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Chapter 25, Invertebrate Enemies and Nest Associates o The Leaf-cutting Ant. . . .

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Invertebrate Enemies and Nest Associates of the Leaf-cutting Ant *Atta texana* (Buckley) (Formicidae, Attini)

D.A. Waller and J.C. Moser

INTRODUCTION

The complex nests of leaf-cutting ants (Formicidae; Attini) provide rich habitats for ant associates. These mounds consist of interconnected subterranean cavities that average 0.002 m^3 in volume (Walter et al. 1938) and extend to depths of 7 m (Moser 1963). Many cavities contain fungus gardens, cultivated on live plant material, frass and debris. Nests of some species include "detritus" chambers filled with discarded fungal garden, exhausted substrate and dead ants. Numerous invertebrate and vertebrate species associate with the ants, their fungus gardens or the detritus (Walter et al. 1938; Moser 1963; Weber 1972; Moser 1983), but little is known about their life cycles or their relationships with the ants. In this paper we review past literature and present observations on *Atta texana* parasites and nest associates in Texas and Louisiana (Table 1).

PARASITES

Leaf-cutting ants have few parasites. Nematodes (Nematoda) have been collected as internal parasites of *Acromyrmex octospinosus* (Weber 1945) and some species are common in deteriorating nests (Weber 1972; DAW). Mites (Acarina) also proliferate in many leaf-cutter colonies and are frequently phoretic on worker ants and alates (Weber 1972; JCM). On nest surfaces, phorid flies (Diptera, Phoridae) are important parasitoids of leaf-cutting ants (Weber 1945; Borgmeier 1926; 1931; 1963 Eible-Eibesfelt and Eible-Eibesfelt 1967; Feener and Moss 1989).

Phorid Flies

Over 20 phorid fly species attack *Atta* and *Acromyrmex* species; parasites and hosts are listed in Borgmeier (1931, 1963), Weber (1972) and Feener and Moss (1989). Females of these minute flies (approximately 1-2 mm body length) oviposit on adult ant workers by inserting their sclerotized ovipositors in the ant head (Feener and Moss, 1989) or thorax (Feener1987). Little is known about the immature stages, but larvae of the phorid,

TABLE 1. Continued.

(Trombidiidae)	
Microtrombidium sp. [Moser 1983 (L)]	F; infrequent
Trombidiid n. gen. n. sp. [Walter et al. 1938 (T)]	F
Typhlotrombidium tridentifer [Walter et al. 1938(T)]	F; common
(Uropodiae)	
Dinychus sp.(=Uraseius)[Moser 1963 (L)&Neff 1971]	D; phoretic on *Pholeomyia comans*,*P*.n.sp.nr. *leucogastra*
Oplitis attaae [Moser 1967] [Hirschmann 1972 (L)]	Phoretic on queen
Trichouropoda (=*Fuscuorpoda*) [Moser 1967 (L)] sp. nr. *marginata*	Phoretic on queen
(Vaigiidae)	
Vaigiidae sp. [JCM (L)]	D; lab colony
Entotrophi (Japygidae)	
Metajapyx n. sp. nr. *subterraneus* [Moser 1963 (L)]	G; infrequent
Thysanura	
Near *Atelura* [Walter et al. 1938 (T)]	F; common, *Grassiella* n. sp.?
Grassiella wheeleri [JCM (L)]	F; infrequent
Grassiella n. sp. [JCM (L)]	F; infrequent
Collembola (Entomobryidae)	
Pseudosinella violenta [Walter et al. 1938 (T)] [Moser 1963 (L)]	D, G; rarely found where ants are abundant; "cave species"
Dictyoptera (Blattidae)	
Arenivaga bolliana [Walter et al. 1938 (T)]	D, G
Arenivaga tonkawa [Walter et al. 1938 (T)]	D, G
Attaphila fungicola [Wheeler 1900, 1907 (T)] [Walter et al. 1938 (T)] [Moser 1964, 1967 (L)]	F; common
Orthoptera (Gryllacrididae)	
Ceuthophilus sp. nr. *umbratilis* [JCM (L)]	G; frequent
(Gryllidae)	
Myrmecophilia nebrascensis [Walter et al. 1938 (T)]	
Myrmecophilia n. sp. [Moser 1963 (L)]	G; infrequent
Hemiptera (*Tominotus unisetosus*) [Moser 1963 (L)]	D; rare
Froeschner (Cydnidae)	
Coleoptera (Carabidae)	
Tachyura dolosa [Moser 1963 (L)]	D; infrequent
(Histeridae)	
Acritus sp. [Walter et al. 1938 (T)] [Wenzel 1939]	D
Acritus attaphilitus [JCM (L)]	D, G; frequent
(type-Acritus sp. Boerne, TX,	Walter et al. 1938)

TABLE 1. Continued.

