

BIOLOGY AND ECOLOGY OF ANTS OF THE  
GENUS APHAENOGASTER IN FLORIDA

By

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Abstract of Thesis Presented to the Graduate Council  
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BIOLOGY AND ECOLOGY OF ANTS OF THE  
GENUS APHAENOGASTER IN FLORIDA

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Investigations were conducted on the biology, ecology and systematics of the Floridian species of the genus Aphaenogaster (Hymenoptera: Formicidae). Nine species of Aphaenogaster occur in Florida: A. ashmeadi Emery, A. carolinensis Wheeler, A. flemingi M. R. Smith, A. floridana M. R. Smith, A. lamellidens Mayr, A. mariae Forel, A. tennesseensis (Mayr), and A. treatae Forel.

A complex of forms, whose constituents have been attributed by various authors to A. rudis Emery, A. texana Emery, A. miamiana Wheeler and varieties thereof, is synonymized under A. carolinensis Wheeler. A. carolinensis was raised to species level from A. texana carolinensis Wheeler on the basis of differences between Floridian forms and Texas specimens of A. texana. Males of A. ashmeadi, A. carolinensis, A. flemingi, A. floridana, A. mariae, and A. tennesseensis females of A. ashmeadi, A. carolinensis, and A. flemingi and a worker of A. carolinensis are described.

In Florida Aphaenogaster spp. occur primarily in wooded habitats. Most species tend to be segregated into characteristic microhabitats. Soil dwelling species predominate in well-drained habitats, while species nesting in rotten wood are most common in moist woodlands. Nests are described and distributions of the species reported.

Aphaenogaster spp. forage chiefly on the ground, only occasionally venturing more than three or four cm up herbaceous vegetation. Species nesting arboreally also forage on the trunks and larger branches of nest trees. The diet of Aphaenogaster spp. consists largely of arthropods, which are captured or scavenged. Seeds and abscised floral parts are collected. Free growing fruiting bodies of mushrooms (Agaricales) comprise a significant portion of the diet of some Aphaenogaster species. Aphaenogaster spp. primarily consume Russula spp. (Russulaceae) but also species of Tricholomataceae and Amanitaccae. Aphaenogaster spp. are virtually free from Formicine competition for this food source. Termites do not constitute a major food source. Confined in the same containers, termite colonies coexisted for months with Aphaenogaster spp. colonies in pieces of rotten wood.

Mating flights of A. fulva are described. A. fulva mating flights are crepuscular, unlike those of A. treatae. Annual cycles of eight Floridian species are reported. Eight species maintained in the laboratory had similar developmental rates. In A. ashmeadi for example the duration of the egg stage is 19 to 22 days, larval stage 14 to 22 days, and pupal stage ten to 13 days.

Toads, spiders, and other ants are important predators of Aphaenogaster spp. workers. Myrmecophilous crickets, Myrmecophila pergandei Bruner, were found in the nests of A. ashmeadi and A. carolinensis. Ant species, nesting in or traversing the various microhabitats utilized by each species of Aphaenogaster, are reported.



## INTRODUCTION

Comparatively little public attention or scientific scrutiny has been directed toward ants of the genus Aphaenogaster. These rather generalized Myrmicine ants exhibit no bizarre or otherwise conspicuous behavior patterns which might pique one's curiosity. They are, however, neither small nor cryptic, nor solely nocturnal or hypogæic foragers. Instead these medium to large ants can be found, often abundantly, in most natural terrestrial ecosystems in Florida. In North America species of Aphaenogaster pose no obvious economic or health problems; thus their anonymity.

Field observations and published accounts of Aphaenogaster spp. being associated with or preying upon termites prompted this investigation. Knowledge of the biology and ecology of these ants, it was felt, might reveal them to be significant biological control agents, limiting termite population levels.

In Florida few ant genera are represented by more species than is Aphaenogaster. This fact raises certain questions regarding inter-specific competition, and the specializations of the different species, individually and collectively. How are so many closely related species able to coexist in such a limited geographic region as north Florida? Do different species feed on different kinds of food or utilize different habitats? Are they different sizes? Hopefully this investigation provides some answers to these questions.

A further indication of the need for studying the genus Aphaenogaster was the number of taxonomic questions which arose at the outset of this investigation and concerned the most common species of Aphaenogaster in Florida.

## REVIEW OF LITERATURE

### Distribution

The genus Aphaenogaster has a worldwide distribution. Wilson (1971) and Wheeler (1922) indicated that species occur in all the major faunal regions of the world except the Ethiopian. At least one species of Aphaenogaster can be found in each of the 48 contiguous states (Smith, 1947). Creighton (1950) provided distribution data for all the then described species of Aphaenogaster in North America north of Mexico. Subsequent work by other investigators has revealed the ranges of several species to be greater than previously supposed. The distribution of each Florida species is discussed individually in the results section. The northward occurrence of species of Aphaenogaster was reported by Gregg (1972). Wheeler (1910) conjectured that A. treatae Forel, A. mariaae Forel, and A. lamellidens Mayr had their evolutionary origin in the southeastern United States, while A. fulva Roger was associated with the northeast.

### Economic Importance

North American species of Aphaenogaster are not significant pests. Nevertheless, Smith (1965) reported A. fulva, A. lamellidens, A. rudis Emery, and A. tennesseensis (Mayr) as occasionally infesting houses.

He had a single record of A. fulva infesting household foodstuffs, but none for the other three species. None of the four species, he believed, were pests of major importance in homes.

In Australia A. (Nystalomyrmex) pythia Forel and A. (Nystalomyrmex) longiceps F. Smith, known as funnel ants, cause serious damage to commercial sugarcane and tobacco operations and to pastures. They tunnel extensively in sugarcane fields and lacerate tender rootlets (Wilson, G., 1969). Funnel ants harm tobacco seedlings by tunneling in the soil and burying the small plants near their numerous nest entrances with excavated soil (Smith and Atherton, 1944). Pastures infested with funnel ants develop bare spots which in turn may be colonized by deep-rooted weeds rather than grasses. Heavy funnel ant infestations are generally associated with the over-grazing of pastures by cattle (Saunders, 1969). Chemicals are used to attempt control of these ants in pastures and sugarcane (Saunders, 1961, 1967, 1969 and Wilson, G., 1969). Smith and Atherton (1944) also report that A. longiceps may tend aphids (Geoica sp.) on the roots of grasses.

As predators of other arthropods Aphaenogaster spp. may benefit man as biological control agents. Jaynes and Marucci (1947) indicate that A. rudis is an important predator of the codling moth, Carpocapsa pomonella (L.) in West Virginia apple orchards. A. rudis attacks C. pomonella larvae which have dropped to the ground prior to hibernation. It also attacks those in cocoons. A large proportion of codling moth larvae released by Jaynes and Marucci near A. rudis colonies were destroyed by the ants before they could make cocoons. Over a three year period A. rudis was one of the most common ants they found in their "biological control orchard." In nearby

commercial orchards where chemicals were heavily used, A. rudis populations were low.

Species of Aphaenogaster have long been reported as predators of termites. This subject was treated in an economic vein in a few publications. In this paper, however, the Aphaenogaster-termite relationship is discussed in the review of literature of Aphaenogaster biology. All economic references are included in that section.

Whitcomb et al. (1973) found A. floridana preyed upon recently mated queens of the economically important red imported fire ant, Solenopsis invicta Buren.

#### Ecology and Biology

Much of the following portions of the literature review is intended to acquaint the reader with the principal sources consulted by the author. The contents of these and other publications are set forth in some detail in the results and discussion sections.

Publications dealing specifically with the ecology or biology of North American species of Aphaenogaster are few. Talbot (1951, 1954) conducted population studies of A. rudis in Missouri and A. treatae in Michigan. In a strip of field 100 by 200 ft she (1954) detected 63 colonies of A. treatae which she calculated to be one colony per 21 sq yds. She (1951) found from 34 to 3,445 individuals (all stages) in 72 A. rudis colonies. She found multiple queens (two to 15) in some colonies excavated in the spring. This led her to suggest that colonies of A. rudis may mingle or coalesce in the spring just after hibernation. Talbot (1953, 1957) studied populations of all ant

species in an old field in Michigan and in a Missouri woodland. In 25 selected plots (each ten sq m) in the Michigan field she found A. treatae nesting in six plots and A. rudis in a single plot. A. treatae colonies ranged in size from 191 to 3,221 individuals (all stages). In 40 plots (each one sq m) in a Missouri woodland she found A. rudis in abundance. Of 206 colonies representing 16 species, 62 colonies were of A. rudis, the most numerous species. A single colony of A. fulva was found. Headley (1949) censused the populations of 46 colonies of A. rudis. They contained 58 to 1,440 individuals (all stages). In the summer there were more brood than workers. He found eggs and larvae in nests excavated during the winter. Only 11 of 36 colonies sampled at the proper time had reproductive forms. Creighton (1951) compared the ecological differences between A. huachucana Creighton and A. texana Emery in Arizona. He found that A. texana occurs at lower elevations, in habitats with a distinct Sonoran character and nests in direct sunlight, while A. huachucana occurs at higher elevations, in habitats with Transitional or Canadian zone affinities and nests in shade as well as sunlight.

Several authors performed ecological studies in which they associated ant species inhabiting an area with particular plant communities and soil types in the area. These papers deal with all the ant species in the areas studied, but they contain much valuable data pertaining to Aphaenogaster spp. Among studies of this genre the most pertinent are those of Van Pelt (1947, 1956, 1958) conducted in the Gainesville area and at the Welaka Conservation Reserve, Putnam County, Florida.

The 1947 paper fails to include two species of Aphaenogaster

occurring in the Gainesville area, but was instrumental in helping me find A. floridana. The later papers provide not only detailed data on the habitats in which Aphaenogaster spp. occur at Welaka, but their nesting habits and some biological information as well. Van Pelt (1966) conducted a similar although less intensive study of the ants of the Savannah River Plant, South Carolina. North Carolina has many of the same species of Aphaenogaster as Florida. Carter (1962a, 1962b) carried out ecological studies similar to Van Pelt's, but encompassing the entire state of North Carolina. He reported on 12 recognizable forms of Aphaenogaster and included data on activity and nesting habits. Dennis (1938) and Cole (1940) undertook investigations of this sort in Tennessee, where several species of Aphaenogaster occur. Talbot (1934) and Gregg (1944), working in the Chicago region studied ant distribution in relation to plant communities. Talbot delved more deeply into the physical factors affecting ant distribution, finding for example that A. rudis picea Emery requires a higher humidity for survival than does A. rudis rudis. She (1953, 1951) conducted similar but less extensive investigations of an old field in Michigan and of a Missouri woodland. In Ohio Headley (1952) studied the ecology of the ants found in locust woods. In 27 sq m plots he found a total of seven colonies of A. rudis in five plots. Three species had more colonies in the study area than A. rudis. A more general work of Headley's (1943) on the ants of Ashtabula County, Ohio, provides some brief ecological and biological notes on Aphaenogaster spp. Saunders (1967) studied some ecological aspects of the pestiferous funnel ants in Australia, but his emphasis was on habitat data.

The most detailed data on the biology of a single species of

Aphaenogaster were reported by Fielde (1901, 1903, 1904a, 1904b, 1905) regarding A. rudis. Although most of her work was carried out in the laboratory and much of it only peripherally pertinent to this study, it does provide basic information on development, annual cycles and reproduction. In her 1901 paper she reported that A. rudis swarms in September in the northeast and that larval development generally takes 18 to 21 days. Some of the experiments she performed on A. rudis were of a rather unique nature and similar comparable data for other species of ants are scant if not wanting altogether. For example, Fielde (1904b) kept an A. rudis worker alive for over three years, a decapitated worker ten days, and another missing its prothoracic legs for one month. She kept a queen without its abdomen alive 14 days. Of 18 workers she submerged in water for four days 12 fully recovered. One unfed worker survived 46 days. Regarding longevity, Haskins and Enzmann (1960) report queens of A. rudis live an average of 8.7 years under laboratory conditions. One survived 13 years.

The only study of actual mating flights of any North American Aphaenogaster is that by Talbot (1966) on A. treatae. Funnel ants, A. (Nystalomyrmex) spp. mate in the spring after a period of cold weather. Apparently copulation takes place in the air. Regarding mating Fielde (1901) found that A. rudis workers carried into their nests and cared for conspecific males from alien colonies. This led her to suggest that "probably cross-fertilization is common if not universal " (p. 131). Ledoux (1971) reported that another form of colony propagation may exist in the European A. senilis Mayr. In the fall all colonies seem to have one dealate female, but in the spring a portion of the colonies are queenless. In the laboratory only colonies from which queens were



removed produced alate females, apparently from eggs of the former queens. Of the orphaned alate females only one survives to mate with one or more of the males which have developed from worker-laid eggs. The number of colonies seems to increase by the budding-off of groups of workers who propagate functional colonies by the means described above. Pleometrosis, the formation of new colonies by budding-off, is known for other Myrmicines, but is often associated with multiple queens. In light of Ledoux' work a statement by Fielde (1901) regarding A. rudis is interesting:

Colonies captured and confined in my nests just before swarming time, within a few days divided into as many groups as there were queens, the queens disposing themselves as far apart as the limits of the nest permitted. When a queen was then removed by me, the workers at once carried the young and settled down by another queen.

(p. 429)

As mentioned previously, Talbot (1951) found multiple dealated females in A. rudis nests in the spring. Headley (1949) also found multiple dealate females in A. rudis nests. Crozier (1973) did not find multiple dealate females in A. rudis colonies in Georgia. His isozyme studies led him to believe that if colonies aggregate in early spring as suggested by Talbot they must separate along original family lines with high fidelity. Crozier (1974) on the basis of allozyme analysis found that in most A. rudis colonies males arise predominantly or only from queen-laid eggs. Colonies with worker-derived males he feels are probably those whose queens have died. Bruniquel (1972b) describes

worker oviposition by the European A. subterranea Latreille. Alimentary and male producing eggs are laid by workers. The alimentary eggs are smaller than queen-laid eggs and male producing worker-laid eggs. Has-kins and Enzmann (1945) report an instance of thelotoky in A. rudis. Of 100 virgin females one produced worker offspring. Only 18 produced any offspring at all. They also mention a possible instance of thelotoky in A. lamellidens. At one Georgia locality Crozier (1972) found that at a cathodal malate dehydrogenase locus A. rudis queens were all heterozygous, while workers were in approximately equal numbers homozygotes and heterozygotes. This genotypic difference suggested to him that differential selection exists between castes and that A. rudis colonies consist of a single once-mated queen and her worker progeny.

Several European authors have studied the biology of Old World species of Aphaenogaster. Bruniquel (1970a, 1970b, 1972a, 1972b) published on the nesting habits, reproduction, and social biology of A. subterranea. He (1970a) found that groups of A. subterranea workers when deprived of their queen had to be comprised of at least 75 to 100 individuals if they were to maintain the semblance of a colony. Over a given period of time the mortality rate for groups of 75 to 100 queenless workers was very low compared to the mortality rate for groups consisting of fewer workers. The mortality rate was inversely proportional to the number of orphaned workers. In the laboratory Bruniquel (1970b) found that when presented a humidity gradient of 35 to 100 percent at 22° C, 92 percent of queenless workers and 93.55 percent of workers with queen and brood nested within the range of 90 to 100 percent relative humidity. This he compares with published data for other ants. In the arboreal Dolichoderus quadripunctatus L., for

example, workers live in the range of 35 to 50 percent relative humidity, while the brood needs a relative humidity of 60 to 75 percent. Bruniquel (1972a) describes two types of nests constructed by A. subterranea; those completely hypogeaic and those partly in rotten logs and extending into the soil. Ledoux (1967) found that the optimal temperature range at which the normal activity of A. senilis took place was 20 to 28° C. This was the temperature within the nest. Temperature outside the nest, with the exception of sub-lethal temperatures, only influenced speed. Above ground activity occurred between ten and 35° C. When confined in a temperature gradient apparatus, A. senilis colonies dwelt in the portion of the gradient having temperatures 23 to 25° C.

Buschinger (1973) noted workers of A. subterranea carrying their larvae to prey which had been brought into the nest. The larvae fed directly on the food item. Fielde (1910) and Wheeler (1901) also report this behavior in A. rudis. Wheeler and Wheeler (1953) gave dead arthropods directly to unattended A. rudis; larvae consumed the items. Fielde (1901) also reports that A. rudis workers regurgitate food to young larvae. Wheeler and Wheeler (1953) describe a generalized Aphaenogaster (Attomyrma) larva.

Moderately stout; constricted slightly at the first abdominal somite; thorax turgid; abdomen swollen; no neck. Submature larva with its diameter greatest at abdominal somites IV and V, diminishing anteriorly; anterior end bent ventrally; no neck; posterior end broadly rounded. Body hairs moderately numerous and rather short. Of two

types: (1) with long stout base and short dichotomizing tip, on the thorax and abdominal somites I, IX, and X; (2) with short base and long flexible dichotomizing branches, on abdominal somites I-VIII; intergrades rare. Head hairs moderately numerous and rather long. Of two types: (1) simple and (2) with bifid tip. Posterior surface of labrum densely spinulose, the spinules minute and in short arcuate rows which tend to form a reticulate pattern. Apex of mandible forming a rather slender tooth which is slightly curved medially; two stout round-pointed medial teeth; medial surface of basal half with several short to very long spinules. Maxillae with the apex spinulose; palp digitiform. Dorsal portion of hypopharynx with sublongitudinal ridges; ventral portion spinulose, the spinules minute and arranged in rows which form a reticulate pattern.

(p. 54-56)

They also describe the larvae of A. fulva, A. rudis, A. rudis picea, A. tennesseensis, A. texana, A. treatae, and A. treatae pluteicornis G. C. and E. W. Wheeler. Biological notes are included for some species. Male and female prepupae of A. flemingi are described by Wheeler and Wheeler (1972).

