Complete Excavation and Mapping of a Texas Leafcutting Ant Nest

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ABSTRACT A medium-sized nest of the Texas leafcutting ant, *Atta texana* (Buckley), in northern Louisiana was excavated completely, and a three-dimensional model of its external and subterranean features was constructed. In total, 97 fungus gardens, 27 dormancy cavities, and 45 detritus cavities were located. At the lower center of the funnel-shaped nest was a large central cavity, which in winter functions as a domicile for the colony and where the alate brood is reared. Vertical tunnels, possibly as deep as 32 m, may serve as wells leading to the water table. Winter mean annual temperatures within the central cavity may limit the northern geographical range of *A. texana* to ≈33° N latitude. The inquilines *Attaphila fungicola* Wheeler, *Pholeomyia comans* Sabrosky, *Ceuthophilus* sp., *Lobopoda subcuneatus* Campbell, *Geomysaprinus* nr. *formicus* (Hinton), species of Aleocharinae, and a species of Annelida were seen in nest cavities and galleries.

KEY WORDS *Atta texana*, nest excavation, central cavity, feeder holes, fungus gardens

During the past 70 years, several nest excavations of *Atta* spp. have revealed the internal architecture of mature nests. Prominent among these excavations are those reported by Jacoby (1955) (*Atta sexdens rubropilosa* Forel), Jonkman (1980a,b) (*Atta vollenweideri* Forel), Moffett (1995) (*Atta capiguara* Gonçalves), Moser (1963) [*Atta texana* (Buckley)], and Stahel and Geijskes (1939) [*Atta sexdens* (L.) and *Atta cephalotes* (L.)]. Because these nests were immense and because resources and labor were limited, only portions of these nests could be excavated. Models were then constructed to show probable locations of the main nest contents.

I report here the complete excavation of a medium-sized nest of *A. texana*, and the subsequent modeling of the exact locations of the major nest features. Two previous publications described other aspects of this nest and its excavation. Neelands (1959) published a popular article narrating the digging events, and Moser (1986) used aerial photographs to summarize the economic implications of damage to the pine plantation where the nest was located.

Materials and Methods

The nest was located ≈3 km north of Lucky, in Bienville Parish, LA, at latitude 32° 17′ N, longitude 92° 59′ W, at an elevation of 61 m above mean sea level. The nest was in a large 4-yr-old pine (*Pinus taeda* L.) plantation (Fig. 1) (Moser 1986). It was bounded by a gully 10 m to the southeast and had excellent surface drainage (Moser 1986).

Care was taken to select a nest located on a relatively flat surface, and where no large trees were present (the roots of such trees can make mapping of nest contents difficult to impossible). Visible surface features of the nest were mapped first. In addition to these entrance holes, the locations of the many feeder holes (Moser 1962) were charted (Fig. 2).

The entire nest was scalped and excavated 15–16 June 1959, by using a Caterpillar D-8 bulldozer. A second and larger D-9 bulldozer also was used solely to remove soil displaced by the D-8 (Neelands 1959). The D-8 bulldozer began slicing ≈9 m left from the nest center, progressing forward for another 9 m, and then repeating this action from left to right and back again. The bulldozers sliced off ≈23 cm of dirt at each pass. Their blades were "delicate enough" to lay open most of the various kinds of ant excavations without crushing or filling them, so that the cavity contents could be measured, collected, and preserved. However, the scalping destroyed most of the smaller galleries connecting the cavities as well as most of the vertical and horizontal tunnels. As cavities and galleries were uncovered, their positions were plotted using a plane table and alidade (Figs. 2 and 4). The dimensions and contents were recorded for each cavity. Depths of the nest features were measured with a rod and level. By the end of the second day, the excavation was terminated at a depth of 4.6 m (Fig. 3), when it was assumed that the last cavity had been uncovered. Vertical tunnels extended downward from the lowest cavity, and a weighted string was use to determine the depth of the deepest of these tunnels (Fig. 5G). These