Geomysaprinus (=*Saprinus*) sp. [Moser 1963&1983(L)]	D; common
Gnathoncus sp. [Walter et al. 1938 (T)]	D *Geomysaprinus?*
Reninus salvini [Walter et al. 1938 (T)]	D
(Hydrophilidae)	
Oosternum attacomis [Spangler 1962 (L)]	D; frequent in active decomp.
(Ptiliidae)	
Acrotichus sp. or *Nephanes* sp. [JCM (L)]	D; rare
(Staphylinidae)	
Atheta sp. [Walter et al.1938 (T)] [JCM (L)]	D
Belonuchus sp. [JCM (L)]	D; common
Tinotus sp. [JCM (L)]	D; common
Gen. sp. 1 [JCM (L)]	D
Gen. sp. 2 [JCM (L)]	D
Gen. sp. 3 [JCM (L)]	D; common
Gen. sp. 4 [JCM (L)]	D
(Pselaphidae)	
Melba sp. [JCM (L)]	D; rare
Pselaphid n. gen. n. sp. [Walter et al. 1938 (T)]	D
(Elateridae)	
?*Conoderus xystus* [Walter et al. 1938 (T)] [Moser 1963 (L)]	D; infrequent
Elaterid adults and larvae [Walter et al. 1938 (T)]	D
(Scydmaenidae)	
Eumicrus sp. [Walter et al. 1938 (T)]	D; *Scydmaenus*?
Scydmaenus sp. [JCM (L)]	D, F; Infrequent
(Lycidae)	
Lycidae sp. [JCM (L)]	F; infrequent
(Alleculidae)	
Hymenorus discretus [Walter et al. 1938 (T)]	D; *L. opacicollis*?
Lobopoda opacicollis=L. aubruneata [Moser 1963 (L) [Campbell 1966 (L)]	D; common in active decomp.
(Scarabidae)	
Cotinus longitarsis [Walter et al. 1938 (T)]	D; common
Euparixia moseri [Woodruff & Cartwright 1967(L)] [Moser 1983 (L)]	F
Euphoriaspis aestuosa [Walter et al. 1938 (T)]	D
(Chrysomelidae)	
Megalostomis major [Walter et al. 1938 (T)]	G
Lepidoptera (Tineidae)	
Amydria confusella [Walter et al. 1938 (T)]	D
Diptera (Psychodidae)	
Phlebotomus n. sp. [Walter et al. 1938 (T)]	D; F
(Ceratopogonidae)	
Forcipomyia sp. [Walter et al. 1938 (T)]	D
(Bibionidae)	
Bibio femoratus [JCM (L)]	D; rare

TABLE 1. Continued.

(Sciaridae)	
Bradysia fenestralis [JCM (L)]	D; frequent
Sciaria varians [Walter et al. 1938 (T)]	D
(Phoridae)	
Apocephalus wallerae [Disney 1980 (T)]	S; frequent
Myrmosicarius texanus [Greene 1938 (L)] [Disney 1980 (T)]	S; frequent
(Fanniidae)	
Fannia moseri [Chillcott 1965 (L)] [Moser & Neff 1971] [Moser 1983]	D; frequent in active decomp.
Fannia sp. [Walter et al. 1938 (T)]	D
(Borboridae)	
Leptocerca sp. [JCM (L)]	?
(Ephydridae)	
Philygria fuscicornis [Walter et al. 1938 (T)]	D
(Milichiidae)	
Megaselia sp. [Walter et al. 1938 (T)]	D
Milichia sp. [Walter et al. 1938 (T)]	D; *P. texensis*?
Pholeomyia comans [Moser 1963 (L)]	D; common
Pholeomyia sp. nr. *leucogastra* [Moser&Neff 1971(L)]	D; infrequent
Pholeomyia texensis [Sabrosky 1959 (T)]	D; common
Hymenoptera (Chalcidae)	
Pheidoloxenus? sp. [JCM (L)]	S; in *Atta* head
(Cynipidae)	
Cynipidae sp. (2) [JCM (L)]	D; infrequent
(Diapriidae)	
Coptera (=*Psilus*) *pholeomyiae* [Moser&Neff 1971(L)] [Muesebeck 1980]	D;infrequent; pupal parasite of *P. comans*
Galesus n. sp. nr *punctiger* [Walter et al. 1938 (T)]	D; specimen is *C. pholeomyiae*
(Scoliidae)	
Scolia guttata [Walter et al. 1938 (T)]	S; entered nests; *Cotinus* parasite?
(Formicidae)	
Ponera trigona [JCM (L)]	D; rare
Neivamyrmex fallax [JCM (L)]	G; rare
Labidus coecus [JCM (L)]	G; rare
Apocrita	
Apocrita sp. [JCM (L)]	F