Behavioral studies on the geotropic response of A. fulva workers placed on an inclined plane were conducted by Barnes (1930) and Barnes and Skinner (1930). They found the ants had a greater positive geotropic response the longer they were isolated from their nestmates.

This change they believed was not due to increasing muscular weakness from lack of food or to the posture the ants assumed in the isolation chamber.

Wheeler (1910) concluded that A. tennesseensis is a temporary social parasite of A. fulva or A. rudis. He found mixed colonies of these ants. This combined with the aberrant appearance of A. tennesseensis females led him to his opinion. He suspected that the rare A. mariae whose females resemble those of A. tennesseensis is also a social parasite.

Little has been reported regarding the predators of Aphaenogaster spp. Edwards et al. (1974) indicate that the jumping spider, Stoidis aurata (Hentz) feeds on species of Aphaenogaster as well as other ants. Brown (1958) describes an unusual instance of a slave-making ant, Formica subintegra Emery, raiding a colony of A. rudis, killing workers and stealing brood. This is peculiar since the usual victims of F. subintegra raids are species of Formica belonging to the fusca and pallidefulva groups.

Aphaenogaster spp. have been generally considered to be largely predaceous and facultative seed collectors (Forel 1901, Wheeler 1910, Talbot 1954, Smith 1965, Wilson 1971). Wheeler (1910) and Hendrickson (1930) describe the collection of seeds and plant parts by A. rudis. Goetsch (1942) reports leaf-cutting and collection by A. testaceopilosa (Lucas) in Spain.

Aphaenogaster spp. predation upon termites has been documented by several authors dating back to Forel (1901). Other authors have reported Aphaenogaster spp. nesting adjacent to termite colonies or preying on them (King 1897, Adams 1915, Van Pelt 1958). Reports of

termite predation were generally instances of the author having broken open a termite nest exposing the inhabitants to attack by Aphaenogaster foragers (e.g. Forel, 1901). More recent papers by Smythe and Coppel (1964, 1973) and Beard (1973) question the actual destructiveness of Aphaenogaster predation to undisturbed termite nests. Their attacks on termites are fortuitous. Referring to Reticulitermes flavipes (Kollar) Beard states:

Compatibility also seems a characteristic of Aphaenogaster spp. in spite of previously reported predatory activity. A. rudis is one of the most frequently encountered ants in termite habitats, and only fortuitous predation has been observed. In laboratory situations, A. rudis and R. flavipes can live in the same container with nonapparent conflict.

(p. 398)

## MATERIALS AND METHODS

### Field Studies

#### Detection of Colonies

I employed a variety of methods to detect field colonies of Aphaenogaster spp. Three techniques were of particular value and frequently used.

1. I broke open rotten logs, limbs, stumps, and cypress knees with an entrenching tool. This was the quickest method of locating nests of several species of Aphaenogaster. Experience soon dictated exclusion from examination dead wood too dry for Aphaenogaster inhabitation.

2. The substrate was scanned for foraging Aphaenogaster workers. Upon spotting a worker, pupae of the red flour beetle, Tribolium castaneum (Herbst), or small particles of old cheese were scattered in the immediate vicinity (one cm) of the ant. Almost invariably the ant picked up the food and returned directly to her nest. Except when she disappeared beneath leaves, the ant was easy to follow as either the dark ant or her light colored burden contrasted with any background. Even if the returning ant was lost from sight, the general direction of the nest was indicated by the

direction she was headed. Often no nest entrance is discernible for soil dwelling species, so disappearance of the ant might mean she entered the nest. In any case, recruited workers soon emanated from the nest toward the food source, thus providing opportunities to pinpoint the nest.

Headley (1949) and Talbot (1954) used a similar technique for locating Aphaenogaster nests, however they sprinkled bread or cake crumbs as bait. Cheese worked well; apparently the ants could detect its odor a few mm away. A major drawback of this method is that its success depends upon the extra nidal activity of the ants. For soil dwelling species, above ground activity was greatly curtailed during cooler and drier months and often during the heat of the day in warmer months. The drawback was particularly serious since no comparably rewarding technique was found for locating nests of soil nesting species.

3. I inspected trunks of living trees for Aphaenogaster workers. Smaller or younger trees generally did not have rotten or termite riddled portions suitable for Aphaenogaster nests. As a rule trees of less than seven cm dbh were not examined by me unless they bore some obvious indication of extensive internal decay. Arboreal nests were discovered by observation of ants carrying food items up the trunks to their nest entrances.



A technique I occasionally employed was overturning stones. Although it may be a rewarding method elsewhere, looking under stones was of little value in Florida. There is in Florida a scarcity of rocks of suitable size and shape beneath which Aphaenogaster spp. might nest. Wilson (1959) reports that in many tropical areas the ant fauna beneath stones is comparatively depauperate. In a New Guinea rainforest less than ten percent of the rocks he overturned had ant nests or foragers beneath them.

Sometimes the nest of a soil dwelling species was detected by my visually recognizing the nest entrance. Such discoveries were usually fortuitous, occurring while looking for foraging workers. However, I found colonies of A. floridana most often by searching for their nest entrances. This species regularly nests in rather open sandy areas where its distinctive thatch encircled nest entrances were easy to see unless situated at the base of a clump of wire grass. A. floridana nest entrances were not always thatched.

A technique I used infrequently was to scrape away surface leaf litter to expose the upper portions of nests of soil dwelling species. This technique was usually much less effective than following workers carrying food. Furthermore, this method was unsatisfactory because it made collection of complete colonies almost impossible. Many immatures and workers were lost in the leaf litter.

#### Collecting Trips

I took collecting trips to nearly every county in peninsular Florida. The panhandle was visited less frequently. Collection and distribution data may be somewhat biased toward north central Florida,

because these areas are more accessible from Gainesville and were examined more extensively and intensively.

### Collection of Colonies

Soil-dwelling colonies with the exception of A. carolinensis were collected without losing significant portions of the population through escape. Having ascertained the main entrance as accurately as possible, I scraped leaf litter away from the entrance for a radius of about 25 cm.

Nests of soil-dwelling species rarely extended laterally more than 20 cm from an imaginary line perpendicular to the ground and passing through the main nest entrance. Since a large portion of a colony usually resided within 13 cm of the surface, one could, by removing in one piece a cylinder of soil, ten cm deep and 36 cm diam with the nest entrance at the center, secure in toto those ants most apt to escape. Such soil cylinders were removed by thrusting an entrenching tool perpendicularly into the soil along the perimeter of the 36 cm diam imaginary circle to a depth of about 20 cm. Soil cylinders were dropped directly into plastic garbage bags. The remaining ants could not readily escape from the hole produced by the removal of the soil cylinder. The rest of the nest was excavated one shovelful at a time. The soil was deposited in an area cleared of leaf litter adjacent to the excavation, and sifted by hand to detect ants. Portions of soil containing large numbers of ants were deposited in a plastic bag. The excavation was expanded downward and laterally until no further ants were discovered for 20 cm in any direction. A. floridana nests were excavated to a minimum depth of 80 cm.

Nests of A. carolinensis were confined largely to the leaf litter stratum. No nest entrances could be discerned among the leaf litter. After several returning foragers disappeared into the leaf litter within a few cm of each other, it was assumed that the nest was directly below that spot. An entrenching tool was thrust into the leaf litter and soil at an angle of about  $20^{\circ}$  from the horizontal and to a depth of about seven cm. One hand was placed on top of this material, pressing it tightly to the blade of the entrenching tool. The entire shovelful was deposited in a plastic garbage bag. The material in the bag was quickly examined for brood to determine if the major part of the nest was where it was suspected to be. Leaf litter adjacent to the excavation was pushed toward the excavated area and examined, making certain no peripheral parts of the colony were missed. Excavation of the remainder of the nest continued as for any soil-dwelling species.

Success collecting in toto Aphaenogaster colonies nesting in rotten logs or stumps depended upon the size of the colony, stage of decay of the log and whether the nest extended into the soil. A large colony in a slightly rotten log was difficult to collect in toto, particularly if some of the nest was in the ground. Well-decayed logs were easily and rapidly broken down by hand or using an entrenching tool. Portions of a nest log containing the colony were dropped into plastic bags. Adults and brood were brushed by hand from large infrangible sections of logs into collecting bags. Occasionally small colonies and specimens hidden in infrangible parts of logs were aspirated. Removal of colonies from cypress knees and logs was especially difficult.

Except in winter, as soon as a nest log was broken open, the workers began to run about rapidly. Many ants ran or dropped from disturbed logs. This posed a serious problem when collecting large colonies. Some nests extended more than a meter along logs. This difficulty was somewhat circumvented by spreading plastic bags along or under nest logs or by clearing leaf litter away from nest logs. Escaping workers were exposed for a longer time and could be aspirated or gathered up by hand.

Colonies nesting in living trees were exceedingly difficult to collect in toto. Often nests penetrated deeply into the heartwood of large trees. Some nests were located several meters above the ground. A colony was collected from a storm-downed tree by cutting a section from the trunk with a chain saw. Nest trees frequently were too large for the use of a chain saw. Trees were chopped open with a hatchet or an axe. Many ants were crushed or escaped during the chopping.

#### Dissection of Colonies

Nests of soil-dwelling species were dissected according to a rather widely accepted procedure. A trench, about 90 cm long, 30 cm wide, and 60 cm deep, was dug tangentially to a 45 cm imaginary radian from the main entrance of the nest. The trench wall nearest the nest was carefully sheared away in decreasing decrements, exposing nest chambers and galleries. Contents of the chambers were aspirated or plucked out with forceps. The initial trench was lengthened as needed. The procedure was continued until after digging 30 cm in any direction no more ants were found.

Nests in wood were broken open carefully and gradually using a

hatchet, entrenching tool or penknife as the situation warranted. The ants nested in preformed cavities in the wood. Sometimes despite being riddled with cavities the wood was extremely hard, making careful dissection difficult. In every case, once the ants were disturbed, they fled, carrying brood, into any tunnels or cavities adjoining the nest proper. The true dimensions of nests in wood were, therefore, always difficult to discern, except for incipient colonies.

### Field Observations

Field observations were made year round. Stations where several congeners coexisted in rather close proximity were frequent observation sites. At stations where several Aphaenogaster spp. occurred I could easily check and compare the activities of the various species under apparently similar temporal and climatic regimes. I observed foragers to determine where and when they foraged and their interactions with other organisms. To study interspecific competition and foraging ranges pieces of cheese and dead insects were set out in natural situations and observed. The feeding habits of other species of ants were noted to determine those competing with species of Aphaenogaster. Observations of competing ant species were corroborated with collections. Within a two m radius of certain Aphaenogaster nests all ants seen foraging on the ground or leaf litter were collected. Collections were limited to one hour. Small ants were collected in an aspirator; large ants by hand or with forceps.

Night observations were made with the aid of a battery powered headlamp. The light from the headlamp seemed to diminish the activity of nocturnal foragers upon which it was shone. A transparent piece of

red plastic affixed to the front of the lamp did not markedly interrupt the activities of the ants, but seriously impaired my ability to see the ants.

To determine some of the vertebrate predators of Aphaenogaster spp., whenever possible amphibians and reptiles were captured and kept until they defecated. The feces were placed in a petri dish with isopropanol and examined microscopically for remains of Aphaenogaster spp.

Cabbage loopers of different instars were released in the field near Aphaenogaster spp. so that attacks upon the larvae by the ants might be observed.

Colonies of A. ashmeadi and A. fulva were watched daily for several weeks in June and July to observe mating flight activity.

#### Foraging Success

I set out 25 dead house flies (Musca domestica L.) several distances from the entrance of an A. ashmeadi nest. Four baits were 15 cm (II), four 21.2 cm (III), four 30 cm (IV), eight 33.5 cm (V), and four 42.4 cm (VI) from the entrance. The remaining bait (I) was placed adjacent to the nest entrance. Each of the baits for distances II, III, IV, VI was on a radian  $90^{\circ}$  from the nearest bait the same distance from the entrance. Each bait at distance V was on a radian 30 and  $60^{\circ}$  from the nearest baits at distance V. The radii of baits of II and IV were identical and offset from the radii of III and VI (also identical). To  $22.5^{\circ}$  either side of radii II/VI were radii of baits of distance V. One at a time each bait was placed down and observed. The species of the first ant to find and begin to feed on or remove the bait was recorded. I placed the baits in a sequence which

avoided the complications of possible recruitment resulting from previously placed baits.

Ten house flies were placed in the area described above. The sequence of ant species removing or feeding on the baits was recorded. Seven house fly heads were placed in the area and observed to see which ants successfully removed to their nests.

Two Pheidole metallescens Emery colonies were in the area between the A. ashmeadi nest and the outermost baits.

### Laboratory Studies

#### Maintenance of Colonies

Colonies of nine species of Aphaenogaster were maintained in the laboratory. When brought into the laboratory field collected colonies were still in the soil or wood in which they nested in their natural situations. This material and the ants within were emptied from plastic collection bags into plastic tubs of various sizes. The sides of the tubs were dusted with talcum powder, preventing the ants from escaping. Some colonies were allowed to remain in the tubs with their natural nesting substrate. Others were transferred to smaller containers permitting better observation.

Plastic shell vials served as artificial nests. A moistened wad of absorbent tissue paper was pushed inside a transparent shell vial, filling about one-half its volume. A plastic snap cap with a hole (five mm across) in the center was affixed to the open end of the vial. The capped vial was placed in a tub containing a newly collected ant colony still nesting in its natural substrate. The vial was buried in

the substrate leaving only the capped end exposed. The natural substrate was allowed to dry for a few days. When the humidity in the natural substrate became low, the colony moved into the more humid vial. Often the vial was not placed in the tub until the substrate had already begun drying for a few days.

Colonies were maintained in plastic vials or transferred into plastic petri dish nests or Wilson cells. Petri dish nests had one or more holes in the lids or sides. Damp tissue paper was placed inside petri dish nests and Wilson cells. Shell vial nests, petri dish nests, and Wilson cells were placed in trays which served as foraging arenas. Sides of the trays were dusted with talcum powder. Individual queens or queens with incipient colonies of less than 20 workers were maintained in closed petri dish or shell vial nests.

High humidity was maintained in laboratory nests. Water from a squeeze bottle was squirted onto natural substrate daily or onto tissue in artificial nests at weekly intervals. Water evaporated rather slowly from the semi-enclosed artificial nests. However, the ants continually tore off small pieces of tissue and carried them from their nests. Therefore, new tissue had to be placed in the artificial nests every few weeks.

I fed the ants largely proteinaceous food principally in the form of larvae and pupae of the red flour beetle, potato tuber moth (Gnorimoschema operculella Zell.) and cabbage looper (Trichoplusia ni Hubner). To a lesser extent a variety of other arthropods and meat table scraps were fed to the ants. Ant media (Bhatkar and Whitcomb, 1970) was frequently fed to the ants.

The laboratory in which the ants were maintained was heated or



cooled by an airconditioner every few days during the course of the year.

#### Determination of Stadial Duration

To determine duration of the egg stage I placed viable queens and four to ten of their workers in closed petri dish nests. The time elapsed between the day the first egg (eggs) was laid and the day of the eclosion of the first larva (larvae) was defined as the duration of the egg stage.

The duration of the larval stage was defined as the time elapsed between the eclosion and pupation of the first larva. Differential feeding of larvae by workers varied the rates of larval development, making it difficult to monitor the development of several larvae in a single colony. The time elapsed between the day of pupation of the first larva and the day of its eclosion was the duration of the pupal stage. Durations of several subsequently pupating larvae were also monitored.

Durations of larval and pupal stages were determined by a similar technique. Eggs were removed from queens and those laid within the next 24 hrs were placed in petri dish nests with four to six sibling workers. The development of eggs could be monitored with more certainty than by the method described above. Eggs were placed in petri dish nests with sibling workers and the duration of larval and pupal stages determined. Prepupae were placed in petri dish nests with sibling workers and the duration of the pupal stage determined.

Development of colonies from founding queens collected in the field were monitored in a similar fashion. Queens and their brood,

if any, were placed in petri dish or shell vial nests and growth of the colonies recorded.

## RESULTS

### General Appearance of Aphaenogaster Spp.

Ants of the genus Aphaenogaster are morphologically rather generalized. They do not depart radically from the basic Myrmicine form. The genus keys out in the final couplet of Creighton's (1950) key to the Myrmicinae of North America. Smith (1947) provides a brief description of the genus.

Monomorphic. Medium-sized (3.25-7mm), slender ants. Head usually distinctly longer than broad; in some forms very noticeably narrowed posteriorly (when the head is much narrowed posteriorly the antennae are usually long and slender). Eye generally prominent, usually not placed far from the middle of the side of the head. Frontal carinae short, not distant from each other. Anterior border of clypeus usually with a distinct median emargination. Antenna 12-segmented, the last 4 segments enlarged but not forming a very definite club, the last 3 segments shorter than the rest of the funiculus. Base of the scape with a prominent lobe in some forms (treatae Forel and its variants). Thorax usually with a

distinct promesonotal suture. Anterior portion of mesonotum sometimes protuberant. Posterior third or more of mesonotum often very noticeably impressed. Mesoepinotal suture distinct. Epinotum usually with a pair of spines of variable length (in only a few forms are the spines vestigial or almost absent). Petiole generally pedunculate anteriorly, sometimes very much so. Gaster oval, not truncate basally, rather shining except for the sculpturing at the base in a few forms.

(p. 555-556)

Brown (1974) synonymized the genus Novomessor, which occurs in the western United States, with Aphaenogaster. Smith's description is still functional for Florida species. See Figure six for line drawing of Aphaenogaster worker.

#### Species of Aphaenogaster in Florida

Eight species of Aphaenogaster, all belonging to the subgenus Attomyrma, were collected in this study.

