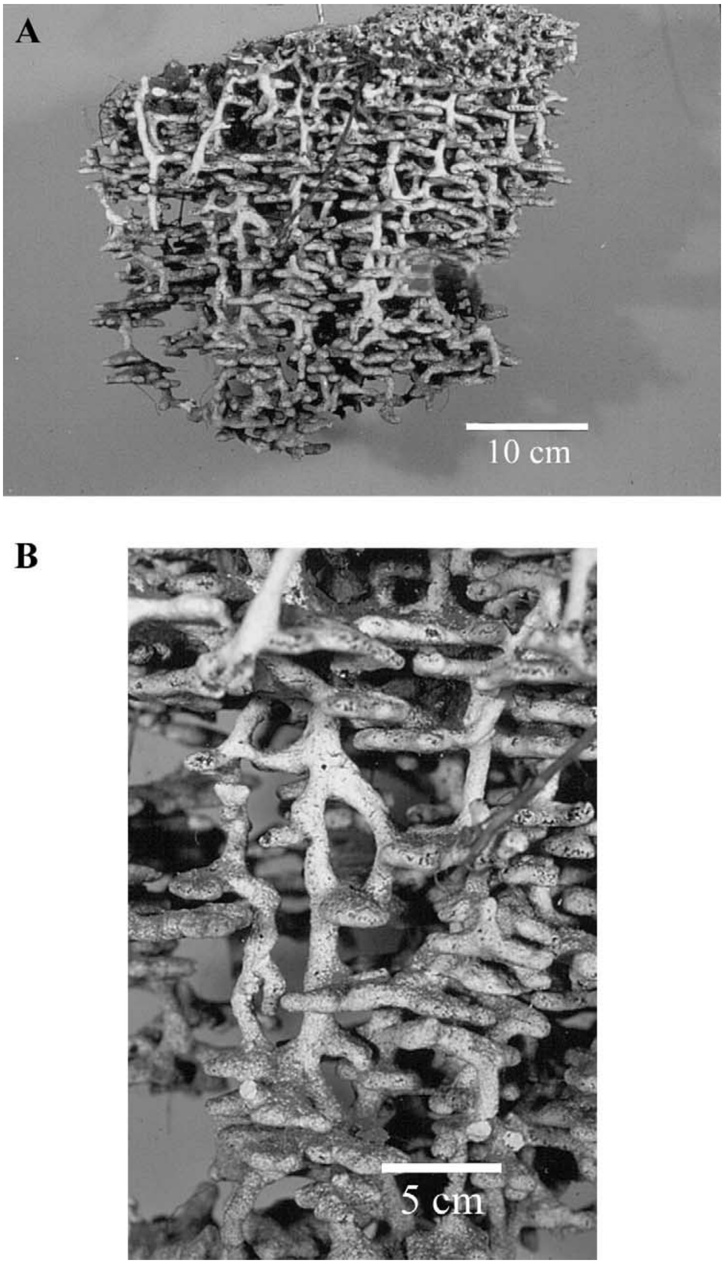

Fig. 8. (A) The fire ant, *Solenopsis invicta*. There are up to 250 000 workers in mature colonies, with nests up to 2 m deep. Although these nests look much more complex than all the previous ones, they nevertheless consist of the same basic units – vertical tunnels connecting horizontal chambers, as seen in B. These units are packed so close together that they merge in many places, but the relationship to the simple nests of Figs. 1–7 remains apparent. $N = 3$ plaster casts and many excavations.

wasp-like ancestor (Hölldobler and Wilson, 1990). These ancestral forms, like many of their modern descendants, dug burrows in soil and stocked them with paralyzed insects as food for their brood. The threshold to sociality was crossed when mother overlapped in the nest with her offspring, giving reproductive division of labor an opportunity to evolve. The nests and colonies of