[1]D = detritus chamber, F = fungus garden or dormancy chamber, G = galleries and empty chambers, S = mound surface.

Apocephalus pergandie develop within the head capsules of *Camponotus pennsylvanicus* (Pergande 1900).

Two phorid species parasitize *A. texana* foragers. *Myrmosicarius texanus* occurs in Texas and Louisiana (Greene 1938; Borgmeier 1963; Disney 1980);

this species hovers over the ants at entrances and along trails and darts down to land on ant heads. In contrast, *Apocephalus wallerae* has been collected only in Texas and rarely hovers but instead runs up to *A. texana* foragers cutting leaves; females then dash between ant mandibles and appear to oviposit behind the occiput (DAW; Disney 1980). Although neither *M. texanus* nor *A. wallerae* has been reared from *Atta* workers, the sclerotized ovipositors of the females and the persistent oviposition behavior strongly suggests parasitism. In Louisiana, a large worker collected by JCM in 1962 had a phorid larva in one side of the head and a chalcidoid larva (*Pheidoloxenus*? sp.), in the other side.

Temporal and Seasonal Patterns. Both *M. texanus* and *A. wallerae* were common from April through November in Austin, Texas (Table 2). In one week in May 1980, DAW collected 162 *A. wallerae* at one ant entrance. Despite three years of careful searching, these phorids were not observed in the winter even though the ants foraged heavily at that time. Phorids did not appear to be active at night, while the ants foraged nocturnally during the summer and diurnally in the winter, and were sometimes active day and night during the spring and fall. Temporal patterns of ant activity may have been related to phorid abundance and/or weather. Figure 1 illustrates that nocturnal *A. texana* foraging and phorid activity occur during the warmest and wettest months in Austin.

Size Selectivity. Leaf-cutter foragers are continuously polymorphic, and *A. texana* workers on a trail can range in headwidth (HW; the measurement across the width of the head at the widest point) from less than 1 mm to over 3.6 mm (DAW). Because fly size is probably constrained by the dimensions of the ant host, phorids may selectively oviposit on hosts of a given size. In Trinidad, Weber (1972) noted large and small phorids attacking *Atta cephalotes* soldiers and workers, respectively, and large phorids pursued *A. cephalotes* soldiers and ignored workers in Vera Cruz, Mexico (DAW). To determine whether *M. texanus* selectively oviposited on *A. texana* workers according to size, DAW collected ants that had been attacked by *M. texanus* and compared HW with those of control ants (all unattacked ants) taken at the same nest entrance. There were usually too few oviposition attempts in a single sample to demonstrate significance, but when samples were combined for each month at a given entrance, the sizes of attacked ants were generally significantly larger than those of control ants (Table 3). Feener (1987) also found that the phorid *Pseudacteon crawfordi* selectively oviposits on larger workers of *Solenopsis geminata* and *S. xyloni*.

Parasitism Rates and Ant Defense. The phorid parasitism rate appears low. Although *M. texanus* females often hovered for up to an hour at an *A. texana* entrance, usually less than a dozen oviposition attempts were made during that time (DAW). A low rate of parasitism might be related to effective ant defensive behaviors. Ant workers fended off *M. texanus* ovipositions by rearing up on their hind legs with mandibles open and abdomens tucked forward, and *Atta* attacked by *A. wallerae* usually stopped cutting leaves. When flies of both species contacted ants during oviposition attempts, the workers vigorously cleaned their heads and mandibles with the forelegs.