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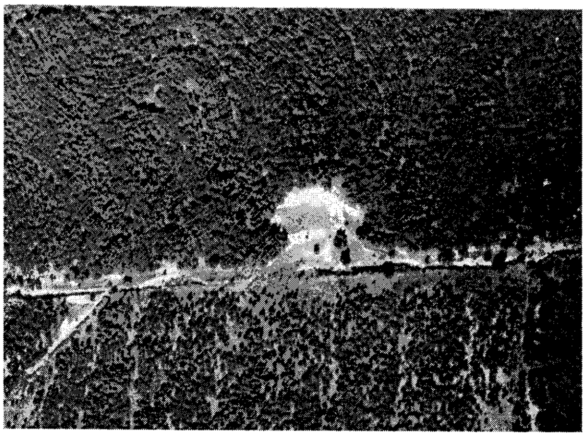

Fig. 1. Enlargement of October 1966 aerial photograph. Nest was killed in 1959 excavation, but damaged area of pine plantation is still clearly evident. Photo courtesy of USDA Farm Service Agency (formerly USDA-Agricultural Stabilization and Conservation Service).

data made it possible to construct a three-dimensional clay model of the nest (Figs. 5 and 6).

Results and Discussion

The Nest Surface. The nest surface was medium-sized and oblong, with mounds and spoil of red soil covering an area of ≈4.5 by 6 m (Figs. 2, 4, 5, and 6). Obvious on this spoil were the many entrance holes within smaller crescent-shaped mounds (Figs. 2 and 4). Soil at the site was Ruston fine sand loam. The topsoil (A horizon) was a black, sandy organic layer ≈30 cm in thickness. The ants had covered the A horizon with a layer of red soil that they brought up from below, and this layer averaged ≈15 cm in thickness. Underlying the A horizon was a red, moderately permeable sandy-clay layer ≈4.3 m in thickness. Below this layer was a soft, white sand that provided excellent drainage. The nest age was estimated to be 4–6 yr, because the nest was within a 4-yr-old plantation of *P. taeda* in which all colonies were thought to have been exterminated with methyl bromide before planting.