- A. ashmeadi Emery
- A. carolinensis Wheeler
- A. flemingi M. R. Smith
- A. floridana M. R. Smith
- A. fulva Roger
- A. lamellidens Mayr
- A. tennesseensis (Mayr)
- A. treatae Forel

The rare A. mariae Forel has been reported from Florida (Creighton, 1950), but I never found this insect in the state. See section on taxonomy for discussion of other species reportedly occurring in Florida.

Key to Workers of Florida Species

1. Antennal scape with rearward extending lobe along at least basal fifth of scape . . . . . 2
- Antennal scape without conspicuous rearward extending lobe . . 3
2. Lobe of scape extending one fifth of scape length, lobe thin and flattened; specimens from peninsula blackish. . ashmeadi  
Lobe of scape extending one quarter of scape length, lobe thick: specimens brown, gaster somewhat darker . . treatae
3. Base of antennal scape with small forward projecting lobe; in frontal view head two times longer than wide. . . . . 4  
Antennal scape without forward projecting lobe; head in frontal view less than two times longer than wide. . . . . 5
4. Propodeum with pair of long slender spines; in profile petiolar node acute . . . . . flemingi  
Propodeum without spines; in profile petiolar node low and rounded . . . . . floridana
5. Postpetiole with laterally compressed anteriorly projecting flange along ventral midline; postpetiole wider than long . . . . . 6  
Postpetiole without forward projecting ventral flange; postpetiole longer than wide . . . . . 7

6. First gastric segment with striations spreading fan-like from point of articulation of postpetiole and covering basal half of dorsum of segment; dorsum of first gastric segment with erect hairs . . . . . mariae  
 First gastric segment without striations, or if present then only extending over basal fifth of dorsum of segment; dorsum of first gastric segment devoid of erect hairs. . . . . tennesseensis
7. Outer face of frontal lobe with rearward projecting tooth-like flange; specimens reddish with yellowish gaster . . . . . lamellidens  
 Outer face of frontal lobe without tooth-like flange; specimens brown to black, or if reddish then gaster dark brown . . . . . 8
- \*8. Anterior border of mesonotum rising abruptly above contiguous portion of pronotum, viewed anteriorly the transverse welt thus formed distinctly depressed in middle; propodeal spines often as long as declivious face of propodeum; in frontal view head, excluding mandibles often as broad as long . . . . . fulva  
 Anterior border of mesonotum not rising abruptly above contiguous portion of pronotum, or if it is higher then anterior edge does not form transverse concave welt; propodeal spines rarely as long as declivious face; in frontal view head, excluding mandibles, not as broad as long . . . . . carolinensis

\*Spines sometimes shorter than declivious face in nanitics of fulva.

Appearance of Workers of Florida Species

See generic description for general appearance.

- A. ashmeadi Emery- Length 6.0 - 7.5 mm. Head 1.4 mm long, 1.2 mm wide.\* Head narrowed posteriorly. Antennal scapes each with flattened rearward projecting lobe. Lobe extending along basal fifth of scape. Propodeal spines shorter than declivious face of propodeum. Postpetiole large as in A. flemingi, A. floridana, and A. treatae. Head with punctations and longitudinal rugae covering frontal and lateral portions. Alitrunk, petiole and postpetiole largely punctate; weak transverse rugae on pronotum and coarse transverse rugae on dorsum of propodeum; some weak granulations and rugae on petiole and postpetiole. Piceous; some specimens from Florida panhandle not as dark. Most similar to A. treatae, but differs in having smaller flatter basal antennal lobes, darker color and fine punctations covering only about basal third of first gastric segment.
- A. carolinensis Wheeler- Length 3.7 - 6.9 mm. Head 1.2 mm long, 1.0 mm wide. Head narrowed posteriorly less than in preceding species. Antennal scapes simple. Propodeal spines rarely longer than declivious face of propodeum. In large specimens spines somewhat incurved, while in smaller individuals spines often diverge. Postpetiole not as voluminous as in preceding species. Head with punctations and longitudinal rugae covering frontal and lateral

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\*For each species head length measurement does not include mandibles, but mandibles included in total length measurements. Head widths measured in frontal view across widest part of heads. Total length equals summation of length of tagma.

portions in larger specimens; in smaller specimens longitudinal rugae confined to area of frontal longitudinal midline and laterally posterior and anterior to compound eyes. Alitrunk, petiole and postpetiole largely punctate; pronotum rather shining in small specimens. Transverse rugae on dorsum of propodeum and in larger specimens on humeral areas as well. Not as rugose as A. fulva. Head, alitrunk, petiole and postpetiole reddish or brown to black; gaster darker in all specimens, sometimes yellowish brown distally. Nanitics of A. fulva are similar; see description of A. fulva for details. Differences between A. carolinensis and A. rudis and A. texana are discussed in "rudis/texana group" taxonomy section.

A. flemingi M. R. Smith- Length 6.5 - 7.6 mm. Head 1.4 mm long, 1.2 mm wide. Head narrowed posteriorly; among Floridian congeners only A. floridana with head as narrowed. Small angular lobe projecting forward from base of each antennal scape. Lobe less than two-thirds the size of basal lobes on scapes of A. ashmeadi and A. treatae. Propodeal spines about as long as basal face of propodeum. Postpetiole voluminous as in A. ashmeadi, A. floridana, and A. treatae. Head with punctations covering frontal and lateral portions. Longitudinal rugae weaker than in A. ashmeadi and A. treatae and largely confined to area of longitudinal midline and laterally anterior and posterior to compound eyes. Alitrunk, petiole and postpetiole largely punctate. Pronotum feebly punctate and smoother; shining even in largest specimens. Alitrunk lacking rugosity; among Floridian congeners only A. floridana with alitrunk devoid of rugae. Castaneous with gaster slightly darker.



A. floridana M. R. Smith- Length 6 - 7.2 mm. Head 1.4 mm long, 1.2 mm wide. Head narrowed posteriorly, more so than in Floridian congeners. Small angular lobe projecting forward from base of each antennal scape; lobes about the size of those on scapes of A. flemingi. Only Floridian Aphaenogaster without propodeal spines. In profile petiole with lower more rounded node than in Floridian congeners. Postpetiole large as in A. ashmeadi, A. flemingi, and A. treatae, but more elongate and with lower node. Head capsule with punctations covering frontal and lateral portions except occipital area which is nearly smooth. Longitudinal rugae largely confined to area of head anterior to compound eyes. Pronotum shining and nearly smooth; remainder of alitrunk moderately to feebly punctate. Petiole and postpetiole punctate laterally; smooth and shining above. Yellow to light orange brown; gaster darker.

A. fulva Roger- Length 4.5 - 6.0 mm. Head 1.1 mm long, 1.1 mm wide. Head excluding mandibles about as long as broad; in frontal view occiput laterally roughly angularly convex. Antennal scapes simple but thicker than in preceding species. Anterior border of mesonotum rising abruptly above contiguous portion of pronotum; viewed from anterior the transverse welt thus formed is distinctly depressed in middle. Propodeal spines generally more upwardly directed than in Floridian congeners; spines about as long or longer than basal face of propodeum. Postpetiole scarcely more voluminous than petiole; postpetiole not as elongate as in any aforementioned species. Heavily sculptured. Punctations and coarse longitudinal rugae covering frontal and lateral portions of

head; in small specimens longitudinal rugae confined to area of longitudinal midline and laterally anterior and posterior to compound eyes. Alitrunk, petiole and postpetiole with more rugosity than in preceding species. Transverse rugae extending across pronotum, particularly in larger specimens. Dorsum of propodeum with transverse rugae. Brown to piceous. Nanitics similar to A. carolinensis and A. rudis; less heavily sculptured, heads narrower and spines often shorter. However, mesonotal welt character seems to hold even in nanitics. Reproductives easily distinguished. Females of A. fulva with mesothoracic sternite and episternite heavily rugose, while in A. carolinensis these sclerites are mostly smooth and shining. Males of A. fulva with pair of thick propodeal spines; males of A. carolinensis rarely with propodeal spines, head narrow.

A. lamellidens Mayr- Length 6.0 - 7.7 mm. Head 1.5 mm long, 1.3 mm wide. Head not as wide posteriorly as in A. fulva, but wider than in A. carolinensis. Antennae simple. Outer face of frontal lobe with posteriorly projecting tooth-like flange. Compound eyes smaller than in A. carolinensis. Propodeal spines shorter than basal face of propodeum. Postpetiole not as large as in A. ashmeadi, A. flemingi, A. floridana, and A. treatae. Punctations and longitudinal rugae covering frontal and lateral portions of head. Alitrunk, petiole and postpetiole largely punctate. Transverse rugae on dorsum of propodeum and pronotum. Brick red with dark legs and reddish yellow gaster; gaster sometimes darker in pinned specimens. In the field A. lamellidens superficially like A. tennesseensis, but morphologically most like larger forms of A.

carolinensis. A. lamellidens distinguished from Floridian congeners by flange on frontal lobe.

A. mariae Forel- Length 5.3 mm. Head 1.1 mm long, 1.0 mm wide. Head shape similar to that of A. lamellidens, but slightly narrower. Antennae simple. Propodeal spines curved and longer than declivous face of propodeum. Viewed dorsally postpetiole broader than long. Postpetiole with laterally compressed anteriorly projecting flange along ventral longitudinal midline; of Floridian congeners only A. tennesseensis with similar flange. Very heavily sculptured. Pronounced punctations and coarse reticulo-longitudinal rugae covering frontal and lateral portions of head. Dense punctations and coarse mostly reticulate rugae over most of alitrunk. Petiole and postpetiole largely punctate. First gastric segment with striations spreading fan-like from point of articulation of postpetiole and dorsally covering basal fifth of segment. Only specimen examined reddish brown. Differs from A. tennesseensis in having erect hairs on dorsum of first gastric segment and in having striations on first gastric segment.

A. tennesseensis (Mayr)- Length 6.0 - 6.6 mm. Head 1.2 mm, 1.2 mm wide. Head wide posteriorly; similar in shape to head of A. fulva. Antennae simple. Propodeal spines curved and longer than declivous face of propodeum. Viewed dorsally postpetiole broader than long; not as elongate or voluminous as in A. ashmeadi, A. flemingi, A. floridana, or A. treatae. Postpetiole with ventral flange as described for A. mariae, but slightly smaller. Heavily sculptured, but less so than A. mariae. Pronounced punctations and reticulo-longitudinal rugae covering frontal and lateral portions of head;

reticulations not as coarse as in A. mariae. Alitrunk except between propodeal spines largely covered with dense punctations and coarse mostly reticulate rugae. Petiole and postpetiole largely punctate. First gastric segment without striations covering basal fifth as in A. mariae. Unique among Floridian species of Aphaenogaster in having dorsum of alitrunk, petiole, postpetiole and gaster devoid of erect hair. Reddish with yellowish gaster.

- A. treatae Forel- Length 6.4 - 7.6 mm. Head 1.4 mm long, 1.2 mm wide. Head narrowed posteriorly; similar in shape to that of A. ashmeadi. Antennal scapes each with thickened rearward projecting lobe. Lobe extending along basal one-quarter of scape; lobe larger and more three dimensional than in any Floridian congener. Propodeal spines shorter than declivious face of propodeum. Postpetiole large and elongate as in A. ashmeadi, A. flemingi, and A. floridana. Punctations and longitudinal rugae covering frontal and lateral portions of head. Alitrunk, petiole and postpetiole largely punctate; transverse rugae on pronotum and coarser transverse rugae on dorsum of propodeum. First gastric segment often with fine punctations basal one-half of dorsum. Brown with darker gaster. A. ashmeadi similar; see description of that species for differences with A. treatae.

#### Taxonomy of rudis/texana Group

The genus Aphaenogaster is in dire need of taxonomic revision. A complex of disputed forms contains some of the most common representatives of the genus in Florida. Other species or forms seem to be

erroneously attributed to the state. Creighton (1950) recognized A. rudis and A. texana as species. Both were originally described as varieties of A. fulva and subsequently reported as occurring in Florida. Under present taxonomy both names are referable to several forms; some of which may well be sibling species, while others may be geographic subspecies or intergrades. A. rudis has a long history of nomenclatorial confusion as well. This is not a taxonomic revision; few specimens from outside Florida were examined and the types of A. rudis and A. texana are not repositied in this country. In lieu of such a desperately needed study, what follows is an attempt to briefly and pragmatically deal with the multiplicity of names and forms involving Floridian representatives of the "rudis/texana group."

For purposes of discussion first A. rudis and associated forms are treated and then A. texana and its associated forms. However, in the ensuing discussion it should become apparent that there does not seem to be, following the current convention, a "rudis group" distinct from a discrete "texana group."

Creighton (1950) recounted the confused taxonomic history of A. rudis and proposed certain changes of his own. In essence Creighton discarded the long standing name aquia as representing an unrecognizable form described by Buckley. According to Creighton aquia had been placed in synonymy with A. fulva by Mayr, perhaps on the basis of type specimens. However, Emery (1895) resurrected the name aquia based on specimens Creighton believed were intergrades, perhaps between the forms rudis and picea also described by Emery in his (1895) paper. All three were considered by Emery as varieties of A. fulva. Creighton suggested Emery's (1895) rudis be recognized as a species and picea as a northerly

and high altitude subspecies of rudis. In addition to the nomenclatorial maze the actual complex of forms is a source of confusion. Karyological and isozyme studies by Crozier (1970, 1973) led him to suggest that at least three distinct forms exist in the eastern United States. Two of these forms he believes may be sibling species. Assuming the validity of Crozier's work and accepting Creighton's abandonment of Buckley's aquia, what in fact is the rudis redescribed by Emery and accepted by Creighton? To what does the name rudis apply? The type locality of Emery's rudis was restricted by Creighton to Virginia.

Smith (1930) and Wheeler (1932) report examining specimens of A. fulva aquia from Royal Palm Park and Dunedin. Smith (1965) stated that A. rudis occurs in Florida. Van Pelt (1958) found specimens at Welaka which he believed resembled A. rudis, but he reserved judgment on the matter. Apart from the questionable application of the name aquia to any form, these records seem dubious. Based on the examination of specimens from Florida I believe that the name A. rudis is not justifiably applicable, even in a rather broad sense, to any form I know to occur in peninsular Florida. Perhaps some isolated enclaves exist near the Georgia border, however, if A. rudis does occur in Florida at all it would seem more likely to be found in the cool shady ravines in the panhandle near the Alabama border, which harbor more northern ant species. The Royal Palm Park and Dunedin records are so far south as to be highly unlikely. Smith's concept of A. rudis must be very broad, because specimens (from Dade County) determined by Smith as A. rudis correspond perfectly with Wheeler's description of A. miamiana. Smith's identification was subsequent to Wheeler's description. Creighton (1950) seemed to support Smith with a statement epitomizing the entire

rudis/texana dilemma. Creighton stated that A. miamiana, which was described as a variety of A. texana, "seems rather closely related" to A. rudis (p. 146). None of the Floridian forms that I have examined have had the smaller compound eyes, thicker prothorax, or shorter post-petiole associated with rudis-like forms from more northern states. Some more northern specimens (Iowa) examined had heads of about the same narrow proportions as A. miamiana. Nanitic specimens with narrower heads and more slender alitrunks lend to the confusion. Carter (1962b) in North Carolina could not determine with certainty some collections from the piedmont and coastal plain forests as either A. rudis or A. texana. In this paper the name rudis is not applied to any Floridian forms.

Emery (1895) described Stenamma (Aphaenogaster) fulvum var. texanum from two workers, which he indicated were honey-yellow. Twenty years later Wheeler redescribed texana, raised it to species level and described two variants of it, furvescens and carolinensis. Menozzi (1929) described A. (Deromyrma) silvestrii from a worker and dealate female collected in Gainesville, Florida. Silvestrii was relegated to the status of a texana variant in 1932 by Wheeler, who at the same time noted Menozzi's error of placing silvestrii in the subgenus Deromyrma. In the same paper Wheeler described two more variants of texana from Florida. Based on specimens from Dade and Monroe Counties he described the variant miamiana, while he described the variant nana from three very small (2.5 mm long) workers from Gainesville. Smith (1934) described A. texana macropsina from coastal South Carolina. In 1950 Creighton attempted to clarify the taxonomy of texana. He dismissed Wheeler's nana and two other more northerly forms, pusilla Emery and punctithorax Cole, as based on nanitics and "impossible of exact

recognition." Creighton acknowledged, in addition to the typical texana, the forms furvescens, carolinensis, and silvestrii. He believed carolinensis exhibits sufficient geographic allopatry warranting subspecific designation, but he synonymized furvescens and silvestrii with the typical texana. He raised macrospina and miamiana to species level. Creighton (1950) and Van Pelt (1958) reported that A. macrospina occurs in Florida. The description of macrospina was based on small specimens from an immature colony, so in 1958 Smith synonymized macrospina with flemingi. A. flemingi, although with definite affinities to the typical texana, is a very distinctive species and concerns us no further in this discussion.

A. texana and its forms have been reported from Florida by several authors. The type locality of Menozzi's silvestrii is Gainesville. Smith (1930) and Wheeler (1932) recorded the variant furvescens from Florida. Wheeler (1932) in addition to describing the variants nana and miamiana from Florida, reported examining silvestrii-like specimens from Gainesville. Creighton (1950) implied that not only the typical texana, but also the variants furvescens and silvestrii occur in Florida. Van Pelt (1958) reported collecting A. texana at the Welaka Reserve.

Certain difficulties arise in the application of the name texana to the Floridian forms of Aphaenogaster examined in this study. Even in a broad sense, including the variants acknowledged by Creighton (1950), silvestrii and furvescens, the name does not seem to refer to Floridian forms.