Eible-Eibesfelt and Eible-Eibesfelt (1967) suggested that minim

TABLE 2. Months during which *Atta texana* parasitoids and nest associates were collected in Austin, TX, during 1979-1981.

Species	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Blattidae (Dictyoptera)												
A. fungicola				x								
Milichiidae (Diptera)												
P. texensis	x	x	x	x	x	x	x	x	x	x	x	
Phoridae (Diptera)												
A. wallerae				x	x	x	x	x	x	x	x	
M. texanus				x	x	x	x	x	x	x	x	
Minim hitchiking	x				x	x	x	x	x	x	x	x

TABLE 3. Mean (± SD) headwidths (mm) of ants attacked by the phorid, *M. texanus*, and unattacked control ants (sample sizes in parentheses) in Austin, TX.

Entrance	Date (1979)	Attacked ants	Control ants
1	June	1.55 ± 0.21 (23)	1.37 ± 0.33 (16)*
1	July	1.53 ± 0.32 (32)	1.28 ± 0.30 (48)***
2	July	1.45 ± 0.32 (21)	1.23 ± 0.29 (43)**
3	July	1.68 ± 0.35 (8)	1.58 ± 0.39 (52)^{NS}
3	August	1.46 ± 0.33 (6)	1.36 ± 0.31 (55)^{NS}
3	September	1.74 ± 0.35 (53)	1.50 ± 0.48 (189)***
3	October	1.76 ± 0.40 (39)	1.59 ± 0.37 (273)**

$^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$, ^{NS}not significant, Student's t-test, 2 tailed.

hitchhiking - in which tiny minim leaf-cutting ant workers ride leaves carried by foragers - deters oviposition by phorids on the foragers. Recently, Feener and Moss (1989) demonstrated that *Atta colombica* foragers carrying hitchhikers on leaves have lower rates of parasitism than undefended ants. Minim hitchhiking probably also serves a nondefensive function, because it reduces the colony's energy expenditure by up to 10% when hitchhikers ride rather than walk to the nest (Feener and Moss, 1989). However, although *M. texanus* and *A. wallerae* were common in Texas, *A. texana* minims rarely rode leaves. When minim hitchhiking did occur, it appeared unrelated to phorid presence (DAW; Table 2).

Social Parasites

The workerless social parasite *Pseudoatta argentina* invades nests of *Acromyrmex lundi* (Weber, 1972), but little is known about this species. Weber (1972) suggested that the host and parasite are closely related.

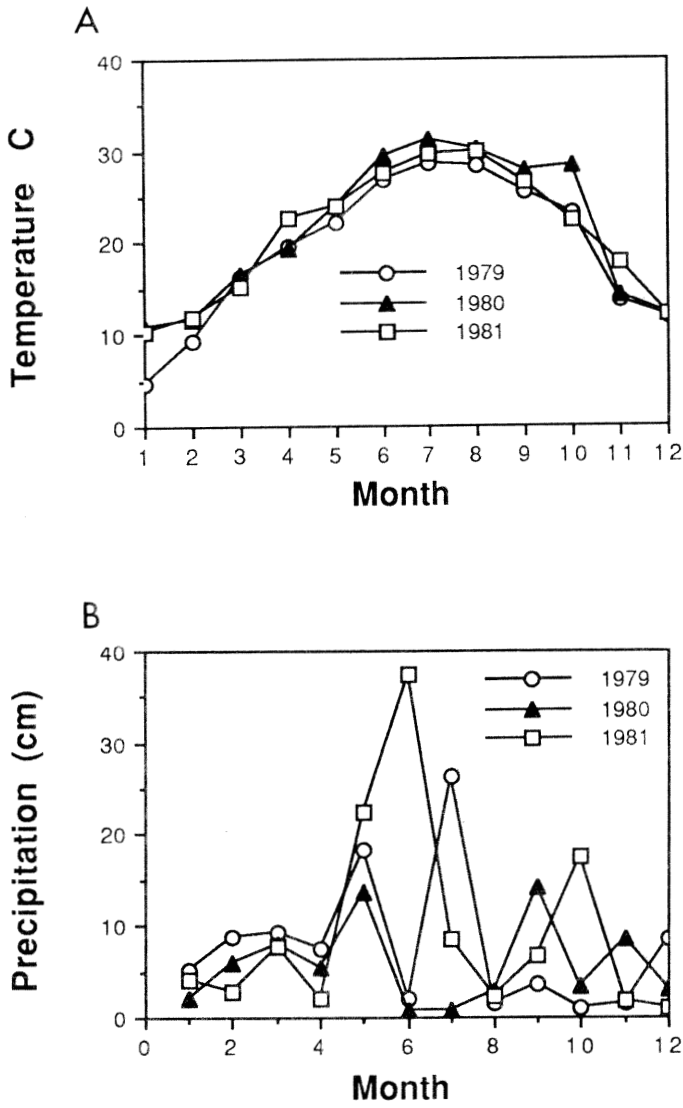

FIGURE 1. Mean average monthly temperature (A) and precipitation (B) in Austin, Texas from 1979-1981.