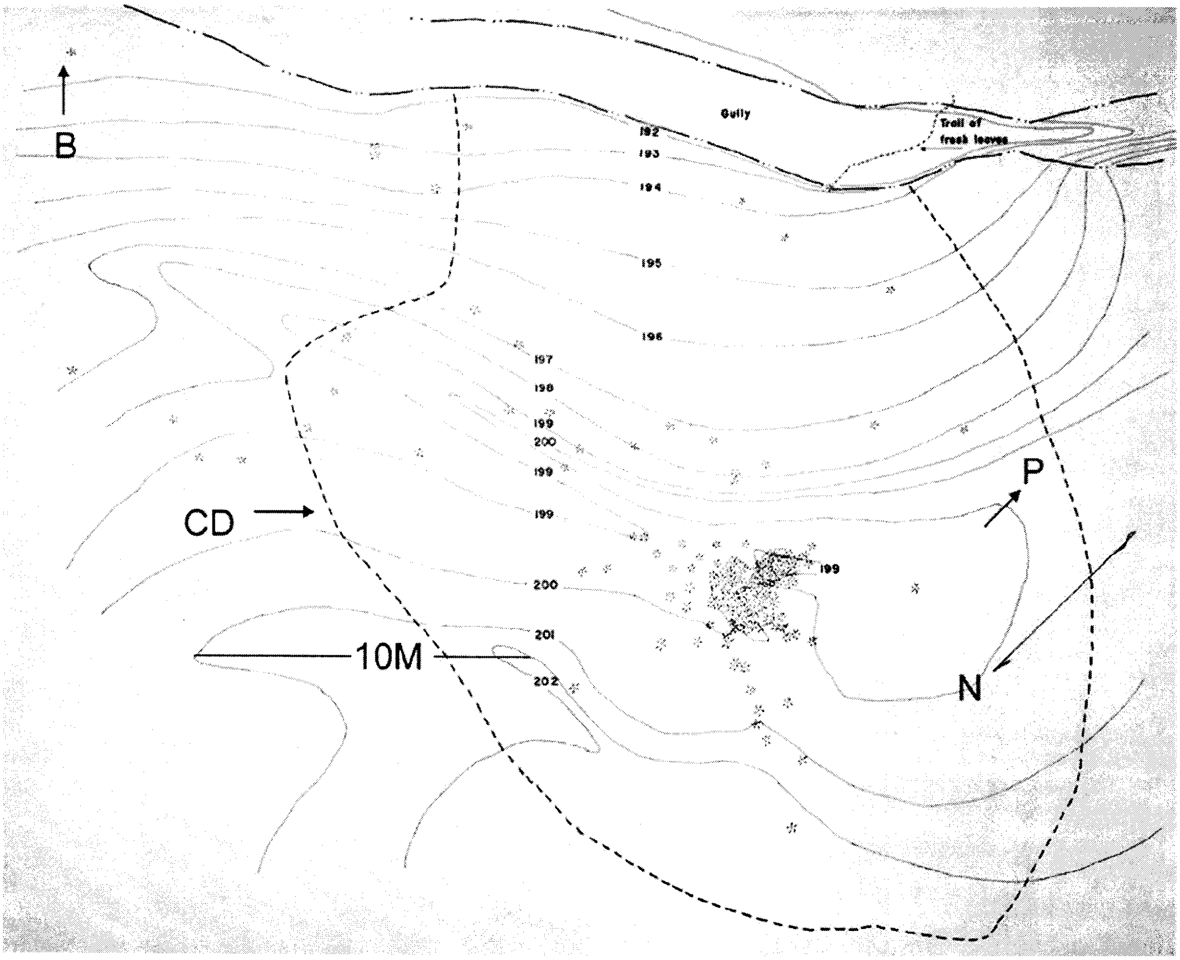

Fig. 2. Major surface features of nest center and surrounding area showing feeder holes marking entrances to horizontal underground tunnels, circle of damage, and location of plane table. B, feeder hole on soil surface; CD, circle of damage; N, north; and P, location of plane table.

Fig. 3. Excavation was terminated at depth of 4.6 m.

The nest was in the center of an ≈0.2-ha circle of damage in the plantation (Figs. 1 and 2). All pines within this circle were dead or stunted; trees nearest the nest were injured the most, with damage progressively lessening toward the periphery (Fig. 2). Most losses apparently occurred in the winter, because there was little evidence by June of needle clipping by workers. Leaves were transported to the nest center by trails on the ground surface and through numerous underground horizontal tunnels, which ran radially from the nest center, at a depth of ≈25 cm below the soil surface (Fig. 7). Presumably, the tunnels kept leaves from becoming desiccated when the workers foraged over long distances and provided protection to the workers from predators and parasitoids, such as phorid flies. *A. cephalotes,* at least, rely on minor workers riding on leaves to protect foragers from phorid flies (Moffett 1995), but *A. texana* does not use this tactic. The reason for this difference in behavior may be that workers of *A. cephalotes* forage primarily by surface trails, whereas those of *A. texana* may rely mostly on tunnels for protection.

Feeder holes are aboveground entrances to these underground tunnels (Fig. 7) and thus indicate the locations of the tunnels, which extended in all directions from the nest center (Fig. 2). These feeder holes were also within crescent-shaped mounds, identical to those on the center surface of the nest, but located away from the nest proper.

Feeder holes were most numerous within the area of tree damage, but some were located as far as 11 m from the outside limits of this circular area. The location of one tunnel terminating at a feeder hole was clearly marked by a trail of fresh leaves laid down overnight at the bottom and sides of the adjacent gully (Fig. 2). Jacoby (1955) notes for *A. sexdens rubropilosa* that similar tunnels (termed Schleppkanäle or drag channels) may radiate as far as 200 m from the nest center.

Surface trails of most other species of *Atta* are far more conspicuous than those of *A. texana,* perhaps indicating that the bulk of leaf material may come to the latter nests via underground tunnels.

Nest Interior. The nest interior was roughly funnel shaped (Fig. 5), with 22 cavities at depth levels of 0–1 m, 96 at 1–2 m, 43 at 2–3 m, and eight below 3 m. The interior nest center was located on the east side of the surface spoil (Fig. 6). The nest contained 169 cavities in total, including 97 fungus garden cavities, 27 dormancy cavities, and 45 detritus cavities (Table 1). Fungus garden cavities are "household" chambers in which the ants raise their brood on a basidiomycete fungus garden that serves as a nutritional basis for their survival. Dormancy cavities may serve as storage areas for excess workers (Moser 1963). Detritus cavities function much as sanitary landfills in human societies.