No specimens of Aphaenogaster from Florida examined by me were colorously honey-yellow and also bore propodeal spines as per Emery's



original description of texana. Specimens from Brownsville, Texas, corresponded closely to Emery's description. They differed markedly from any specimens from Florida. The Brownsville specimens, aside from color differences, had heads distinctly more narrowed posteriorly, less rugosity, and larger size. If texana is a monotypic species then I know of no specimens of it from Florida.

Wheeler (1915), however, complicated matters. Making no mention of a honey-yellow form, he redescribed the typical texana as uniformly light ferruginous. Much of the description is in the form of a comparison with the very different A. fulva and thus of limited value. Morphologically the Brownsville specimens fit Wheeler's description. According to Wheeler's description, the variant furvescens differs from the typical texana only in its coloration. Furvescens is reddish brown with a dark brown gaster. He fails to offer an explanation regarding the disparity between the sizes he gives for females of the two forms; texana 11 - 11.5 mm and furvescens 7.5 mm. Creighton (1951) interpreted this incongruity as that the texana measurement included the wings, while the furvescens measurement was based on a dealated specimen. Judging from the size of the Brownsville workers, their queen (dealated) would be surprisingly small if it were only 7.5 mm long. In fact in a later paper Wheeler (1932) mentioned that the female of the typical texana measured 8 - 8.5 mm. If furvescens differs from the Brownsville specimens only in color, the author has seen no Floridian forms referable to furvescens. Some Floridian forms fit the description of the coloration of furvescens, but most of these conform closely to Wheeler's (1932) description of miamiana. Wheeler, author of both furvescens and miamiana maintained that both occur in south Florida.

Could he have mistaken some nanitics of miamiana for furvescens? He (1932) stated regarding miamiana that it is "More robust and averaging larger than other forms of texana: head broader and less narrowed behind, ... antennal scapes stouter and slightly shorter; ... sculpture decidedly coarser throughout " (p. 5). The characters quoted all would serve to separate workers from mature miamiana colonies from nanitics of the same species. The unquoted characters are also rather variable in miamiana-like specimens examined by the author and in many instances would not permit separation of texana from miamiana. Wheeler (1932) cited only a single record of furvescens from Florida, that being from Royal Palm Park. One further anomaly, miamiana-like specimens examined by the author tended to be smaller than the Brownsville specimens just the opposite of Wheeler's description. It would seem that if furvescens occurs in Florida it must be extremely rare.

Having disposed of the names texana and furvescens, there remains the problem of the forms themselves. That is, what names do we apply to them. A major difficulty is the question of sibling species in the "texana group." Reproductive isolation has not been demonstrated between any of the Floridian forms with affinities to texana. Based on morphology and coloration there seems to be a gradation of forms with the typical miamiana at one extreme. Creighton (1950, 1951) in his treatment of the forms of texana neglected to mention the possibility of sibling species. The fact that dark forms and light forms could be found throughout most of the range of texana led him to conclude that these forms, except for carolinensis, were merely variants. Because of their sympatry they could not be considered subspecies. However, carolinensis occurred in rather pure stands so he felt it was a true

geographic subspecies. In his 1951 paper Creighton recited the diverse localities and habitats from which texana sensu latu has been reported; abundant in Miami, Florida, damp woods at an elevation of 1800 feet in the Great Smoky Mountains, at an elevation of 900 feet in the plains of central Kansas, shady ravines in central Texas, Grand Canyon, Arizona, and at the 6,000 foot level on sunny slopes in canyons of mountains in southern Arizona. Responding to this data, Creighton (1951) stated:

All these stations lie south of the 38th parallel, but I fail to see that there is any other feature which they share that could be cited as a reason why they were selected as nest sites by texana. Under such circumstances it appears hopeless to attempt a generalization which will cover the behavior of texana over its entire range. However the situation is by no means difficult if field observations are limited to a particular part of the range.

(p. 90)

Such ecological data would seem to indicate the existence of, if not more than one species, then at least of geographic subspecies. An ant species with such a range would be rather unique among the North American fauna. In this regard the original appellation of furvescens to an Arizonan form makes its application to a Floridian form slightly more suspect. Until evidence of reproductive isolation between any of the forms in the "texana/rudis complex" is demonstrated taxonomic judgment on various forms is tentative at best.

At one extreme among the Floridian forms are specimens recognizable

as Wheeler's A. texana carolinensis. Some of these Floridian specimens were compared by Dr. W. F. Buren with type material. This form was characterized by its small size (all castes), minimal rugosity, faint femoral punctation, slender alitrunk, rather short propodeal spines, comparatively convex compound eyes. It differs most markedly from the typical miamiana. See Figure six. Specimens examined included many from mature colonies containing reproductive forms. This small form diverges from the typical miamiana in the size of its colonies, which are less populous. The carolinensis-like form regularly constructs small rather superficial nests in leaf litter and soil. In north Florida it is commonly found in drier habitats in areas where miamiana-like forms are largely restricted to river swamps or hydric hammocks. Mating flights of the two extreme forms do not seem to be chronologically isolated from one another. The smallest specimens of the carolinensis-like form approach the measurements given by Wheeler (1932) for nana.

At the opposite extreme is the typical miamiana. Specimens from south of Lake Okeechobee fit Wheeler's (1932) description very closely. Figure one depicts the distribution of miamiana-like and more carolinensis-like forms in Florida. These specimens are readily distinguishable from carolinensis-like forms by the characters given above. I found only the miamiana-like form south of Lake Okeechobee. Forms less typical of miamiana occur in central and north Florida. These specimens are generally darker, with the head, alitrunk, petiole and post-petiole brown to almost piceous. In north and central Florida those specimens resembling the typical miamiana in color are more restricted to drier habitats; however, they are morphologically more similar to the carolinensis-like form. The small specimens of the northern forms

do not seem distinct from larger carolinensis-like specimens in morphology or color. The description of Menozzi's A. silvestrii seems to be of such intermediate forms.

The two extreme forms in the absence of demonstrable reproductive isolation will have to be treated as a single species. To assign a name to these forms one must go back to A. texana carolinensis (Wheeler, 1915), which preceded silvestrii (Menozzi, 1929) and miamiana (Wheeler, 1932). As discussed above Floridian forms seem quite distinct from the typical texana and the variant furvescens as I interpret them. In my opinion the Floridian forms represent a separate species from texana and the name A. carolinensis is being applied to them. The only other name possibly applicable is furvescens (Wheeler, 1915), and only if the type material does conform to the description. Described from Tryon, North Carolina, carolinensis has not been previously recorded from Florida. Carter (1962) reported it from the piedmont and fall line sand hill areas of North Carolina, but did not find the typical texana in that state. If one only considers the populations in Florida, one might interpret the frequent occurrence of small forms (typical carolinensis) in drier areas in north and central Florida as a response to adverse conditions in such habitats. Females produced in such enclaves might also tend to be small being reared under less than optimal conditions. Congeneric competition might be important in this regard. In south Florida miamiana-like forms occur in a wide variety of habitats but have little or no congeneric competition. Judging from some collections from central Florida one might also hypothesize a north-south color cline exists in the complex. Considering the overall distribution of the typical carolinensis and the miamiana-like forms another

interpretation is possible. The two extreme forms may be geographic subspecies with a zone of hybridization in north and central Florida. In North Carolina carolinensis seems to be prevalent in the same general habitats as in Florida. According to Carter (1962b), in North Carolina carolinensis is common in upland forests and "bottomland collections were generally made in well-drained, sunny and sandy locations." Perhaps, resolution of the problem rests in karyological and isozyme studies like those of Crozier (1970, 1973) and Imai (1971), laboratory mating tests or nutritional investigations.

#### Findings on A. ashmeadi

##### Description of Female

TL 9.3, HL 1.8, HW 1.5, SL 1.9, AL 3.1 mm.\* General appearance as in Figure three. Head shape as in Figure three; not as narrowed posteriorly as in workers. Conspicuous rearward projecting lobe extending along basal one-fifth of antennal scape. Lobe flatter than in A. treatae females. Lobe in A. treatae females longer, extending one-quarter scape length. Scape bent at slight angle at distal end of lobe. Anterior margin of clypeus somewhat more deeply incised than in A. treatae females.

Alitrunk as in Figure three; propodeum with pair of short posteriorly directed spines, as in females of treatae and floridana. Spines shorter than declivious face of propodeum.

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\*TL=total length; HL=head length; HW=head width; SL=scape length; AL=alitrunk length.

Petiole and postpetiole as in Figure three; rather similar to those of A. treatae females. Postpetiole distinctly more voluminous than in females A. carolinensis, A. fulva, A. lamellidens, and A. tennesseensis.

Mandibles with longitudinal striae which spread slightly as they approach the masticatory border. Clypeus with slightly wavy longitudinal rugae. Clypeal rugae distinctly less coarse and less reticulate than in A. treatae females. Coarse longitudinal rugae over front and lateral portions of head. Some transverse connections between rugae. Punctations interspersed between rugae. In occipital region rugae weaker and reticulate to transverse. Pronotum with rugae parallel to suture between pronotum and scutum. Scutum longitudinally rugose; rugae somewhat fainter along longitudinal midline of scutum. Longitudinal rugae continue across parapteron to scutellum, where rugae are slightly more reticulate. Propodeum with transverse rugae; area between spines with more feeble rugae. Mesothoracic sternite and episternite with rather longitudinal rugae; rather smooth and shiny ventrally. Coxae and femurs shining, but with some punctations. Coxae with a few weak rugae. Petiole punctate with some dorsal and lateral rugae. Postpetiole punctate with dorsal and lateral rugae tending to be transverse. Basal half of first gastric segment finely punctate; basal one quarter finely striate (Florida females of A. treatae have punctations covering basal four fifths and striations basal one third of first gastric segment). A. treatae females from more northern states may have less gastric sculpture. Remainder of gaster rather shining.

Erect hairs on head, alitrunk, petiole, postpetiole and gaster

arranged in typical Aphaenogaster fashion. Hairs on scutum slightly shorter than those of A. floridana females. Piceous; some workers from Florida panhandle are lighter brown, but no females from such enclaves were found.

#### Description of Male

TL 5.6, HL 1.0, HW 0.8, SL 0.35, AL 2.2 mm. General appearance as in Figure four. Head shape as in Figure four; more elongate than in males of A. fulva, A. mariae, and A. tennesseensis; in transverse cross section head more rectangular, not distinctly wider ventrally than dorsally as in A. fulva, A. mariae, and A. tennesseensis males. Head wider than in male of A. flemingi.

Alitrunk as Figure four. Dorsum of propodeum with pair of short denticles. Metathorax with pair of latero-ventrad swellings, each narrowing distally into a blunt point. Swellings not nearly as well developed as those of A. mariae and A. tennesseensis males.

Petiole and postpetiole as in Figure four. Petiolar node in profile more acute than in A. floridana males. Viewed dorsally postpetiole distinctly wider than petiole.

Less sculptured than males of A. treatae. Mandibles smooth, shining, with feeble punctations and hint of longitudinal striations. Clypeus shining and feebly punctate. Frontal and lateral portions of head punctate with faint transverse rugae between ocelli; faint longitudinal rugae directly anterior and posterior to compound eyes. Alitrunk largely shining and feebly punctate except scutum. Scutum densely punctate with feeble rugae originating along longitudinal midline on anterior half of scutum and running roughly longitudinally



the length of the scutum. Scutellum punctate and with faint rugae. Dorsum of propodeum and lateral sclerites mostly glassy smooth and very shiny in A. ashmeadi, but in A. treatae largely punctate. Punctations and transverse rugae on declivous face of propodeum and laterally between spines and lateral protuberances. Some rugae between meso- and metathoracic wing articulations. Petiole and postpetiole shining but punctate particularly laterally and posteriorly. Gaster shining; weak punctations at base of first segment.

Pilosity characteristic of genus. Few short hairs on dorsum of alitrunk. On posterior of postpetiole six setae which overlap base of first gastric segment. Piceous.

#### Distribution

According to Creighton (1950), A. ashmeadi occurs in the eastern Gulf Coast states. In the Atlantic Coastal Plain it has been found as far north as New Bern, North Carolina (Carter, 1962b). Cole (1940) reported A. ashmeadi from the Great Smoky Mountain National Park at an altitude of about 500 m. Carter (1962a) did list this species among the ants he collected in the North Carolina Piedmont.

In Florida, its type locality, A. ashmeadi occurs throughout the panhandle and northern portion of the state. The extent of its southward distribution in Florida is uncertain. The southernmost collection was made near Trilby in northeastern Pasco County. Habitats ostensibly similar to those in which A. ashmeadi regularly occurs in north central Florida exist as far south as Highlands County. It was specifically sought for in Highlands and southern Polk Counties. However, soil nesting species such as this are usually difficult to find unless they

are active above ground. A. ashmeadi was found in the following counties: Alachua, Franklin, Hamilton, Hernando, Leon, Levy, Marion, Okaloosa, Pasco, Putnam, Sumter, and Union. A. ashmeadi was quite common in the Gainesville region.

#### Habitats

Among those species of Aphaenogaster consistently nesting in the soil A. ashmeadi was found in the widest range of habitats. See Table one. Although A. ashmeadi occurs in well-drained sand pine and turkey oak-longleaf pine communities as well as mesic hammocks, it is most abundant where the soil is moderately well-drained sand, as in scrub oak communities and xeric hammocks. In Gainesville this insect is particularly common in scrub oak woods and upland open mesic woodlands. Although pine woods generally harbored rather sparse populations of A. ashmeadi, at one pine woods site in Union County it was abundant. A. ashmeadi often nests in shaded lawns and parklike areas. At Welaka Van Pelt (1958) found it common in xeric hammocks, occasionally in blue jack oak woods, mesic hammocks, Leon scrubby flatwoods and scrubs, and rarely turkey oak woods and bayheads.

The microhabitat of A. ashmeadi nests in Florida was characterized by moderately to well-drained sandy soil. Only once was a colony found nesting in a log and then only partially. Leaf litter and midday shade also characterize its microhabitats. However, leaf litter was not always present, but was generally rather thick in natural A. ashmeadi microhabitats. Generally herbaceous vegetation was rather sparse in A. ashmeadi microhabitats, except in parklike situations where it is regularly cut.

### Nests

Nests of A. ashmeadi rarely extended below a depth of 40 cm. The deepest nest I found extended down about 60 cm. A. ashmeadi nests have one to six entrances, but usually only one or two. Generally there is one larger primary entrance used by foragers returning with food. The main entrance may change every few days or weeks. This main entrance is often surmounted by a turret of short (less than eight mm) slender twigs, bits of wood, caterpillar droppings, and other debris. Arthropod remains are frequently included in turrets. Heads of Odontomachus brunneus (Patton) and Camponotus floridanus (Buckley) were regular constituents of turrets. One colony was found to have incorporated white pin feathers in its turret, while the turret of another colony was strewn with entire corpses of the bibionid, Plecia nearctica Hardy. When nests were in heavy leaf litter distinct turrets were not always visible. However, the same materials which comprised turrets were used by the ants to form the walls of an entrance-way among the leaves. A superficial chamber among the litter or between the leaf litter and the soil was delimited by vertical walls of debris. Pupae and prepupae are usually kept in the superficial chamber. Winged reproductives often frequent the superficial chamber. The superficial chambers were variously shaped and up to three cm across and one to two cm deep. One to three large tunnels up to a cm in diameter open into the superficial chamber. The tunnels descend to large chambers three or four cm across and one to two cm high. The chambers have rather flat floors and curved ceilings. The uppermost chambers are only about two to 16 cm below the surface. The queen was frequently found in a chamber about

25 cm below the surface. Brood may be in upper and lower chambers. There are usually five to seven subsurface chambers. One chamber contains refuse, mostly arthropod remains. Refuse is also brought to the surface and deposited. Workers carrying refuse from the nest deposited the refuse 30 to 80 cm from the nest entrance.

### Foraging

A. ashmeadi foraged both day and night during the warmer months. Colonies in deeper shade tended to forage more in the mid-afternoon than those exposed to more direct sunlight. All were somewhat more active in the evening than midday. Foraging decreased considerably during winter and was confined to the warmer hours of the day. As late in the Spring as mid-March it was hard to find A. ashmeadi foragers in the Gainesville region. Regarding A. ashmeadi, Carter (1962b) reported that in North Carolina: "Activity was observed from June to August "(p. 173).

Foraging of A. ashmeadi was typical of most species of Aphaenogaster, particularly those nesting in the soil. Workers of A. ashmeadi forage singly, recruiting co-workers when a large or appealing food source is found. Foraging was almost completely restricted to the ground and leaf litter strata. Foragers were rarely found on herbs, grasses or trees. The maximum height at which an A. ashmeadi forager was seen on a plant was approximately six mm. Foragers sometimes searched fallen logs. They investigated beneath leaves and into curled leaves. As the ants traveled slowly about, they moved their antennae right and left, frequently touching them to the substrate or raising them in the air. Foragers were sensitive to sudden vibrations of the leaves. If a vibration was caused by dropping a pin-head-sized

pebble upon a dry leaf, an ant on or under the leaf would run to the vicinity where the pebble hit and search actively.

Foragers apparently found food by other modes of perception as well. Items of food incapable of movement were detected by foragers. Antennal contact was not necessary for some inert food items to be detected. If an ant's antenna passed within less than two or three mm of the food, the ant would turn toward the food and find it. Apparently scent trails of other ant species or the food carried by those ants also can be sensed by Aphaenogaster foragers. A. ashmeadi workers crossing the path just traversed by a returning forager of another species would stop and run rapidly in the direction taken by the burdened ant even if she were a cm distant. The A. ashmeadi worker would sometimes lose the trail and run from side to side and backtrack to pick it up again. Often the ant carrying the food outdistanced the A. ashmeadi worker who would then lose the trail altogether.