NEST ASSOCIATES

Moser (1983) briefly summarized the roles of tne nest associates and natural enemies of *A. texana*. In general, these associates can be divided into broad habitat categories including fungus gardens, detritus, galleries and empty cavities, and dormant cavities which have characteristics of both the detritus and fungus gardens (Moser 1963). Some associates feed on the detritus (mostly remnants of fungus gardens) or fungi, others seem to be general feeders, and still others are predators or parasites. Internal detritus chambers occur in *A. texana* nests (Moser 1963), but the ants sometimes discard small quantities of garden material on the mound surface (DAW; JCM). In contrast, *Atta colombica tonsipes* and "*A. fervens*" (*A. mexicana*) deposit large amounts of waste outside the nest (Hinton 1935; Weber 1969). The common groups of associates (fungi, nematodes, mites, histerids, staphylinids and fly larvae) found in *A. texana* detritus cavities often bear striking similarities to those found in detritus habitats of other insects such as bark beetle galleries (Moser et al. 1971; Moser and Roton 1971). There are three stages of detritus decomposition: 1) recent (little, if any breakdown); the substrate looks and smells somewhat like cigarette tobacco and few associates are present, 2) active decomposition; maximum numbers of both associate species and individuals, 3) mature; where the substrate has changed to a "black humus," and fauna consists mostly of nematodes and earthworms. The biologies of species commonly found in detritus chambers, fungal gardens/galleries and empty cavities are discussed below:

Thysanura

Grassiella. Grassiella wheeleri, when present, seems to be the most common silverfish; JCM collected as many as 22 in galleries of one nest in Louisiana. However, it was not often found (JCM). Wheeler collected *G. wheeleri* from a number of ant species in Texas, including *Pachycondyla harpax* (P. Wygodzinsky, personal communication). *Grassiella* n. sp. was found in fungal gardens from two separate nests in Glenmora and Flatwoods, Louisiana (JCM). This species does not appear to be associated with nest galleries, and so may be ecologically distinct from *G. wheeleri*. Walter et al. (1938) recorded a species "near *Atelura*" (apparently a misspelling of *Attatelura*) common on walls of fungus garden chambers which may be *Grassiella* n. sp. The only other species of silverfish known to occur with *Atta* is *Attatelura geijskesi*, found with *A. sexdens* in Surinam (Wygodzinski 1942).

Dictyoptera

Attaphila. Attaphila is a small cockroach (to 3.5 mm long) that lives within leaf-cutting ant fungus gardens and disperses by riding leaf-cutter alates on the mating flight (Bolivar 1901; Moser 1964; DAW) (Fig. 2). Wheeler (1900) considered *Attaphila* to be the only insect that lives in close association with the ants. *Attaphila fungicola* follows the pheromone trails of *A. texana* and *Trachymyrmex* in the laboratory (Moser 1964), and *A. schuppi*. has been found on trails of *Acromyrmex* prob. *niger* (F. Smith) (Bolivar 1905). Within the nest, *A. fungicola* frequently rides upon soldiers (Wheeler 1900), while the related species *A. bergi* from Acromyrmex lundi nests in Argentina and

FIGURE 2. *Attaphila fungicola* phoretic on *A. texana* alate.

Uruguay apparently rides only alates (Bolivar 1901). Wheeler (1900) observed that *Attaphila*'s gut contents are whitish, and he initially suggested that the cockroaches feed on fungus, but he later believed that the roaches ingest ant secretions while riding upon the soldiers (Wheeler 1907). The ants generally ignore *Attaphila* in the nest (Wheeler 1900; DAW).