Fig. 4. W. H. Bennett (deceased) examining nest center. Plane table is at top center.

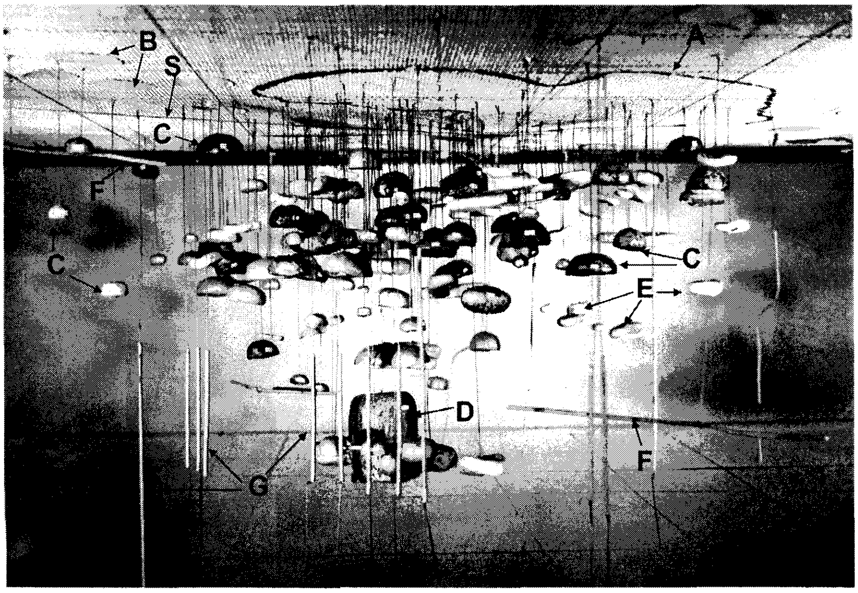

Fig. 5. Clay model viewed form ESE, showing funnel-shaped underground structure of nest and major features. A, edge of excavated surface subsoil; B, feeder holes on soil surface; C, typical fungus garden cavities are shaped like inverted mixing bowls (those colored black were largely full of fungus); D, central cavity at nest bottom; E, irregularly shaped detritus cavities; F, horizontal tunnels; G, vertical tunnels; and S, south end of north–south line on ground surface of nest.

These cavities were connected by galleries (Fig. 5), which were usually short and sometimes curved, whereas both horizontal and vertical tunnels are long and straight.

The three cavity types occurred in fairly distinct areas of the nest. All but one of the dormancy cavities (Moser 1963) were under the surface spoil. Detritus cavities were mostly E of the surface spoil, and many were concentrated under a lush, grassy area ≈3 m northeast of the surface spoil (Fig. 6). Grass in this location was noticeably greener and denser than in any other area around the nest, possibly because it used nutrients from the detritus below. Fungus garden cavities that were full or partially full of garden material were mostly located in a line E of the surface spoil and between the detritus and dormancy cavities, but a