A. ashmeadi foragers generally stayed in shaded leaf litter microhabitats. Rarely did this species venture into extensive areas of hot bright sunlight. However, Whitcomb et al. (1972a) reported this species foraged in Florida soybean fields.

### Feeding

The diet of A. ashmeadi consists mostly of other arthropods, which are captured or scavenged. According to Carroll and Janzen (1973) very few ant species are exclusively hunters, and may supplement their diets by scavenging. Unless disabled or molting, large or quick arthropods (e.g. locusts, many Diptera) escaped predation. Insect larvae were more susceptible. Large lepidopterous larvae were attacked, whereas

adult beetles of similar size repelled A. ashmeadi foragers. A. ashmeadi workers were able to capture apparently healthy noctuid larvae up to four cm long. Capture of such large larvae required the combined efforts of at least four or five A. ashmeadi workers. Aphaenogaster workers appeared rather clumsy in cooperative attacks. They often seemed to be working against one another, biting and seizing co-workers, thereby frequently allowing the prey to escape. Jaynes and Marucci (1947) described similar counter-productive behavior in attacks of A. rudis upon codling moth larvae. Individual A. ashmeadi foragers were able to capture naked lepidopterous larvae up to 1.3 cm long. No field observations were made of successful A. ashmeadi predation upon hairy lepidopterous larvae. In closed arenas in the laboratory the ants subdued larger hairy larvae only after a prolonged struggle. Most of the field observations of A. ashmeadi predation upon large lepidopterous larvae were after heavy rainfalls, which might have dislodged the larvae from vegetation, or of attacks upon prepupal larvae. On several occasions while excavating A. ashmeadi nests, unharmed prepupal notodontid larvae were discovered just below the soil's surface within ten cm of the nests' entrances.

I released cabbage loopers near an A. ashmeadi nest, so that the ants' predatory behavior might be observed in the field. One fourth instar looper attacked by a worker managed to escape in a manner which emphasizes the terrestrial nature of A. ashmeadi foraging. The ant bit the larva several times. One time when the larva broke free it climbed a small plant instead of running along the ground. The larva climbed to a height of only about 2.5 cm, but the ant was unable to find it. The ant was soon joined by two nestmates and all searched

unsuccessfully about the base of the plant for nearly five minutes, never climbing it. Large lepidopterous larvae were capable of killing Aphaenogaster workers by biting them.

Arthropods living on plants are virtually free from A. ashmeadi predation as long as they do not venture to the ground. Some quite desiccated arthropods brought in by foragers were obviously scavenged. I assumed that any worker returning with a piece of a larger arthropod had scavenged it unless other workers returned with pieces of the same organism. Crushed or flattened arthropod remains brought in by foragers were assumed to have been accidentally stepped or knelt upon by me. Small spiders, Diptera, Orthoptera, ants, and various larvae brought in by foragers generally appeared to have been captured. Food items too large to be brought to the nest whole were dismembered and dissected on the spot.

Other ants were regularly among the items brought in by A. ashmeadi foragers. Most of the smaller ants appeared to have been attacked by A. ashmeadi, while most larger ants appeared to have been scavenged. Pheidole dentata Mayr and a small species of Paratrechina (Nylanderia) predominated among the victims. At times individual A. ashmeadi workers were observed carrying two of these smaller ants. The smaller ants were gripping each other with their mandibles as if they were captured while fighting each other. Considering their abundance in A. ashmeadi microhabitats and their numerous encounters with the larger ant, relatively few P. dentata and P. (Nylanderia) sp. were captured by it. Corpses of Odontomachus brunneus, Pseudomyrmex brunneus F. Smith, Camponotus floridanus, and C. (Colobopsis) sp. were also brought in by A. ashmeadi foragers. Van Pelt (1958) reported seeing A. ashmeadi

workers carrying dead bodies of O. brunneus. An A. ashmeadi forager rarely attacked larger ants, but was sometimes able to kill one when attacked itself.

Termites seem to be of little significance in the diet of A. ashmeadi. Once a termite worker was observed being brought into an A. ashmeadi nest. An A. ashmeadi worker was seen carrying a nearly dead alate Kalotermes approximatus Snyder. On another occasion I saw an A. ashmeadi worker leaving her nest carrying a termite wing, which she deposited on an external refuse area.

Small oligochaetes were preyed upon occasionally. A. ashmeadi workers often scavenged larval exuviae of various arthropods. Pupal skins were usually ignored. Lepidopterous feces were sometimes observed being carried by A. ashmeadi workers. A bird dropping was visited by several A. ashmeadi foragers, which were removing lepidopterous eggs from the excrement. According to Van Pelt (1958), A. ashmeadi is attracted to raw liver.

Fruiting bodies of certain fungi comprise a significant part of the diet of A. ashmeadi. Although during the course of a year the greater part of the food of A. ashmeadi consisted of arthropod flesh, there were times when mushroom tissue was brought into nests in quantities surpassing that of arthropod flesh. A. ashmeadi most frequently brought back pieces of Russula spp. and Marasmiellus sp. These two genera are not closely related; the former belonging to the family Russulaceae and the latter to the Tricholomataceae. Occasionally taken was Amanita vaginata of the family Amanitaceae. A rotting clump of Clitocybe tabescens, Tricholomataceae, was visited for at least seven days by workers from a nest by A. ashmeadi colony.



All are members of the order Agaricales. Usually no more than two or three mature Russula sp. grew within the foraging territory of an A. ashmeadi colony.

Workers tore off chunks (two to four mm diam) of Russula pusilla. (The gills and cap were the most frequent sites of attack, but pieces were removed from the stalk or stipe as well. See Figure two.) A maximum of five or six, usually one to three, workers visited a mushroom at one time. In comparison a large dead lepidopterous larva might attract 20 or more workers. A mushroom, however ephemeral, constitutes a more permanent food source than a dead insect. Individual Russula sp. were visited rather continuously by A. ashmeadi workers over a period of three to five days, until the mushrooms decayed or were consumed by other organisms. Pieces of mushroom were generally carried nestward at a rather slow gait compared to the speed of a forager returning with a dead insect of equivalent size. Perhaps running back with a dead insect lessens the chances of the forager being waylaid by a larger stronger species and having the food stolen. There seems less need for an A. ashmeadi forager returning with a piece of fungus to run fast, since no larger ant species foraging in its microhabitats was known to feed on fungi and therefore apt to steal its burden. General foraging continued while mushrooms were being visited.

Marasmiellus sp. is a small mushroom. The ones harvested by A. ashmeadi had not fully expanded their caps. They were about five mm high. An A. ashmeadi worker would cut one off at the base and carry it back to the nest. The stalk was grasped just below the cap so that the cap was anterior to the ant's head and the stalk directly beneath

her body. Marasmiellus sp. were brought in while other workers continued general foraging. Several other genera of mushrooms, bracket and other fungi were available in A. ashmeadi microhabitats but were not seen being taken by the ants.

Occasionally unidentified seeds were collected by A. ashmeadi workers. A. ashmeadi was never seen associated with honeydew excreting Homoptera except in a predator - prey relationship. Sucrose and water solutions presented to colonies of this species in the laboratory were imbibed by workers rather than pure water simultaneously presented them. Sometimes workers filled the liquid with grains of sand or wood chips. The particles were later carried into the nest.

The artificial diet (Bhatkar and Whitcomb, 1970) used to feed laboratory colonies was taken readily by the ants at first. After several weeks the quantities consumed by the colonies gradually decreased.

#### Coexistence with other Ants

Several species of ants traverse and nest in microhabitats in which Aphaenogaster spp. occur. The term Aphaenogaster sp. microhabitat is used in discussing coexistence of various Aphaenogaster species with other ants. For our purposes an Aphaenogaster microhabitat is defined as the portion of the habitat directly influencing or interacting with an Aphaenogaster sp. colony. Interspecific competition among social insects is exceedingly complex, involving many parameters beyond the scope of this study; e.g. source of food items, criteria for selection of food items, energy requirements of colonies, recruitment of workers. I will make no attempt here to draw definite conclusions regarding

interspecific competition. The data in Tables three, four, and five and the ensuing remarks may indicate areas of potential overlap in food and nest site requirements of the more common ant species utilizing Aphaenogaster spp. microhabitats.

Table three shows the relative abundance of workers of various ant species traversing the ground within a two m radius of A. ashmeadi nests. Foragers of many species traversed to the very edge of A. ashmeadi nest entrances and picked up baits in such proximity. The ubiquity of foragers of other species about an A. ashmeadi nest is further indicated in Table five. Also suggested in Table five are the capabilities of different sized ants to successfully remove food items to their nest without having the items taken by larger ants. Not shown in Table five is the ability of certain species (e.g. Solenopsis spp.) to monopolize large immovable food items. Large items of animal tissue (dead mammals) are infrequent food sources of Aphaenogaster spp.

Those ants commonly nesting in or traversing microhabitats of A. ashmeadi are:

- Ponerinae- Hypoponera opaciceps  
Odontomachus brunneus
- Myrmicinae- Aphaenogaster carolinensis  
A. lamellidens  
Pheidole dentata  
P. floridana  
P. metallescens  
Crematogaster ashmeadi  
C. clara  
Solenopsis geminata

Solenopsis (Diplorhoptum) sp.

Leptothorax pergandei

Cyphomyrmex rimosus minutus

Trachymyrmex septentrionalis

Formicinae- Brachymyrmex depilis

Camponotus floridanus

C. castaneus

Paratrechina (Nylanderia) sp.

Prenolepis imparis

Formica pallidefulva

Remarks on individual species. Not listed above is the red imported fire ant, Solenopsis invicta Buren. In northwest Florida S. invicta is known to be a serious competitor of native predaceous ants (Whitcomb et al., 1972). Bhatkar (1973) computed an index quantifying aggression between the two species.

Although it forages on the ground like A. ashmeadi, Hypoponera opaciceps (Mayr) is more specifically a subsurface forager in leaf litter. A. ashmeadi tends to forage on the surface of the leaf litter layer. This indicates a partitioning of the leaf litter layer into different foraging zones. I have observed Odontomachus brunneus preying upon and scavenging the same sort of arthropods in the same stratum as A. ashmeadi. With their long powerful mandibles and potent sting O. brunneus workers are formidable predators. Although Table three indicates few O. brunneus workers were collected around A. ashmeadi nests, the large O. brunneus workers appeared to be able to search an area rapidly. Recruitment does not seem important in the foraging strategy of O. brunneus. As in A. ashmeadi, workers of O. brunneus take food

items from smaller ants; they also take food items from A. ashmeadi workers. O. brunneus workers regularly attack A. ashmeadi foragers, but not vice versa unless within one cm of the latter's nest entrance. Attacked A. ashmeadi workers were often killed or maimed, while only once was an A. ashmeadi worker seen killing an attacking O. brunneus worker. I frequently saw O. brunneus workers visiting mushrooms, but never observed them removing or carrying pieces of the fungi. Occasionally O. brunneus workers were seen visiting extrafloral nectaries; a dimension not known in the feeding habits of A. ashmeadi.

Interspecific coexistence among the various species of Aphaenogaster is discussed in a subsequent section.

In all A. ashmeadi habitats examined at least one species of Pheidole was common. See Table three. Table five shows the ubiquity of Pheidole foragers about one A. ashmeadi nest. Fifteen of 25 dead house flies placed around the nest were first attacked by a Pheidole. Despite their ubiquity Pheidole spp. may lose many food items they find to A. ashmeadi workers as suggested by the limited data in Table five. Size of the food item may be a factor in the ability of Pheidole spp. to collect it from an A. ashmeadi foraging area (Table five). Single A. ashmeadi workers took cheese baits and dead house flies from as many as three P. dentata Mayr workers and seven P. metallescens workers. P. morrиси Forel and P. metallescens occur in well-drained rather open A. ashmeadi microhabitats. I never found P. floridana Emery in abundance in A. ashmeadi microhabitats. On one occasion a P. metallescens worker was seen removing a piece of a mushroom, Russula sp.

Crematogaster ashmeadi Mayr and C. clara Mayr often nest arboreally or at least in wood rather than the soil. It is doubtful that they are

nest space competitors of A. ashmeadi. Solenopsis geminata (Fabricius) is common in more open drier A. ashmeadi microhabitats. Hamburger baits set on the ground in microhabitats where S. geminata was present were in a few hrs covered with hundreds of S. geminata workers. A hypogeaic species of Solenopsis (Diplorhoptum) sometimes nests near A. ashmeadi nests. Some S. (Diplorhoptum) species are known to infiltrate nests of larger ants and take food (Wilson, 1971). Leptothorax pergandei Emery often occurs in A. ashmeadi microhabitats, but its colonies were small and few. Cyphomyrmex rimosus minutus Mayr usually nests in decaying wood, but was sometimes found nesting in the soil. In addition to plant material it collects insect remains to use in its fungal substrate.

Brachymyrmex depilis Emery tends to forage more nocturnally. According to Whitcomb et al. (1972b), sweet liquids are an important part of the diet of Camponotus floridanus (Buckley). Although I have found it nesting in the soil C. floridanus generally nests in wood. Both C. floridanus and C. castaneus tend to forage more at night. The Paratrechina (Nylanderia) group is in need of taxonomic revision. At least two forms occur in A. ashmeadi microhabitats; one form more prevalent in drier areas, the other common in more mesic habitats. I observed A. ashmeadi workers taking small cheese baits and dead mosquitoes from P. (Nylanderia) sp. foragers. In the Gainesville area Prenolepis imparis (Say) is very active above ground from November to April, but is difficult to find during the warmer months when A. ashmeadi is most active above ground. More needs to be known about what P. imparis does during the summer in order to properly speculate on the competitive relationship between P. imparis and A. ashmeadi.

Formica pallidefulva Mayr is common in more open or parklike habitats which have thin leaf litter. It seems to nest in sunnier areas than A. ashmeadi.

A. ashmeadi workers were seen carrying corpses of two arboreal ants, Pseudomyrmex brunneus F. Smith and Camponotus (Colobopsis) sp.

#### Annual Cycles and Colony Size

Large female larvae were found in field colonies in mid-March in the Gainesville region. Pupal females appear during early April. Alates were found in mid-April. Males usually reach adulthood ahead of females, but there is overlap in most colonies. Mating occurs in July and August. I regularly observed reproductives at nest entrances during late afternoon from early June to early July. Alates are present in the superficial nest chambers of some colonies in late July. A male was found at a light on 7 July. I observed a dealated female crawling among leaf-litter on 22 July. On 8 August I discovered a founding queen with a few eggs in a small cell (one cm across) just below the loose leaf-litter at the base of an oak tree. Her original eggs were lost when I collected her. She laid eggs her first day in captivity. Her first larva eclosed on 28 August. On 10 September the colony consisted of the queen, five eggs, seven larvae, and one pupa. Small colonies with less than 30 small workers, which I discovered in the spring, may have been founded by queens mated the previous summer.

The largest colony of A. ashmeadi I collected contained a queen, 423 workers, 46 male and 15 female pupae, 6 female and 53 male or worker prepupae, 50 larvae, and at least 30 eggs. Most colonies producing alates had only 100 to 250 workers and fewer males. Van Pelt

(1958) collected a large A. ashmeadi colony at the Welaka Reserve containing a queen, 333 workers, 250 pupae, workers and eggs.

### Development

Duration of the egg stage for workers of A. ashmeadi is 19 to 22 days. Larval development is more variable in duration; 14 to 22 days. The shortest duration for larvae, 14 days, occurred in incipient colonies having no older larvae. The longest elapsed times were for larvae in colonies where older sibling reproductives were present. The pupal stage lasts ten to 13 days. A few females remain in the pupal stage eight to ten days.

### Findings on A. carolinensis

#### Description of Female

TL 7.0, HL 1.4, HW 1.2, SL 1.4, AL 2.3 mm. for typical Floridian carolinensis to TL 8.2, HL 1.6, HW 1.5, SL 1.6, AL 2.7 mm. for south Florida specimens. General appearance as in Figure five. Head shape as in Figure five; more convex posteriorly than females of ashmeadi, flemingi, floridana, and treatae, but less so than fulva. Base of antennal scape without lobe.

Alitrunk as in Figure five. Propodeum with pair of posteriorly directed spines. Spines shorter than declivous face of propodeum.

Petiole and postpetiole as in Figure five. Postpetiole less voluminous than in ashmeadi, flemingi, floridana, and treatae, but more voluminous and elongate than in fulva.

More sculptured than flemingi, but less than fulva. Mandibles



with longitudinal striae which spread as they approach the masticatory border. Clypeus punctate and with slightly wavy longitudinal rugae. Coarse longitudinal rugae over front and lateral portions of head; less coarse near occipital border. Punctations between rugae. Pronotum with rugae parallel to suture between pronotum and scutum. Rugae originating along longitudinal midline of scutum and running roughly longitudinally the length of the scutum. Longitudinal rugae extend across parapteron and scutellum. Propodeum with transverse rugae; area between spines with feebler rugae. Mesothoracic sternite and episternite with rather longitudinal rugae, but smoother and shinier ventrad; large specimens with more and coarser lateral rugae. Coxae and femurs largely shining, but punctate, and in large specimens fore coxae with some striations. Petiole punctate and longitudinally rugose, particularly posteriorly. Postpetiole punctate and with rugae rather longitudinal anteriorly, but transverse posteriorly. Gaster rather smooth and shining and with only faint punctation.

Erect hairs on head, alitrunk, petiole and postpetiole arranged characteristically for genus. Brown or reddish brown to piceous; gaster dark brown to piceous in all specimens.

#### Description of Male

TL 4.5, HL 0.75, HW 0.75, SL 0.4, AL 1.7 mm. for typical carolinensis to TL 5.0, HL 0.9, HW 0.75, SL 0.4, AL 2.0 mm. for south Florida specimens. General appearance as in Figure four. Head shape as in Figure four; narrower posteriorly than in fulva, mariae, and tennesseensis, but less so than in flemingi. In transverse cross section head rather rectangular instead of wider ventrally than dorsally as in

fulva, mariae, and tennesseensis.