Both male and female of *A. fungicola* have been collected from Texan *A. texana* nests (Wheeler 1900; DAW), but only females have been collected from Louisiana (Moser 1964). In Louisiana there is one generation per year. JCM observed females and nymphs in the fungus garden cavities in Louisiana as early as March 24, and noted that the ratio of females to nymphs increased until after the first mating flights in late May when few, if any, of the large nymphs were seen. Small nymphs then appeared in early June, and nymphs predominated in nests until the following year. However, JCM has observed *A. fungicola* females in nests in July, September and January, suggesting that females can live over a year, and a female lived for one year in an artificial nest. During mound excavations in Austin, Texas, in June 1983, DAW recovered males (M), females (F) and nymphs (N) from fungus gardens in three separate mature nests. JCM has collected *Attaphila* oothecae in large numbers by capturing *Atta* alates on nest surfaces prior to the mating flights and placing them in jars. Oothecae were deposited at the bottoms of the jars within a few days. Information on the ovarioles and ooethecae of *A. fungicola* can be found in Roth (1968, 1971).

Wheeler (1900) noted that *Attaphila* adults and nymphs have never been collected with intact antennae and suggested that they are clipped by the ants

tending their fungus gardens, although it is possible that the cockroaches practice antennal mutilation, as do many termite species (Hewitt et al. 1972).

Orthoptera

Ceuthophilus spp. These crickets are associated with the nest galleries, especially the upper galleries. Others are seen in tunnels, a type of gallery normally 0.3 m deep which may radiate as far as 300 m from nests. They occur in most nests, although not in great numbers, perhaps due to their large size. It is difficult to say how many species are involved because most specimens collected have been nymphs. In 1963, JCM collected females identified as members of a group that includes *C. umbratilis*, and *C. uhleri* complex nymphs. Unfortunately, males are required for a positive identification.

Myrmecophila n. sp. This tiny cricket was collected six times in nests in Louisiana by JCM under the following conditions:

Date	# found	Cavity type	Depth	Comments
8/60	1	Empty F.G.	3 m	Few workers present (Moser 1963)
4/61	1	Full F.G.	30 cm	Many workers, no brood
3/61	1	Gallery	8 cm	Nest dead; *2 Ceuthophilus* present
3/61	2	Gallery	8 cm	Worker present
2/61	1	Gallery	15 cm	Worker present

It seems likely that *Myrmecophila* merely coexists with the ants and, from the dead nest observation, may be more dependent on the nest than on the ants. Walter et al. (1938) noted that *Atta* workers in Texas become annoyed when groomed by *Myrmecophila*, and the crickets nibbled at the chamber walls and runways encrusted with waxy ant secretions. Walter et al. (1938) listed this associate as *M. nebrascensis*, but A. B. Guerney identified the Louisiana specimens as a new species.

Hemiptera

Tominotus unisetosus. Five adults and several large and small nymphs of this cydnid bug were taken from a cavity containing mature detritus in Louisiana (Moser 1963). This species has only been found in Texas, Mexico, Guatemala and Costa Rica; we know little about its biology (Froeschner 1960). Cydnids feed on roots, but it is unclear how they sustain themselves in *Atta* nests.

Coleoptera

Geomysaprinus sp. Probably a predator, this histerid beetle is commonly found in detritus cavities. Moser (1963) cited it as *Saprinus*, and it may be the *Gnathoncus* sp. in Walter et al. (1938). The Louisiana material (Walter et al. 1938) is deposited at the Field Museum of Natural History.