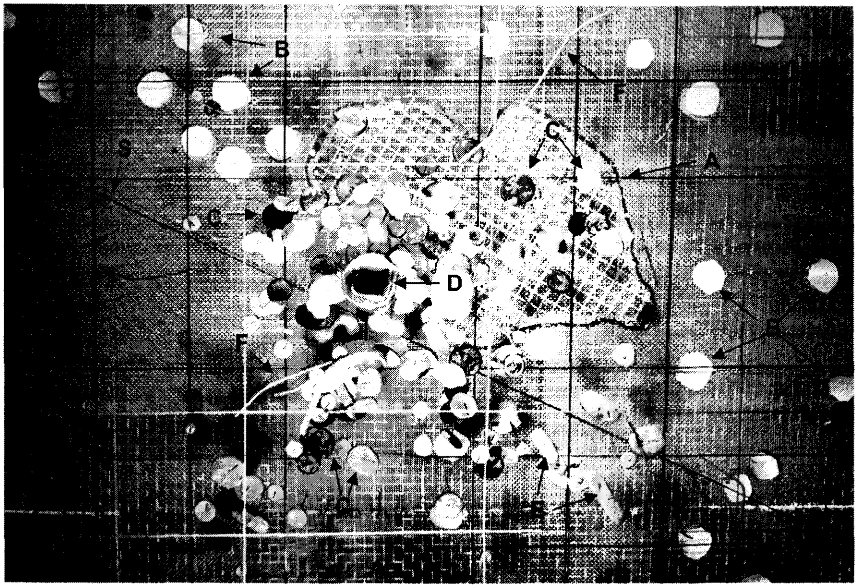

Fig. 6. Clay model of nest viewed from bottom of central cavity. Note that underground features are concentrated on east edge of excavated surface subsoil. A, edge of excavated surface subsoil; B, feeder-holes on soil surface; C, typical fungus garden cavities (those colored black were largely full of fungus); D, central cavity at nest bottom; E, irregularly shaped detritus cavities; F, horizontal tunnels; N, north end of north–south line on ground surface of nest; and S, south end of north–south line on ground surface of nest.

Table 1. Types of cavities at various depths

Depth (m)	Fungus garden ≈full	Fungus garden ⅛ to ½ full	Fungus garden trace-empty	Fungus garden sand-filled	Dormancy	Detritus	Total
0–1	10	0	1	0	5	6	22
1–2	5	15	27	5	19	25	96
2–3	0	4	20	2	3	14	43
3–4.6	0	0	7	1	0	0	8
Total	15	19	55	8	27	45	169

few were scattered in peripheral areas and under the spoil (Fig. 6). Empty fungus garden cavities and those with a trace of garden substrate were situated mostly below the full cavities and at the periphery of the nest.

Fungus Garden Cavities. Of the 97 fungus garden cavities, 34 were wholly or partially filled with active fungus gardens, 55 were mostly empty, and eight were partially or completely filled with sand (Table 1). Most cavities with fungus gardens were in the upper 2 m, whereas most empty cavities were at depths >2 m. Sand-filled cavities were found at most depths. Fungus garden cavities are typically the size and shape of an inverted mixing bowl (Moser 1963). The long diameters of cavities ranged from 7.6 to 90 cm and averaged 29 cm. Most gardens rested on the bottoms of cavities with roots penetrating the cavities for support of these fragile gardens (Moser 1963). Only a few workers were present in empty cavities and in cavities with sand. Only nine of the 34 fungus gardens contained worker larvae and pupae. The nest soil temperatures were 26, 25, 21, and 20°C at 0.45-, 1.2-, 2.4-, and 2.6-m depths, respectively. Generally, broods were largest in fungus gardens in the upper 0.6 m of the nest, confirming that warmer temperatures are preferred for rearing worker brood. Almost all active adult workers were in fungus gardens and in galleries.

Only 15 winged males and queens were in several cavities above 0.6 m, suggesting that most of the alates produced that year had previously flown from this nest; none of these queens were fertile. Peak flight times for alates from most nests are from the last week of April to ≈1 June (Moser 1967). Because this nest was thought to be 4 yr old, the presence of alates indicates that vigorous nests may produce sexual forms at least as early as age 4.

Two departures were noted from the typical size and shape of fungus gardens. The first was that only a few of the numerous galleries were filled with fungus gardens. Galleries that are filled with fungus gardens are larger than the usual gallery size (Fig. 7). We typically use 13-mm-i.d. plastic tubing to connect various portions of our laboratory nests, but when this size is replaced with tubing 16 mm or larger internal diameter, the workers soon fill this tubing with fungus gardens, leaving only enough room for normal traffic between the smaller feeding and detritus canisters and the much larger canister normally used by the ants to build fungus gardens.

Central Cavity. The second departure from the typical fungus garden cavity was the central cavity (Figs. 5, 6, and 8) (Moser 1967), which measured ≈1 m in width and depth. It approximated the size and shape of a large oil drum and was located near the center and