Alitrunk as Figure four. Dorsum of propodeum with pair of slight protuberances, not quite denticles but more prominent than corresponding raised areas in flemingi. In one specimen examined protuberances were drawn out into denticles. It is not rare for Aphaenogaster males to have one propodeal protuberance drawn out twice the length of the other. Metathorax with pair of latero-ventrad swellings, each narrowing distally into a dull point. Swellings only slightly more developed than in flemingi and less so than other Floridian congeners. Mid dorsum of propodeum tends to collapse in some pinned specimens.

Petiole and postpetiole as in Figure four. Postpetiole not as voluminous as in flemingi, but more elongate than in fulva.

Rather weakly sculptured. Mandibles smooth, shining (less so in large south Florida specimens), and with feeble punctations. Clypeus shining and with faint punctations. Frontal and lateral portions of head punctate, most pronounced punctations between ocelli. Scutum shining, with some faint punctation; humeral areas particularly smooth and shining. Scutellum punctate laterally, smooth and shining along longitudinal midline. Dorsum of propodeum largely smooth and shining, punctate laterally and dorsally between protuberances. Mesothoracic sternite and episternite somewhat punctate, but with rather smooth shining appearance. Petiole shining, but with punctations. Postpetiole shining, punctate, but smoother dorsally. Gaster smooth and shining.

Pilosity generally characteristic of genus. A few hairs on scutum and on protuberances of propodeum. Light brown with head darker.

Description of Worker

TL 4.0, HL 1.0, HW 0.9, SL 1.3, AL 1.6 mm. for typical Floridian carolinensis to TL 6.5, HL 1.3, HW 1.2, SL 1.6, AL 1.9 mm. for large specimens particularly those from south Florida. General appearance as in Figure six. Head shape as in Figure six; very similar to that of lamellidens, particularly in larger carolinensis specimens. In frontal view head more narrowed posteriorly than fulva and rudis, lacking roughly angular convexity near occiput characteristic of non-nanitic forms of those species. Head not nearly as narrowed as in flemingi and typical texana. Base of antennal scape without lobe.

Alitrunk as in Figure six. Prothoracic region more slender laterally and dorsoventrally than in fulva and rudis; somewhat less slender in largest carolinensis specimens. Propodeal spines shorter than declivious face of propodeum; generally shorter and more divergent in smaller specimens, longer and rather incurved in larger specimens. Spines project posteriorly but at various angles above the horizontal; rarely as upwardly directed as in fulva. Spines somewhat laterally compressed.

Petiole and postpetiole as in Figure six. Postpetiole less voluminous than in ashmeadi, flemingi, floridana, and treatae; more elongate than in fulva.

Larger specimens with more and heavier sculpture. Mandibles with faint longitudinal striations; more shining in smaller specimens. Clypeus punctate and with rugae that tend to be longitudinal toward middle of clypeus. Most of head capsule punctate. Longitudinal rugae covering frontal and lateral portions of head in large specimens; in

smaller more typical carolinensis specimens longitudinal rugae more confined to area of longitudinal midline between and posterior to frontal lobes and laterally anterior and posterior to compound eyes. Head shinier near occiput; rugae and punctations weaker. Alitrunk largely punctate; pronotum less so. Middle of pronotum smoother and shinier in small specimens. Larger specimens with some transverse rugae along humeral areas. Mesonotum and metanotum with somewhat longitudinal rugae especially in larger specimens. Dorsum of propodeum with reticulate and transverse rugae; rugae coarser and tend to be more transverse in large specimens. Area between spines shiny and with feeble transverse rugae. Coxae and femurs shining and faintly punctate; punctations most noticeable on fore coxae, particularly in large specimens. Petiole punctate, especially posteriorly and laterally; shining dorsally in small specimens, some rugae in large specimens. Postpetiole punctate, particularly laterally and posteriorly; shining anteriorly, more so in small specimens. Dorsal posterior of postpetiole of large specimens granulo-rugose. Gaster shining. Head, alitrunk, petiole and postpetiole orange-red to brown to piceous. Gaster dark brown to piceous; distally yellowish brown in some specimens.

#### Distribution

According to Creighton (1950), A. carolinensis occurs in the Piedmont region from southwestern Virginia to northwestern Alabama. Carter (1962b) collected A. carolinensis in the fall-line sandhill region of North Carolina, but not in the Coastal Plain. Warren and Rouse (1969) stated that A. carolinensis can be found as far west as

Oklahoma. In a foregoing section on the taxonomy of the species of Aphaenogaster of Florida A. miamiana was synonymized with A. carolinensis. Consequently the range of A. carolinensis is expanded to include that of the former A. miamiana, which Creighton (1950) reported to be Florida and northward and westward into Alabama and Mississippi. Smith (1933) and Wheeler (1932) had previously reported the occurrence of A. miamiana from Florida.

A. carolinensis has not previously been recorded from Florida. Smith (1930, 1933), Wheeler (1932), and Van Pelt (1947, 1958) mentioned the occurrence of forms of A. texana in Florida, some of which may be attributable to the typical A. carolinensis. The typical form occurs at least as far south as Marion County. No collections of the typical A. carolinensis were made in the panhandle west of Leon County, although it probably occurs there. It is quite abundant in Alachua and Marion Counties.

Atypical forms of A. carolinensis, i.e. miamiana-like and intermediate forms here referred to as A. carolinensis\*, occur throughout the state of Florida. A. carolinensis\* was collected in the panhandle in Leon and Santa Rosa Counties. The southernmost collection site for carolinensis\* was Key Largo, Monroe County. Wilson (1965) also found A. carolinensis\* in upper Key Largo. A. carolinensis\* was also collected in the following counties: Alachua, Broward, Collier, Columbia, Duval, Gadsden, Gilchrist, Hamilton, Levy, Marion, Nassau, Okeechobee, Palm Beach, Pasco, Putnam, Sumter, and Volusia. I examined specimens from Dade, Dixie, and Hendry Counties. Forms closely resembling Wheeler's (1932) description of A. miamiana seem to be restricted to south Florida. See Figure one. A. carolinensis\* seemed to be common

except in the central portion of the peninsula. Several attempts to find this ant in Polk County proved fruitless. Since A. carolinensis\* generally nests in rotten logs, its presence was readily surveyed. I scanned tree trunks and the ground for strays if no colonies were found in logs. Van Pelt (1958) did not list A. miamiana among the ants he collected at the Welaka Reserve. I found dark miamiana-like specimens there in a mesic hammock. Van Pelt apparently identified specimens of miamiana as A. fulva or A. texana. Furthermore, he mentioned some Aphaenogaster specimens which seemed to key out to A. rudis in Creighton's (1950) key. Some of the specimens he believed might be A. fulva he sent to M. R. Smith for examination.

#### Habitats

In the Alachua, Marion County area the typical A. carolinensis is most common in upland mesic hammocks, having rather open understories. This ant is often associated with the presence of pines in such hammocks. At one station it was abundant in a grove of loblolly pine, where little other woody or herbaceous vegetation grew. At the Welaka Reserve typical A. carolinensis was numerous in a mixed slash pine-blue jack oak woods. Specimens attributable to this species were collected in wet mesic hammocks in Leon County. Van Pelt (1958) reported collecting A. texana rarely in hydric hammocks at the Welaka Reserve.

Nests of A. carolinensis are often confined to the leaf litter-humus layers and the upper ten cm of the soil. The leaf mold layer is sometimes wetter than the soil immediately beneath it. A. carolinensis is not "restricted" to soil-nesting as A. ashmeadi, A. flemingi, A. floridana, and A. treatae are in Florida. A. carolinensis nests are

frequently associated with buried pinecones or small branches the diameter of one's finger. Varying portions of a colony reside within the wood. Colonies collected in Leon County were usually nesting in moist rotten stumps or logs. There was heavy leaf litter present, but the site appeared subject to frequent saturation or flooding. Wheeler (1915) and Carter (1962b) reported that A. carolinensis often nests beneath stones.

In the northern half of Florida A. carolinensis\* is most commonly found in mesic and hydric hammocks, bayheads, cypress domes, and river swamps. It is not as prevalent in upland mesic hammocks as in the lower more moist woodlands. I rarely found A. carolinensis\* in xeric hammocks in north Florida and never found it in fields or unwooded habitats. It occasionally occurs in shaded lawn or parklike areas. In south Florida A. carolinensis\*, i.e. the typical miamiana, occupies a much wider range of habitats. It not only occurs in the same type habitats as in northern Florida, but also in pastures, sugar cane fields, sand pine dune areas, willow and pond apple quasi-marsh land, cypress - red maple strand forests, tropical hardwood hammocks and habitats disturbed by man (i.e. Australian pine, Casuarina sp., groves).

A. carolinensis\* nests in rotten logs, stumps, and cypress knees, in rotten portions of live trees, and in the soil, sometimes under stones. No arboreal nests were found in living pine or sweetgum trees. One nest was found in the Australian pine. All arboreal nests of A. carolinensis\* I found were less than three m above ground level. Some A. carolinensis\* arboreal nests were higher than the highest A. fulva arboreal nests. None were as high as most A. lamellidens and many A. tennesseensis nests. Most A. carolinensis\* arboreal nests are in

habitats subject to frequent yearly flooding. Few arboreal nests were found in cypress domes. A. carolinensis\* sometimes nests in smaller trees than do A. fulva, A. lamellidens, and A. tennesseensis.

Epiphytes, mosses, lichens, and vines contribute to the micro-habitat about arboreal nests. Most arboreal nests are in the core or heartwood of trees. Stumps, logs, and cypress knees occupied by A. carolinensis\* colonies may be in various stages of decay, but least often in early and advanced stages of decomposition. The wood was moderately dry to saturated. Nests were rarely found in logs containing passalid beetles. In floodplain situations, however, nests are occasionally immediately beneath the bark of slightly decayed logs. Nests wholly in the soil are less common than nests in wood. Nests frequently extend from logs or stumps into the soil. The soil in which A. carolinensis\* nests is highly organic in content in mesic and swamp situations. The hummocks in which this species may nest in hydric hammocks, bayheads, and cypress swamps consist almost entirely of decayed vegetable matter. At the other extreme soil nests in sand pine woods are partially in very well-drained sand. Nests in such xeric situations occur at the shaded base of shrubs such as rosemary, Ceratiola sp., where organic matter has accumulated. Nearly all the nests of A. carolinensis\* were shaded, but more so in north Florida. The amount of leaf litter around A. carolinensis\* nests in flood plains varies depending on its deposition by water currents. There is heavy leaf litter in mesic, hydric, and tropical hardwood hammocks. Leaf litter is thin in sand pine woods except beneath shrubs. In cypress domes, hydric hammocks, and river swamps flood waters often isolate colonies on small hummocks connected only by the tree canopy.



## Nests

Nests constructed in leaf mold consist of one to three chambers, the largest not more than three cm across. The pupae, prepupae and some older larvae are usually in the uppermost portion of the nest among newer drier leaf litter. Ants enter their nest by descending into the leaf litter. No external sign of an entrance could be detected for these nests; thus differing from the nests of A. ashmeadi, A. flemingi, A. floridana, and A. treatae in which a turret of debris usually surmounts at least one entrance. Chambers in newer leaf litter are often cells between two superimposed rather horizontal leaves. The lateral boundaries of the cell are walls of minute wood chips or where the leaves are tightly appressed. Portions or all of some ground nests are in buried small branches or pine cones. All the pine cones containing A. carolinensis colonies appeared to have been gnawed by squirrels and tunneled by insects other than ants. The cones and branches were moderately well decomposed, breaking apart easily when handled. The deepest any colony was found to penetrate the soil was about 25 cm, and this was in well-drained sand in a bluejack oak-slash pine woods. Nests in logs or stumps consist of one to five chambers. Pupae are usually in the most exterior chamber, where it is drier.

It was difficult to determine the number of chambers used by large carolinensis\* colonies nesting in rotten wood. See explanation in materials and methods section. Apparently no more than five chambers usually contained brood. Nest chambers appeared to be preformed by termites or other wood boring or tunneling insects. One colony was found nesting adjacent to a colony of Reticulitermes virginicus in

a rotten stump. Pupae and prepupae are usually in the outermost chambers. Often they are just beneath a layer of loosened bark rather than in a distinct chamber. I rarely found the queen in outer chambers. Winged reproductive forms tend to congregate in the outer chambers. Eggs, younger larvae, and the queen are in inner and outer chambers. Chambers opening to the outside or beneath bark partly enclosed by walls constructed of wood chips and other debris. Nests in living trees often open to the outside via a hole or crack in the tree trunk. Such cracks are sealed with a wall of wood chips or carton-like material leaving open only a small entrance hole. Workers returning to log nests use one or sometimes two entrance holes. Soil nests may extend as deep as 50 cm or more. In nests beneath stones the older brood is just beneath the stone. When a nest is in both log and soil the older brood is in the log except in winter.

### Foraging

When A. carolinensis nests in the ground it forages almost entirely among leaf litter. Foragers were not observed climbing higher than five cm on vegetation. Log nesting colonies also forage largely on the ground. It does more subsurface foraging among leaf litter than do other Aphaenogaster spp. Foraging continues through the day in the summer.

A. carolinensis\* forages primarily on the ground. Foragers were occasionally seen climbing trees other than those in which they nested. However, foragers were not observed on foliage of trees or higher than five cm on herbs or grasses. Foragers from arboreal colonies generally descend to the ground to forage. They search among leaf litter, rotten

logs and hummocks in river swamps. A. carolinensis\* forages on mud flats of flood plains. Carroll (1970) found strays of A. carolinensis\* in sugar cane fields in south Florida in January. Foraging continues throughout the day. In north Florida foraging is reduced during winter months, but in south Florida it is not so curtailed.

### Feeding

A. carolinensis workers brought into their nests the same type food items as the preceding species. If the comparatively small size of A. carolinensis workers is a factor in the size of the food items taken, it was not discernible on the basis of observation alone. I saw A. carolinensis foragers bringing in dead or dying Pheidole dentata minor workers. Although A. carolinensis was not observed collecting seeds, it was often seen visiting and removing pieces of mushrooms, particularly Russula sp. and occasionally Amanita vaginata. Bhatkar and Whitcomb (1975) found workers of this species associated with bracket fungi and the mushroom, Agaricus sp. I never saw A. carolinensis tending Homoptera, but Bhatkar and Whitcomb (1975) report that workers occasionally visit the extrafloral nectaries of Cassia sp. In the laboratory workers imbibed solutions of sucrose and water rather than plain water proffered them.

The feeding habits of A. carolinensis\* are similar to those of the typical A. carolinensis and A. fulva. In south Florida A. carolinensis\* feeds on a wider variety of species of organisms, because it occurs in a broader range of habitats. It also feeds on tropical organisms whose range is restricted to south Florida. In river swamps A. carolinensis\* feeds on mollusks and oligochaetes stranded by receding waters. I

infrequently observed termite predation in the field except when I broke open termite nests. In the laboratory colonies of A. carolinensis\* and termites coexisted in the same logs for months. Instances of field predation on termites consisted of only one or two termites being brought in by A. carolinensis\* foragers during a period of one or two hr. A. carolinensis\* workers were seen collecting seeds of sweet gum, Liquidambar, and dogwood, Cornus, and fallen floral parts of elderberry, Sambucus. Foragers were observed collecting pieces of mushrooms, Russula sp., in the field. I never saw workers tending Homoptera. In the laboratory workers imbibed sucrose and water solutions proffered them. Workers were seen visiting a mass of freshly oozing sap on a winged elm, Ulmus alata, trunk.

#### Coexistence of A. carolinensis with other Ants

Several species of ants share nesting or foraging microhabitats with A. carolinensis. Among the most common of those ants are:

Ponerinae- Hypoponera opaciceps

H. opacior

Odontomachus brunneus

Myrmicinae- Aphaenogaster ashmeadi

A. carolinensis\*

A. fulva

A. lamellidens

Pheidole dentata

Crematogaster ashmeadi

C. clara

Solenopsis (Diplorhoptum) sp.

Leptothorax pergandei

Cyphomyrmex rimosus minutus

Trachymyrmex septentrionalis

Formicinae- Camponotus floridanus

C. castaneus

Paratrechina (Nylanderia) sp.

Prenolepis imparis

Remarks on individual species. Most of the species occurring in A. carolinensis microhabitats are also present in A. ashmeadi microhabitats. A. carolinensis is smaller than its Floridian congeners. Although it remains to be demonstrated, A. carolinensis workers may not be able to take food items as easily as its larger congeners do and its workers may be more susceptible to having items taken from them.

Like A. carolinensis, Hypoponera opaciceps, and H. opacior (Forel) frequently nest in leaf mold. I observed Odontomachus brunneus taking food items from A. carolinensis foragers.

Coexistence among the Floridian species of Aphaenogaster is treated in a subsequent section.

Pheidole dentata is abundant in A. carolinensis microhabitats. A. carolinensis foragers were often seen carrying dead P. dentata minor workers or with P. dentata workers clinging to their appendages. Although Solenopsis (Diplorhoptum) sp. occurs in A. carolinensis microhabitats, I never found it nesting adjacent to A. carolinensis nests. Leptothorax pergandei often occurs in A. carolinensis microhabitats, but its colonies are small and few.

In A. carolinensis habitats Camponotus floridanus generally nests in logs or stumps. On one occasion I saw a C. castaneus major worker

take a dead mosquito from an A. carolinensis forager. Paratrechina (Nylanderia) sp., a dark species, is abundant in A. carolinensis microhabitats. See collections one and two under A. ashmeadi in Table three. In upland mesic hammocks where A. carolinensis is common P. (Nylanderia) sp. nests chiefly in leaf mold, while in wetter areas it often nests in rotten logs or stumps.