Geomysaprinus sp. has been seen following foraging trails of *A. texana*

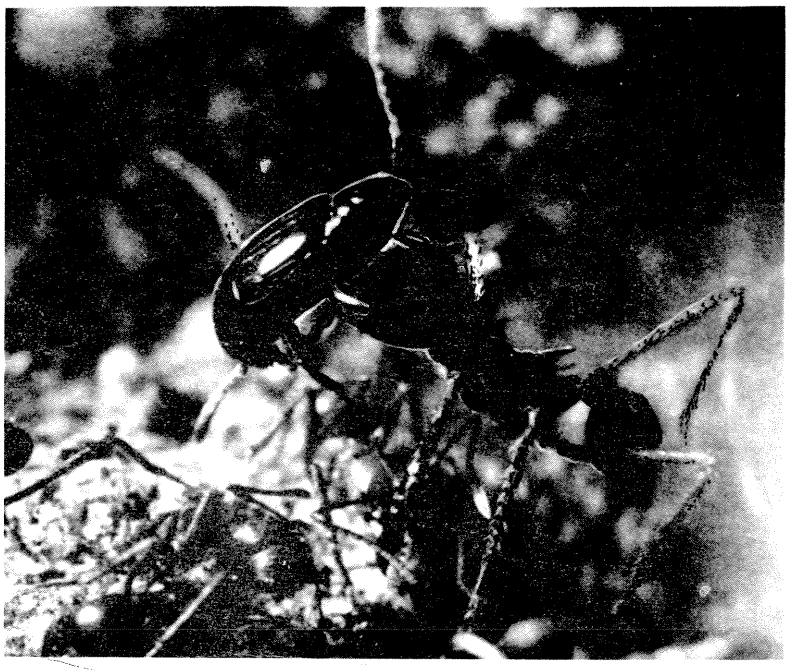

FIGURE 3. Adult histerid *Geomysparinus* n. sp. nr. *formicus* carried from the nest with refuse.

in Louisiana (JCM). Worker ants on the trail ignored the beetle. *Geomysaprinus* sp. followed an artificial trail made from major worker poison sacs dissolved in methylene chloride (JCM), but did not perform as well as the inquiline cockroach *Attaphila fungicola* (Moser and Blum 1963).

An *Atta* worker carried an adult *Geomysaprinus* from the nest (Fig. 3). Workers excavate dirt from mounds in October and November, but this rarely includes detritus and any associates. When a beetle was dropped on a previously removed refuse pile, the beetle immediately revived and ran off.

Staphylinidae. Rove beetles are common in detritus cavities (Moser 1963), but grouping these species produced a taxonomic quagmire. Recently, seven species were resolved (S. Ash, unpublished) from several hundred specimens collected from active detritus cavities in Louisiana (JCM). These include *Belonuchus* sp. (Staphylini), *Tinotus* sp. (Hoplandriini), *Atheta* sp. (Aleocharini) (Fig. 4) and four separate unknown species in the Aleocharini. All of these groups are probably predators and may feed on mites and/or nematodes. Kistner (1982) reviewed the relationships of staphylinid nest associates with their leaf-cutting ant hosts.

Scydmaenus sp. (Fig. 5). A total of eight adults of this small ant-like stone beetle were found in three nests. Two each occupied detritus cavities at

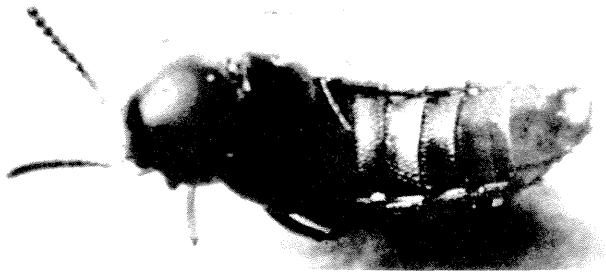

FIGURE 4. Staphylinid adult from detritus cavities.

FIGURE 5. Adult of *Scydmaenus* from detritus cavities.

depths of 2.5 and 2.75 m, one in a dormancy cavity at 3m, and three in a fungus garden at 4 m. All specimens are apparently the same species. The *Eumicrus* sp. listed by Walter et al. (1938) may be this species.

Lycidae sp. (Fig. 6). Small, probably first-instar larvae of this net-winged beetle were found in a central Louisiana detritus cavity (January 18, 1960), and large late-instar larvae were collected once in a dormancy cavity (February 6, 1959), and once in an active fungus garden with ants and brood (March 24, 1960). Arnett (1960) states that the larvae are carnivorous, so this species may eat *Atta* workers and/or their brood.

Lobopoda opacicollis. The known information for this large alleculid beetle is summarized by Campbell (1966). Larvae (Fig. 7) help decompose detritus. The *Hymenorus discretus* listed by Walter et al. (1938) may be this species. The presence of *L. opacicollis* in Mexico, Guatemala, and British Honduras suggests an association with the detritus of *A. cephalotes* and possibly *A.*