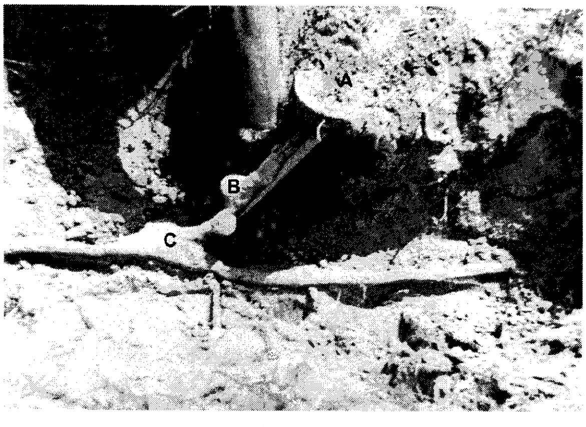

Fig. 7. Cement cast of feeder hole and horizontal tunnel. Feeder hole is on soil surface with small gallery at 45° angle entering horizontal tunnel ≈25 cm below soil surface. Photo was taken at another nest in central Louisiana. A, entrance to feeder hole; B, 45° gallery to horizontal tunnel; and C, horizontal tunnel.

Fig. 8. John Moser inside central cavity.

lowest level of the nest (Fig. 5). The central cavity and most other cavities were not centered under the surface spoil of mounded red dirt (Fig. 6). All ants and fungus gardens reside in the central cavity in winter, and this is where the alate larvae and pupae are produced (Moser 1967). In contrast, worker broods are reared only in the upper cavities during warm weather. Air temperature was ≈32°C in the shade at 1300 hours on 15 June 1959. In Louisiana, at least, the upper cavities apparently become too cold in winter to support the colony, so the ants must relocate to cavities below 3 m, where the temperature of the soil approximates the mean annual temperature of the area (17.9°C) throughout the year (NRCS 2001). The latter temperature is somewhat lower than the 20°C soil temperature that we measured at 4 m for the central cavity. Temperature patterns cause two vertical nest migrations each year—workers move to the upper cavities in spring to construct gardens, but in late fall they retreat to the lower cavities, where they begin constructing new gardens. The metabolic heat produced by large quantities of fungus garden in the central cavity might be able to produce temperatures much warmer than the surrounding soil at that depth. If so, then the purpose of the central cavity may be metabolic heat production enabling this ant to survive in cool climates. These migrations may have little to do with the ability of the ants to procure adequate forage for their gardens. Workers are seen on surface trails at trail temperatures ranging from 13 to 29°C; in summer the ants travel at night, but in winter workers forage during daylight (Moser and Blum 1963). It would be interesting to know whether this vertical migration pattern inside nests and the presence of the central cavity also holds true for *A. texana* in warmer, southern regions, such as the Rio Grande valley and the east coast of Mexico. Use of a single, large central cavity for habitation in cold weather may be unique to *A. texana*. Although mention is made of similar large cavities below the fungus garden cavities of other *Atta* species (Stahel and Geijskes 1939, Jonkman 1980b), these large cavities were either empty or contained detritus. No mention was made of them containing fungus gardens.

Mean annual climatic temperatures also may explain why *Atta* spp. are not found north of ≈33° N or south of ≈33° S. For *A. texana*, at least, soil temperatures in cavities below a depth of 3 m must exceed a minimum to sustain the life of the fungus and the ant. Temperatures at such depths are largely a function of mean annual climatic temperature, so the geographical distribution of *A. texana* and perhaps that of *A. vollenweideri* in Argentina may be governed by mean annual climatic temperature and not by climatic temperature extremes. Although the vertical migration of *A. texana* to the central cavity may explain the northern distribution limits of this species, the picture may be more complicated for the distribution of *A. vollenweideri*. This is because the external environment and architecture of *A. vollenweideri* nests, which may lack a central cavity (Jonkman 1980b), are very different from those of *A. texana*.

Winter migrations to the central cavity were of importance to those wanting to exterminate colonies of *A. texana* with methyl bromide (now prohibited for this use in the United States). Winter is an ideal time to use this fumigant, because it liquefies below 4°C and can be easily poured into the nest. Once inside the nest, the liquid warms and the resulting gas, which is heavier than air, sinks to the central cavity, where the majority of the colony is concentrated in winter. If the theories of Jacoby (1955) regarding the internal circulation of air within *Atta* nests are correct, then it may be better to inject fumigants into galleries at the periphery of *Atta* spp. nests, rather than those in nest centers.

Females and last instars of the roach *Attaphila fungicola* Wheeler occupied most larger fungus gardens, but other inquilines were seen only in the empty fungus garden cavities. Two adults of the fly *Pholeomyia comans* Sabrosky were seen (one in each of two empty cavities), and another empty cavity contained two nymphs of the cave cricket *Ceuthophilus* sp. (Waller and Moser 1990).