Coexistence of A. carolinensis\* with other Ants

The following ants were found nesting in or traversing microhabitats used by A. carolinensis\*

- Ponerinae-           Platythyrea punctata  
                           Hypoponera opaciceps  
                           H. opacior  
                           Leptogenys manni  
                           Odontomachus brunneus
- Pseudomyrmecinae- Pseudomyrmex brunneus  
                           P. mexicanus
- Myrmicinae-         Aphaenogaster ashmeadi  
                           A. carolinensis  
                           A. fulva  
                           A. lamellidens  
                           A. tennesseensis  
                           Pheidole dentata  
                           P. floridana  
                           Cardiocondyla spp.  
                           Crematogaster ashmeadi  
                           C. atkinsoni

	<u>C. clara</u>
	<u>C. vermiculata</u>
	<u>Monomorium floricola</u>
	<u>Xenomyrmex stollii</u>
	<u>Solenopsis geminata</u>
	<u>S. invicta</u>
	<u>Tetramorium guineense</u>
	<u>Cyphomyrmex rimosus minutus</u>
Dolichoderinae-	<u>Iridomyrmex pruinosus</u>
	<u>Conomyrma</u> sp.
	<u>Tapinoma melanocephalum</u>
Formicinae-	<u>Camponotus floridanus</u>
	<u>C. castaneus</u>
	<u>C. (Myrmentoma) sp.</u>
	<u>C. (Colobopsis) impressus</u>
	<u>Paratrechina (Nylanderia) spp.</u>
	<u>Lasius alienus</u>

Remarks on individual species. The long list of species which co-exist with A. carolinensis\* reflects this ant's distribution from the panhandle to subtropical south Florida.

Platythyrea punctata F. Smith is a south Florida species common in tropical hardwood hammocks. I frequently found Hypoponera spp. nesting in logs containing A. carolinensis\* nests. Leptogenys manni Wheeler feeds primarily on Isopods (Wheeler, 1910), but will also scavenge other dead arthropods.

Pseudomyrmex brunneus and P. mexicanus Roger forage chiefly on foliage and slender twigs and stems. P. mexicanus, although expanding

its range, is not yet known from north Florida (Whitcomb et al., 1972).

Coexistence among Floridian species of Aphaenogaster is discussed in a subsequent section.

Pheidole dentata colonies were often found in rotten logs and stumps containing A. carolinensis\* nests. However, in many river swamps where P. dentata is common, A. carolinensis\* is scarce or absent. P. dentata often nests in drier logs than does A. carolinensis\*. P. floridana is more common in south Florida than northward. Four species of Cardiocondyla occur in A. carolinensis\* microhabitats. C. venustula Wheeler is not known from north Florida and the other three species are more common in south Florida. Crematogaster vermiculata Emery occurs mainly in cypress and river swamps. Monomorium floricola (Jerdon) and Xenomyrmex stollii Forel are primarily south Floridian. Tetramorium guineense (Fabricius) is common in south Florida, but is scarce in the northern part of the state.

Iridomyrmex pruinosus (Roger) and Conomyrma spp. occur in more xeric or open A. carolinensis\* microhabitats. Tapinoma melanocephalum (Fabricius) occurs in a variety of habitats in south Florida. It uses many different types of nest sites.

Twice Camponotus floridanus foragers entered the laboratory and raided and destroyed A. carolinensis\* colonies nesting in Wilson cells. C. (Colobopsis) impressus (Roger) forages chiefly on foliage and slender twigs and stems. I found at least one form (species) of Paratrechina (Nylanderia) in every A. carolinensis\* microhabitat I examined. Lasius alienus (Foerster) occurs in the northern part of the state and most abundantly in the northern tier of counties.



### Annual Cycles and Colony Size

In Marion County alates of both sexes of A. carolinensis were found in field colonies in May. Males and winged females occur in field colonies in Alachua County at least as late as early July. No colony found had more than ten females or 15 males, while some contained alates of only one sex, usually male. Large colonies have 200-300 workers.

An A. carolinensis\* colony collected on Key Largo in mid-March contained female larvae and adult males. Most of the female larvae pupated during the first two weeks of April. Prepupal females were found in colonies from Sumter and Duval Counties in mid-April. I found adult males in a colony in late April in Sumter County. Pupae and larvae of females and male pupae and imagines were found in an A. carolinensis\* colony in Gainesville in late May. Alates were found in a colony in Palm Beach County in early June. Alates of both sexes were found in field colonies as late as mid-July in Gainesville. Founder queens with brood were discovered in cells in wet rotten wood in late June and early July in Gainesville. No flights of this species were witnessed. In laboratory colonies sometimes females shed their wings. Such dealates seemed to function as workers, while sibling alate females behaved and were treated by workers as sexuals. These dealate females foraged and defended the rest.

One colony with only about 50 workers contained six males and seven alate females. Mature A. carolinensis\* colonies contain an estimated 800 or more workers. Small colonies with less than 30 workers were found in the early spring and fall. These probably represent first year colonies.

### Development

The duration of the egg stage of A. carolinensis and A. carolinensis\* is 16 to 22 days. The larval stage lasts 13 to 17 days. The elapsed time of the pupal stage is nine to 11 days. One male pupa enclosed after ten days. The only recorded duration of a female pupa was 21 days.

### Findings on A. flemingi

#### Description of Female

TL 9.5, HL 1.8, HW 1.5, SL 1.9, AL 3.0 mm. General appearance as in Figure seven. Head shape as in Figure seven; narrower than in A. floridana, but distinctly less narrowed posteriorly than heads of own workers. Base of each antennal scape with small angular forward projecting lobe. Lobes approximating size of those of A. floridana rather than much larger, rearward projecting, ones on scapes of antennae of A. ashmeadi and A. treatae.

Alitrunk as in Figure seven; propodeum with pair of somewhat upwardly directed spines. Spines as long as declivious face of epinotum. No females of similar Floridian species possess such long propodeal spines.

Petiole and postpetiole as in Figure seven. In profile petiole with rather acute node compared to females of A. ashmeadi, A. treatae, and particularly A. floridana. Postpetiole proportionally more voluminous than in females of A. carolinensis, A. fulva, A. lamellidens, and A. tennesseensis.

Considerably more sculptured than workers. Mandibles with longitudinal striae, which spread slightly as they approach the masticatory margin. Clypeus with slightly wavy longitudinal rugae. Coarser longitudinal rugae over front and lateral portions of head. Some transverse connections between rugae. Punctations interspersed between rugae. Posterior to ocelli, rugae weaker and reticulate to transverse. Pronotum with rugae parallel to suture between pronotum and scutum. Scutum longitudinally rugose. Longitudinal rugae continue across parapteron to scutellum where they are more reticulate. Propodeum with transverse rugae; area between spines with more feeble rugae. Mesothoracic sternite and episternite with rather longitudinal rugae, but smoother and shinier ventrally. Coxae and femurs shining, but with some punctations. Petiole punctate with some dorsal and lateral rugae. Postpetiole punctate with dorsal and lateral rugae which tend to be transverse. Basal one quarter to one third of first gastric segment finely punctate. In A. ashmeadi, A. treatae, and A. floridana basal gastric punctation more extensive and fine striations are more apparent. Remainder of gaster of A. flemingi rather shining.

Hairs on scutum slightly longer, more slender and less numerous than in A. floridana. Castaneous with gaster slightly darker.

#### Description of Male

TL 5.0, HL 0.85, HW 0.7, SL 0.35, AL 1.95 mm. General appearance as in Figure eight. Head shape as Figure eight; narrower posterior to eyes than Floridian congeners. Distinct depression between lateral ocelli. In transverse cross section head rather rectangular. Antennal scapes more slender than in A. floridana males.

Alitrunk as in Figure eight. Dorsum of propodeum posteriorly with pair of slight protuberances each surmounted by a "Y"-shaped carina. Metathorax with pair of latero-ventrad swellings each narrowing distally to rather blunt point. Swellings less well developed and less pointed than in Floridian congeners except A. carolinensis.

Petiole and postpetiole as in Figure eight. Petiolar node in profile less rounded than in A. floridana, but not as raised as in A. ashmeadi. Viewed dorsally postpetiole nearly twice as wide as petiole.

Mandibles smooth, shining, and with feeble punctations and hint of longitudinal striations. Clypeus shining and feebly punctate. Remainder of head mostly punctate and devoid of rugosity except for a few feeble transverse rugae between lateral ocelli. Alitrunk more feebly punctate than in A. ashmeadi, A. floridana, and A. treatae. Scutum weakly punctate and smooth at dorsal midline. Scutellum with denser punctations and tending toward longitudinal rugae. Dorsum of propodeum glassy smooth and shining. Mesothoracic sternite and episternite mostly glassy and shining. Petiole and postpetiole shining, but largely punctate particularly laterally and posteriorly. Gaster shining.

On posterior of postpetiole six setae overlap base of first gastric segment. Brown with head darker brown.

#### Distribution

As recently as 1950 Creighton reported that A. flemingi was known only from its type locality in Mississippi. At that time, however, A. macrospina had not yet been synonymized with A. flemingi. This ant has since been found in the Atlantic Coastal Plain as far north as Pine Bluff and New Bern, North Carolina (Carter, 1962b). I have seen

specimens from Louisiana.

This may be the least common of the soil-dwelling species of Aphaenogaster in Florida. It is not nearly as abundant as A. ashmeadi or A. floridana. In light of its known distribution in Florida, Mississippi, and Louisiana its occurrence in the Florida panhandle west of Leon County seems predictable. A. flemingi was not collected south of Alachua and Putnam Counties in Florida. I collected this species several times in the Gainesville area. Van Pelt (1958) found A. flemingi occasionally at the Welaka Reserve. I have seen specimens from Columbia County.

#### Habitats

In the Gainesville area I found A. flemingi, like A. ashmeadi and A. treatae, most commonly in xeric scrub oak woods. It was not found in turkey oak woods or mesic hammocks, but occurs in pine woods where A. ashmeadi and A. treatae are scarce or absent. At the Welaka Reserve Van Pelt (1958) found A. flemingi in bluejack oak, longleaf pine and Rutlege slash pine flatwoods. He believed the distribution of A. flemingi on the reserve indicated a preference for pine growths. In North Carolina Carter (1962b) found A. flemingi had a "distinct preference for open, grassy sites of dry sandy soil " (p. 173). He too found it in pine woods. I did not find A. flemingi in fields. Van Pelt (1966) in his study of old field ants of the Savannah River Plant in South Carolina did not find A. flemingi.

A. flemingi nests in only slight shade, often provided by herbaceous vegetation alone. Neither A. ashmeadi nor A. treatae nests are exposed to as much direct midday solar radiation. The soil in which A.

flemingi nests is often not as well-drained as where A. floridana nests. The soil in pine flatwoods is frequently near saturation and temporary surface water collects in lower areas. Usually the nest is at the base of a clump of grass or a herb. In Mississippi Smith (1928) collected a colony of A. flemingi from the base of a rotten stump. I found no nests associated with logs, stumps, or stones.

### Nests

Nests of A. flemingi are of the same general structure as those of A. ashmeadi. However, A. flemingi nests extend deeper and more laterally. There are one or two entrances, one of which is surmounted by a thatched turret of small pieces of dried grass and plant parts. Turrets of A. flemingi nests, which sometimes appear woven, contain arthropod remains less frequently than do those of other Aphaenogaster species. The turreted entrance serves as the passageway for foragers. Woody roots usually obstructed excavation of A. flemingi nests. Brood was often found directly beneath the clump of grass where the main nest entrance was located.

### Foraging

A. flemingi forages mainly on the ground. Foragers were not observed climbing higher than two cm on plants. Workers forage among the herbaceous vegetation. I never saw foragers in the deep shade of scrub oak thickets. Foragers wandered farther from their nests in open areas than into nearer shady thickets. No foragers were seen more than about 5.5 m from their nest. Foraging activity is greater in the evening than at midday during the summer, particularly when the colony is

shaded only by herbaceous vegetation. On most summer days I could find a few foragers in mid-afternoon. On summer afternoons colonies of A. ashmeadi and A. treatae within 11 m of an A. flemingi foraged moderately to actively, while very few workers were seen leaving or entering the A. flemingi nest. Foraging activity decreases in winter. However, on rather cool days in late November there is moderate foraging activity. Van Pelt (1958) called A. flemingi a moderately active forager. In North Carolina Carter (1962b) found A. flemingi active from May to September.

### Feeding

The feeding habits of A. flemingi are like those of the preceding species. However, foragers tend to bring in organisms associated with A. flemingi nesting microhabitats. A. flemingi seems no more adept than its congeners at cooperative attacks involving several workers against rather large prey. A lepidopterous larva about two cm long, starting to spin its cocoon between two overlapping leaves, was attacked by A. flemingi workers. Ten workers surrounded the larva, yet it escaped. On only one occasion a forager was seen bringing in a termite. In the laboratory A. flemingi workers readily attacked termites proffered them. Smith (1928) reported breaking open a rotten stump containing a termite colony and an A. flemingi colony. The ants did not disturb the termites. However, this took place in Mississippi in January. I did not see A. flemingi collect seeds. It fed on pieces of mushroom, Russula sp. in the laboratory and was seen visiting Russula sp. in the field. A. flemingi was never seen tending Homoptera, but in the laboratory workers drank sucrose and water solutions rather than

plain water proffered them. Van Pelt (1958) remarked that on several occasions A. flemingi workers were attracted to molasses traps.

Coexistence with other Ants

The following species were found nesting in or traversing A. flemingi microhabitats:

Ponerinae-	<u>Odontomachus brunneus</u>
Pseudomyrmecinae-	<u>Pseudomyrmex pallidus</u>
Myrmicinae-	<u>Aphaenogaster ashmeadi</u>
	<u>A. treatae</u>
	<u>Pheidole dentata</u>
	<u>P. metallescens</u>
	<u>P. morrisi</u>
	<u>Crematogaster ashmeadi</u>
	<u>C. clara</u>
	<u>Monomorium viridum</u>
	<u>Solenopsis geminata</u>
	<u>S. invicta</u>
	<u>S. (Diplorhoptum) sp.</u>
	<u>Leptothorax pergandei</u>
	<u>L. texanus</u>
	<u>Cyphomyrmex rimosus minutus</u>
	<u>Trachymyrmex septentrionalis</u>
Dolichoderinae-	<u>Iridomyrmex pruinosus</u>
	<u>Conomyrma sp.</u>
Formicinae-	<u>Camponotus floridanus</u>
	<u>Paratrechina (Nylanderia) sp.</u>



Prenolepis imparisFormica archboldiF. pallidefulva

Remarks on individual species. Many of the species listed above are discussed regarding A. ashmeadi. For special remarks about those species listed but not mentioned below see corresponding sections under A. ashmeadi or A. floridana.

In A. flemingi microhabitats Pseudomyrmex pallidus frequently nests in hollow grass stems. It appears to forage very little on the ground.

Coexistence among the various Aphaenogaster species is treated in a subsequent section.

Pheidole metallescens was nesting or foraging within one m of every A. flemingi nest I found in the Gainesville area. Except in some pine flatwoods around Gainesville either Solenopsis geminata or S. invicta was abundant wherever I found A. flemingi colonies. S. geminata was seen raiding a small A. flemingi colony and routing the inhabitants from their nest. In northwest Florida S. invicta has largely replaced S. geminata in most habitats except mesic hammocks. Leptothorax texanus Wheeler was found more regularly in A. flemingi microhabitats than in those of other Aphaenogaster species.

Iridomyrmex pruinosus and Conomyrma sp. occur in the more xeric A. flemingi microhabitats.

At least two forms (species ?) of Paratrechina (Nylanderia) occur in A. flemingi microhabitats. A yellow nocturnal form lives in the more xeric A. flemingi microhabitats, while at least one dark form occurs where there is moist leaf litter. Formica archboldi M. R. Smith

was more often seen foraging in A. flemingi microhabitats than in those of other Aphaenogaster species.

#### Annual Cycles, Mating Flights, and Colony Size

A colony excavated in Leon County on 28 April, 1973, contained last instar female larvae. Males produced in a queenless laboratory colony flew from their nest on several nights during May. These males were active above ground or flew from 7:30 - 9:30 p.m. EDT. Another laboratory colony contained both males and females, which intermittently attempted nocturnal mating flights during August. The alates were active from about nine p.m. to 12 a.m. The colony was placed in the observation cage described in the materials and methods section. Eight females and four males were present in the colony. No more than four females flew on any one night. Alates flew no longer than one or two seconds at a time. They alighted on the screened walls of the cage and crawled about, usually upward. Encounters between opposite sexes were frequent, but no copulations were observed. When a female encountered a male she followed him for two or three cm. Females stroked males with their forelegs and antennae, but the males moved away after a few seconds or minutes. Flight activity would continue for two to 2.5 hrs. Males appeared fatigued after 1.5 hr. They sometimes fell from the walls, and landed upside down unable to right themselves.

Eight females which had flown in the cage were removed and placed in separate shell vial nests. Two laid no eggs and died in early September. Six intermittently laid one or two eggs which they ate after a few days. No larvae were produced. No copulations, therefore, seem to have taken place at any time among this colony. The lights in the

laboratory were turned off for several minutes during flights. The darkness elicited no observable change in their activities. Alates still climbed toward the top of the cage and did not copulate. Perhaps mating only takes place between non-siblings.

A few larvae and many teneral workers were found in an A. flemingi colony excavated in late November. No colony excavated contained over 300 workers. The colony collected by Smith (1928) in mid-January in Mississippi had 90 workers and "many larvae."

#### Development

The duration of the pupal stage of A. flemingi is ten to 13 days. Larvae are in the prepupal state three or four days.