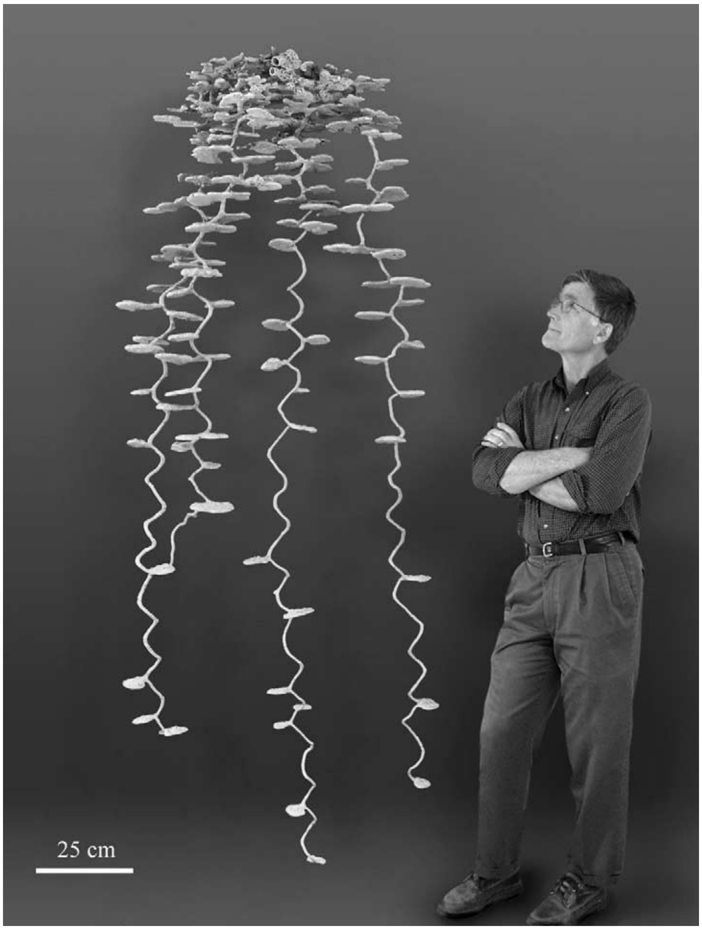

Fig. 9. *Pogonomyrmex badius*, the Florida harvester ant, and the best-studied of the species presented here. Colonies of up to 8000 workers make nests up to 3.5 m deep, with up to 150 chambers in four or five vertical series connected by helical tunnels that may spiral clockwise or counter-clockwise. Details of structure are discussed in the text. Height of person is 1.78 m. $N=3$ plaster casts and 35 excavations.

these proto-ants were almost certainly small and simple. The evolutionary path between these beginnings and modern ants led to larger, more integrated colonies and larger, more complex nests. Still, the ancestral legacy remains visible – it seems likely that the ground-nesting habit and the tunnel+chamber structure are both primitive features of ant nests that were already present in the pre-social ancestors of the ants. Evolution always molds the clay already in its hands. It is likely that branching, large chambers and many other features of modern ant nests are elements added after sociality arose. Trace fossils of these nests may someday allow us to describe the course of this evolution through the ages.

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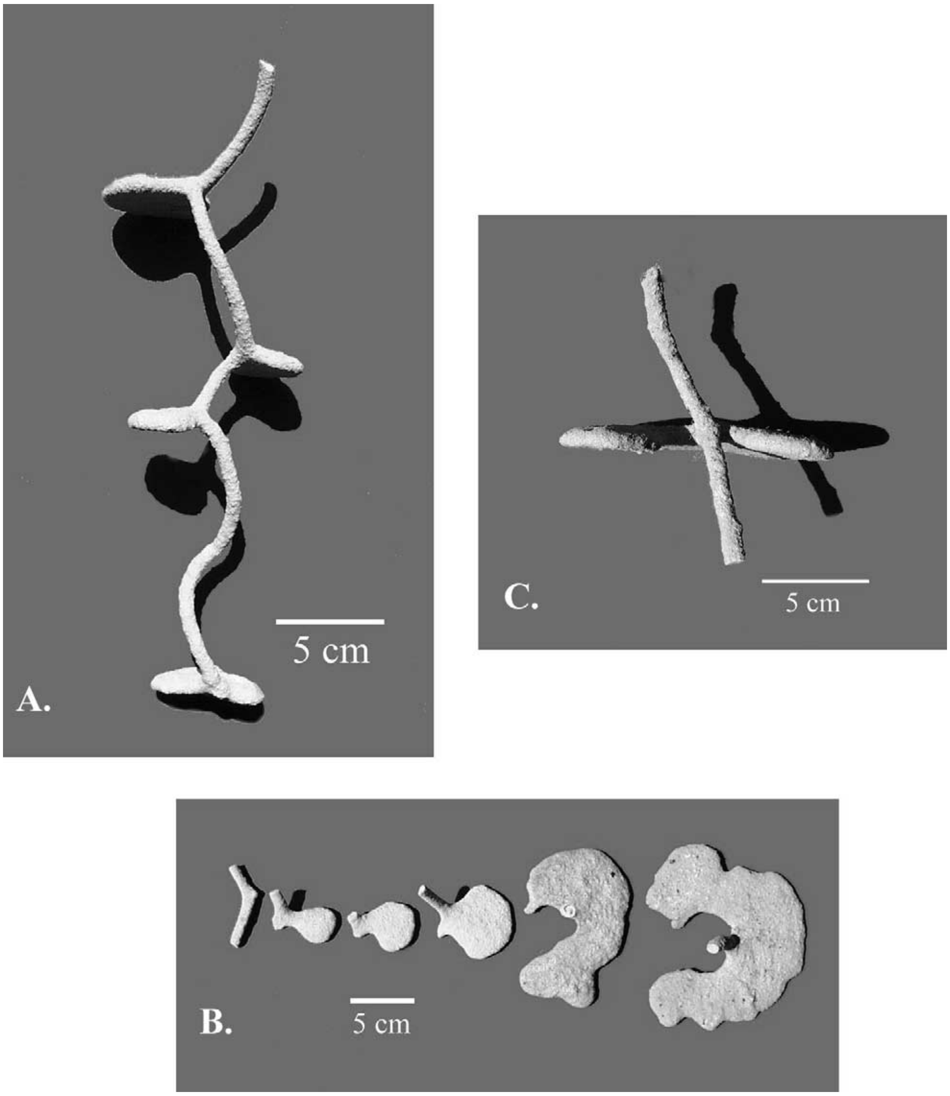

Fig. 10. (A) A segment from the bottom of a *Pogonomyrmex badius* nest, showing the helical tunnel connecting the chambers. Tunnels may branch, usually at the base of a chamber, and may reverse direction. (B) As chambers are enlarged, their outlines become multi-lobed and complex. Chambers near the surface are always more complex than deeper chambers. (C) Chambers are initiated on the outside of the helical tunnel, and are enlarged outward from the point of initiation. Although chambers may 'wrap around' the tunnel, the tunnel never passes through the center of deeper chambers.

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