Dormancy Cavities. Dormancy cavities (Moser 1963) are about the same size as fungus garden cavities, but more irregular in shape. These cavities are often packed tightly with leaves and contain torpid workers and inquilines, although no insect associates were seen in dormancy cavities of this nest. Twenty-seven such cavities were seen. Twenty-four were situated in the upper 2 m of the nest, with only three below this level. Most contained fungus-bearing substrate, dormant workers, and brood in about the same abundance as in fungus gardens. Fungus was present on the substrate in most cavities and at all depths. Fresh leaves also were found in some cavities. The worker brood was mostly above 1 m, although some pupae were present in one cavity at 2 m. Cavities with large numbers of brood always had correspondingly large numbers of teneral or callow workers, but some cavities without brood also contained teneral workers. Contents of cavities at the lowest levels were different. The cavity at 3 m was packed only with dormant mature workers; but the lowest dormancy cavity, at 3.6 m, contained fungus-bearing substrate with many workers; these workers seemed dead and did not revive when exposed to air. Dead workers are typically disposed of in detritus cavities.

Detritus Cavities. Forty-five detritus cavities (Moser 1963) (Figs. 5 and 6) were observed. Thirty-nine were irregularly shaped holes, two used old fungus garden cavities, and four were galleries packed with detritus. Contents of these cavities consisted mostly of brown or black material resembling peat moss, but a few contained a wet, pitchy substance. A white fungus that resembled the ant fungus was found growing on the substrate in one of the former fungus garden cavities. Twenty-three detritus cavities contained inquilines (Waller and Moser 1990), but 22 had none.

Practically all inquilines were in detritus cavities nearest to the surface spoil. Cavities with few or no inquilines were mostly below 1.6 m and further from the surface spoil. The beetle *Lobopoda opacicollis*

Campbell (=*L. subcuneata* Casey) was the most common inquiline, and occurred in 17 cavities. Larvae were found at depths from 0.3 to 2.4 m, but pupae and adults were located only in the upper 1.2 m. A few larvae were found in one of the cavities containing the black, pitchy substance.

Adults, puparia, and larvae of the fly *P. comans* were found in seven detritus cavities above 0.6 m, and a few of the adults were seen in two detritus cavities at depths of 1.5 and 1.8 m.

A few adults of the histerid beetle *Geomysaprinus* (=*Saprinus*) n. sp. nr. *formicus* (Hinton) were found in two cavities in the center of the nest at a depth of 0.6 m and in two cavities at the periphery of the nest at 1.2 m. This species is presumably a predator, feeding on small arthropods in the detritus cavities. But the lower two cavities only contained small, red earthworms, which may have been a source of prey. These earthworms were present in two cavities in the center of the nest and in three cavities at 1.4 m at the nest periphery. Adult staphylinid beetles (species of Aleocharini) occurred in the same two peripheral cavities where for *G. ?formicus* were found.

Vertical Tunnels. Below the 4 m level of the deepest cavity, several vertical tunnels extended to unknown depths. It was possible to lower a weighted string 3 m beyond a depth 4.6 m, the lowest depth dug (Fig. 5). Depth of the water table under this nest was unknown, but at this writing, depth of the water table at wells in similar soil types ≈1.6 km north and ≈1.6 km south of the nest was 32 m. Because water levels vary little at this depth, and assuming that these vertical tunnels dug by the ants are used as wells, then this ant may burrow down at least 32 m to reach water. Stahel and Geijskes (1939) and Jonkman (1980b) suggested that similar vertical tunnels in nests of *A. sexdens* and *A. vollenweideri*, respectively, may be used to supply colonies with water. However, Stahel and Geijskes (1939) doubted that *A. cephalotes* digs tunnels for wells, because the shallow nests of this species are located in rain forests, where the water tables are normally high. Termites are reported to penetrate to depths as great as 100 m to reach water (Cloud et al. 1980).

In conclusion, although the techniques described here are almost 50 yr old, this technology is still as useful as it was when the operation was conducted. Future innovations may include the use of ground penetrating radar, an untested, noninvasive idea that might be used alone or in combination with excavations.

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