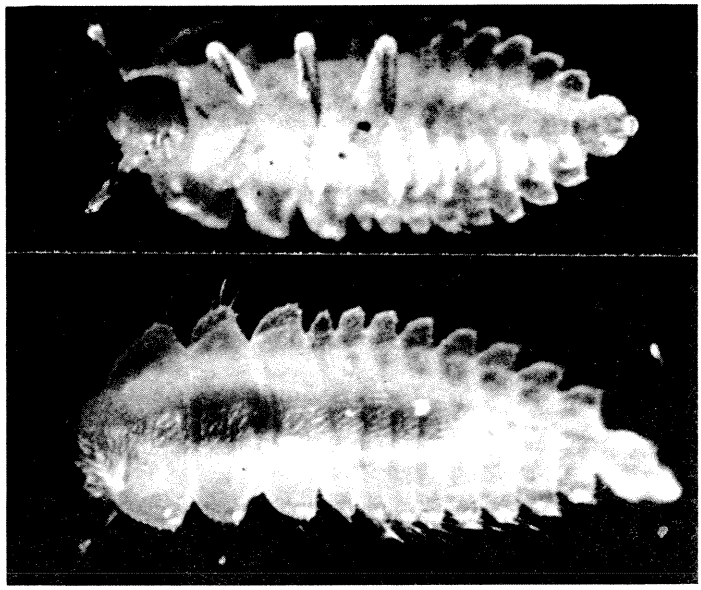

FIGURE 6. Lycid larvae from fungus gardens.

FIGURE 7. Larvae of various instars of *Lobopoda opacicollis* from detritus cavities.

mexicana. Adults of a closely related species, *L. granulata* (Campbell 1966) have been collected near a large *A. cephalotes* nest in Panama (Campbell 1971).

Euparixia moseri. This small scarab commonly inhabits *A. texana* fungus gardens, but is almost never in detritus cavities where "dung" beetles would be expected. Woodruff and Cartwright (1967) give a thorough review of five species that associate with *Atta* nests.

Diptera

Milichiidae. In Louisiana, the milichiid flies *Pholeomyia comans* and *P.* n. sp. nr *leucogastra* inhabit detritus cavities of *A. texana* where the larvae feed on nest wastes (Moser and Neff 1971). *P. comans* is probably the most common insect in the active detritus decomposition when all stages of this fly are present. *P.* n. sp. nr. *leucogastra* has been found only in galleries, but it carries a species of *Macrocheles* mite found in the detritus (JCM). *P. texensis* appears to replace *P. comans* in Texas (Sabrosky 1959; Waller 1980, 1984). Walter et al.'s (1938) report of *Milichia* sp. reared from nest refuse in Texas may be *P. texensis*. Females of *P. texensis* enter *Atta* nests either by hopping onto leaves carried by ants and riding them into the entrances (Waller 1980) or by waiting beside entrance holes and then dashing inside (DAW). Milichiids also rode leaves carried by *A. cephalotes* in Vera Cruz, Mexico (DAW), and Sabrosky (1959) reported that W.L. Brown and E.O. Wilson observed the milichiid *P. decorior* closely following a forager of the attine *Trachymyrmex septentrionalis* in Florida. *Pholeomyia texensis* rode leaves and was collected near *A. texana* entrances throughout the year (Table 2). *P. texensis* males, which have silvery abdomens, frequently occurred near *Atta* entrance holes, with mating observed on one mound in early June 1979 (Waller 1980). Sex ratios of *Pholeomyia* appear equal. Of 196 *P. comans* adults reared from nest detritus, 87 were males (JCM). Waller (1984) found that *P. texensis* females produce an average of 14.1 ± 5.3 SD females and 15.3 ± 7.7 males. Female *P. texensis* frequently had large red mites attached to their abdomens (DAW); Moser and Neff (1971) found three macrochelid mite species phoretic on both *P. comans* and *P.* n. sp. nr. *leucogastra*.

Hymenoptera

Coptera pholeomyia. This small diapriid wasp is an internal pupal parasitoid of *P. comans* (Moser and Neff 1971). The type series consists of females and a male collected in Louisiana by JCM, and a female collected in San Antonio, Texas, by Walter et al. (1938) who listed it as *Galesus* n. sp. nr. *punctiger* and noted that adults escaped by crawling into refuse rather than by flight.

Apocrita sp. This hymenopterous larva was found lying on a fungus garden containing a large number of workers and brood on May 15, 1964, in central Louisiana (JCM). B.D. Burks (personal communication) determined that it did not belong to the Formicoidea, Ichneumonoidea, Cynipoidea, Dryinidae, Bethylidae, Chalcidoidea or any of the Aculeata groups. Hence he concluded that it probably belonged to the Apocrita. Because many of the Apocrita are parasitic, it may parasitize the ant.

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