#### Findings on A. floridana

##### Description of Female

TL 9.9, HL 1.9, HW 1.7, SL 2.1, AL 3.0 mm. General appearance as in Figure nine. Head shape as in Figure nine; narrowed posteriorly, but less so than in worker. Head wider than in female of A. flemingi. Antennal scapes exceed occipital margin by at least one quarter their length. Base of scape with small angular forward projecting lobe about the same size as lobe on base of an A. floridana antenna. Occipital margin with more developed rim than females of Floridian congeners.

Alitrunk as in Figure nine. Propodeum with pair of short posteriorly directed spines, like those of A. ashmeadi and A. treatae females, but differing markedly from the unarmed propodeum of own worker. A. flemingi female similar in many respects, but has long rather upwardly

directed propodeal spines.

In profile petiolar node slightly more rounded than in similar A. ashmeadi, A. treatae, and A. flemingi; considerably more acute than in own workers. Viewed dorsally postpetiole as broad as long; not as elongate as in worker. In profile postpetiole rather evenly convex above, more so than in Floridian congeners.

Far more heavily sculptured than workers. Mandibles with longitudinal striae, which spread slightly as they approach masticatory margin. Clypeus with slightly wavy longitudinal rugae. Coarser longitudinal rugae over front and lateral portions of head. Some transverse connections between rugae. Punctations interspersed between rugae. Rugae weaker and reticulate to transverse posterior to ocelli. Pronotum with rugae parallel to suture between pronotum and scutum. Scutum longitudinally rugose. Longitudinal rugae continue across parapteron to scutellum, where they are more reticulate posteriorly. Propodeum with transverse rugae; area between spines with more feeble rugae. Mesothoracic sternite and episternite with rather longitudinal rugae, but smoother and shinier ventrad. Coxae and femurs shining, but with some faint punctations. Petiole punctate, with some dorsal and lateral rugae or granulation. Postpetiole punctate, with dorsal and lateral rugae tending to be transverse posteriorly. Basal segment of gaster finely punctate.

Hairs on scutum longer than those of A. ashmeadi and thicker and more numerous than those of A. flemingi. Yellowish to light-orange brown, gaster slightly darker. Females of Floridian congeners darker.

Description of Male

TL 5.5, HL 0.8, HW 0.8, SL 0.4, AL 2.2 mm. General appearance as in Figure eight. Head shape as in Figure eight; not as elongate as heads of males of A. ashmeadi or A. flemingi. Only slight depression between lateral ocelli. Head rather rectangular in transverse cross section as in A. ashmeadi, A. carolinensis, A. flemingi, and A. treatae.

Alitrunk as in Figure eight. Dorsum of propodeum with pair of spines which in some specimens may be three times as long as figured. Metathorax with pair of latero-ventrad swellings, each narrowing distally into blunt point. Swellings not as well developed as in A. ashmeadi, A. mariae, or A. tennesseensis.

Petiole and postpetiole as in Figure eight. Petiolar node in profile more rounded than in Floridian congeners. Postpetiole more elongate than in males of A. fulva, A. mariae, and A. tennesseensis.

Mandibles smooth, shining, feebly punctate, and with hint of longitudinal striations. Clypeus shining and feebly punctate. Remainder of head mostly punctate and without rugosity. Alitrunk largely shining and weakly punctate. Scutum with faint longitudinal striations. Scutellum more densely punctate than scutum and with feeble reticulate rugae. Dorsum of propodeum shinier with slight punctation. A few weak rugae spread fan-like from propodeal spines. Petiole and postpetiole punctate, but somewhat shiny. Gaster smooth and shiny.

On posterior of postpetiole six setae which overlap base of first gastric segment. Dark brown to nearly piceous.

### Distribution

In 1950 Creighton remarked that A. floridana was known only from Florida. Subsequently, however, A. floridana has been found occurring in the Atlantic Coastal Plain as far north as Pine Bluff and Morehead City, North Carolina (Carter, 1962b). Krombein (1958) listed A. floridana from Alabama.

A. floridana occurs throughout the Florida panhandle. Its type locality, Gretna, is in Gadsden County in the panhandle. Collection sites in the panhandle were in Escambia, Okaloosa, Santa Rosa, and Wakulla Counties. Although I have not collected or seen specimens of A. floridana from south of Alachua or Levy Counties, habitats ostensibly suitable for A. floridana exist in central Florida and further south along the coasts. Even though A. floridana is a soil nesting species its presence in an area could be detected when its workers were not foraging. Its nest entrances can be recognized at a glance in open sandy areas. I unsuccessfully sought A. floridana on several trips to south and central Florida. This species was also found in Clay, Putnam, and Hamilton Counties.

### Habitats

A. floridana appears restricted to very well-drained sandy open woodlands, fields, or ruderal areas. It is most characteristically associated with turkey oak - longleaf pine sandhills, but also regularly occurs in sand pine scrub and open areas in xeric hammocks. It has not been found at the Tall Timbers Research Station despite the considerable attention paid to the ant fauna there. The apparent

absence of A. floridana there may be due to a lack of suitably drained sandy soil. Carter (1962b) in North Carolina, Van Pelt in South Carolina (1966) and at Welaka found A. floridana in similar habitats.

A. floridana nests are exposed to more direct sunlight than those of any of its Floridian congeners. In wooded habitats nests are situated in open areas away from trees, except in turkey oak woods where the canopy is not dense. Nest entrances are not usually among leaf litter, but are often located at the base of a clump of grass or an herb. Herbaceous vegetation in the vicinity of A. floridana nests is rather sparse. The soil is always well-drained. A. floridana nests were never found associated with stones or rotten logs.

#### Nests

The structure of A. floridana nests resembles that of A. ashmeadi. Like those of A. flemingi, nests of A. floridana have no superficial chamber among leaf litter. A. floridana nests extend deeper than those of other Floridian Aphaenogaster species. During the drier spring months nests extend more than 1.3 m deep. There may be as many as three nest entrances, but generally only one or two. Only one entrance is usually used by foragers on a given day. This main entrance is changed every few days or weeks. The main entrance usually has a characteristic turret of debris surrounding it. The turret is comprised of slender twigs (less than ten mm long), dried vegetation, and arthropod remains. The presence of arthropod remains in a turret may not indicate they are former food items. I have seen an A. floridana worker pick up a dead Trachymyrmex septentrionalis worker, return to her nest and place the carcass on the turret. Several Trachymyrmex bodies were

already on the turret. It is not uncommon to find heads of Odontomachus brunneus and Camponotus socius imbedded in turrets. As in A. ashmeadi, A. flemingi, and A. treatae, A. floridana moves its nest entrances or nests every few weeks in the summer. Such moves are usually less than one m. Workers were often seen carrying brood and callows from an old entrance to a newly excavated one. Brood is near the surface in the spring and fall. At other times the brood is in two or three chambers more than 15 cm below the surface. Occasionally no ants were found in the upper 35 to 40 cm of excavated nests.

#### Foraging

A. floridana forages on the ground. I never saw workers climbing herbs or trees, except an occasional partially recumbent stem or blade of grass. Foragers generally do not penetrate the dense leaf litter which accumulates beneath some trees and shrubs in turkey oak woods. The ants searched open sandy areas having only sparse grassy or herbaceous vegetation. Foraging tends to be crepuscular and nocturnal, except in winter when diurnal foraging is proportionally greater than in summer. In mid-December on warm days heavy foraging may take place at midday, but on the whole foraging is somewhat curtailed in winter. In the summer extensive foraging begins about five p.m. EDT. In late July foragers left the nest of one colony during the afternoon only when the temperature at ground level outside the nest fell below 34° C, as when a dark cloud passed. Nest entrances were not sealed during daylight hours. In mid-April I observed foragers in late morning and early afternoon. Carter (1962b) reported A. floridana is active from May to December in North Carolina. In sandy soybean fields in Florida



Whitcomb et al. (1972a) found foragers, but no nests of A. floridana. In many respects sandy soybean fields are similar to the natural habitats in which this species forages.

### Feeding

The feeding habits of A. floridana differ little from those of the preceding species. The prey of A. floridana and the items it scavenges differ from those of other species of Aphaenogaster primarily in that many items are organisms characteristic of xeric habitats. For example, A. floridana frequently preys on the xerophilic Pheidole morrisi, while A. ashmeadi attacks P. dentata, a species common in mesic habitats. Whitcomb et al. (1973) reported that A. floridana preys upon newly mated queens of the imported fire ant. Foragers from a single colony of A. floridana killed three recently mated females of the native fire ant, Solenopsis geminata, in one half hr. A single A. floridana worker was able to kill the larger S. geminata female. In less than 30 seconds an A. floridana worker paralyzed an S. geminata female. A. floridana preyed on termites in the laboratory. However, few field observations of such predation were made. On one occasion three termites were brought in by workers of one A. floridana colony in one hr. It is uncertain whether A. floridana captured the termites, because I saw the third termite taken from a P. morrisi worker by an A. floridana forager.

A. floridana workers were seen scavenging the external refuse heaps of Pogonomyrmex badius after the harvester ants had closed their nests for the day. A. floridana collects seeds of the xerophilic comb-leaved false foxglove, Aureolaria pectinata. Seeds of this plant were

proffered to a laboratory colony of A. floridana, but only one was taken. A. floridana was seen removing portions of the mushroom, Russula sp. (in one instance R. aff. subflava). I never saw this ant tending Homoptera. In the laboratory A. floridana workers imbibed water with sucrose in it in preference to plain water. Often workers filled the liquid with grains of sand. In the field workers were seen carrying grains of sand into their nest.

#### Coexistence with other Ants

Several species of ants share nesting and foraging microhabitats with A. floridana. The most common of these are:

- Ponerinae-      Odontomachus brunneus
- Myrmicinae-    Pogonomyrmex badius
- Aphaenogaster ashmeadi
- A. treatae
- Pheidole metallescens
- P. metallescens splendidula
- P. morrisi
- Crematogaster ashmeadi
- Monomorium viridum
- Solenopsis geminata
- S. invicta
- S. (Diplorhoptum) sp.
- Leptothorax pergandei
- Cyphomyrmex rimosus minutus
- Trachymyrmex septentrionalis

Dolichoderinae- Iridomyrmex pruinosus

Conomyrma flavopecta

Conomyrma sp.

Formicinae- Camponotus floridanus

C. socius

Paratrechina (Nylanderia) sp.

Prenolepis imparis

Formica pallidefulva

Remarks on individual species. Some species listed above are discussed in greater detail regarding A. ashmeadi. Unless otherwise noted the following species are diurnal or continuous foragers. This is significant in light of the fact that A. floridana is chiefly a nocturnal forager.

Odontomachus brunneus foragers tend to keep to patches of leaf litter rather than open sandy areas which are frequented by A. floridana. O. brunneus is a continuous forager and takes food items from single A. floridana foragers. It also kills A. floridana foragers.

Coexistence among the various Aphaenogaster species is discussed in a subsequent section.

I always found Pheidole metallescens or P. metallescens splendidula Wheeler nesting and foraging in A. floridana microhabitats. See Table three. Individual A. floridana foragers were seen taking food items from foragers of P. metallescens, P. metallescens splendidula, and P. morrиси. P. morrиси is quite active at night. Monomorium viridum Brown occurs in many A. floridana microhabitats. M. viridum is not as regularly associated with any other Aphaenogaster as with A. flemingi. Solenopsis geminata is more common in ruderal situations

than in turkey oak sandhills sand pine areas. I have observed A. floridana preying upon alate S. geminata females. Whitcomb et al. (1973) reported that A. floridana attacks founding queens of S. invicta. Trachymyrmex septentrionalis (McCook) is more common than Cyphomyrmex rimosus minutus in A. floridana microhabitats.

Iridomyrmex pruinosus is often abundant in A. floridana microhabitats. At least two forms of Conomyrma occur in A. floridana habitats; one or two forms in ruderal areas and another one or two in turkey oak and sand pine habitats.

Camponotus socius characteristically occurs in turkey oak woods, while C. floridanus is more often found in more moist habitats. C. socius is a more distinctly nocturnal forager than C. floridanus. A yellow nocturnal species of Paratrechina (Nylanderia) is abundant in A. floridana microhabitats. Formica pallidefulva is not as common in A. floridana microhabitats as in those habitats which are not as well-drained.

#### Annual Cycles and Colony Size

Alate males and females were in field colonies excavated in late June and early July. On late afternoons and evenings during late August and early September alate females were seen appearing at the nest entrance of a field colony. The females waved their antennae about and disappeared into the nest after a few moments. Brief showers were not followed by any increased above ground activity by these alate females. Flights were never witnessed. Four apparently unmated females which dealated in laboratory colonies were placed in separate shell vial nests. All four females laid eggs intermittently for as

long as two months, but they ate the eggs and no larvae ever developed.

Colonies are not populous compared to other species of Aphaenogaster. The largest colony collected contained an estimated 200 workers. One colony collected in early May had only 34 workers, a queen and two larvae. This colony existed at least since the previous August. A colony excavated in June contained seven females and no males. Both sexes were present in a partially collected colony in early July. One male of that colony was just inside the nest entrance while no other reproductives or workers were found within 45 cm of the surface.

#### Development

Larvae of A. floridana were kept 17 days but did not pupate. The duration of the pupal stage is ten to 12 days.

#### Findings on A. fulva

#### Distribution

Creighton (1950) reported that A. fulva occurs in the northeastern United States to northern Alabama and west to Ohio. More recently Carter (1962b) collected A. fulva in the Coastal Plain of North Carolina and Van Pelt (1966) found it at the Savannah River Plant in South Carolina. Smith (1965) stated that the range of A. fulva extends as far north as Nebraska, south as Florida, and west as Colorado. Gregg (1972) considered A. fulva a Carolinian life zone species.

I collected A. fulva in peninsular Florida as far south as southern Pasco County, where several colonies were found. It was collected

frequently at Tall Timbers Research Station in Leon County, but records from further west in the panhandle are wanting. There seems to be no reason to suspect that A. fulva does not occur throughout the panhandle. Collecting trips to Polk County and further south in the peninsula indicate that A. fulva is rare, very local, or not present in south Florida. Van Pelt (1958) found A. fulva at the Welaka Reserve in Putnam County. A. fulva was also collected in Alachua, Gilchrist, Levy, Marion, Sumter, Suwannee, and Union Counties.

### Habitats

Nests of A. fulva are common in mesic and hydric hammocks, bayheads, cypress domes, and river swamps. According to Van Pelt (1958) at the Welaka Reserve: "A. fulva prefers the lower areas of the Reserve" (p. 12). He took A. fulva commonly in the river swamp, occasionally in scrub, longleaf pine flatwoods, hydric hammocks, and bayheads; and rarely in Rutlege slash pine flatwoods, xeric hammocks, and marshes. However, Van Pelt (1958) admitted uncertainty about the taxonomy of some of his fulva-like collections. In South Carolina Van Pelt (1966) found A. fulva in hardwood forests, while in North Carolina Carter (1962b) likewise generally found A. fulva in moist mesic wooded habitats rather than in xeric ones. A. fulva seems to be more restricted to river swamps and similarly moist habitats in central Florida. Smith (1965) stated that A. fulva is "very characteristically found in wooded areas, but also shows a high adaptability to various types of ecological habitats" (p. 25). In Florida, however, this species seems absent from non-forested habitats.

Rotten logs, stumps, and cypress knees are common nesting sites of

A. fulva in Florida. The stumps containing nests are usually quite moist. No colonies were found in wood as dry as that in which A. lamellidens or A. tennesseensis often nest. A. fulva nests in logs partially suspended off the ground and those completely recumbent. It frequently nests in rotten parts of living trees. Such nests are within two m of the ground. Some A. fulva nests are wholly in the soil, while others extend from logs into the soil. Nests completely in the soil are more characteristic of upland mesic hammocks rather than river swamps where arboreal nests are frequent. In North Carolina Carter (1962b) found A. fulva nests in rotten logs and stumps and in the soil under stones. At Welaka Van Pelt (1958) found A. fulva nesting in similar microhabitats. He added, however, that nests were usually in logs in the last stages of decay. I often found A. fulva nests in fairly hard logs. In very moist habitats nests were found just beneath the bark of slightly decayed logs, while there was an abundance of unoccupied well decayed logs within two m of the nests. The extent to which A. fulva nests penetrate the soil from logs seems to depend upon moisture. During dry periods river swamp colonies migrate from logs into hummocks and soil. At times arboreal, log, stump, and hummock nests in river swamps are isolated by water; the only connection being the tree canopy. In A. fulva habitats there is usually ample leaf litter. In river swamps, however, leaf litter is variable in depth depending upon where flood currents deposit it. Around some nests there is virtually no leaf litter. All A. fulva nests were shaded. Smith (1965) reported that A. fulva occasionally infests houses.

### Nests

The nests of this species are similar in structure to those of A. carolinensis\*.

### Foraging

A. fulva generally forages on the ground. Foragers were rarely found on vegetation except when their colony was arboreal and they were on the nest tree. Upon leaving their nests foragers from arboreal colonies sometimes ascend the trunk of their nest tree, but most descend directly to the ground. Foragers search leaf litter and logs. In river swamps foraging is limited to hummocks, logs, and trees during flood conditions. When the waters recede foragers search the mud flats between hummocks. Foraging continues throughout the day. Foraging occurs at a reduced level during the winter months; particularly in December and January. I found no foragers farther than five m from their nest or nest tree. The foraging of A. fulva is similar to that of A. carolinensis\*.

### Feeding

Foragers of A. fulva bring in the same type of food items as other species of Aphaenogaster. Colonies in river swamps feed on oligochaetes, snails, and clams in addition to the usual fare of arthropod flesh. Aquatic organisms often become stranded on mud flats in river swamps, while arboreal larvae which fall into the mud become mired and subject to A. fulva predation. In the laboratory A. fulva were observed capturing house flies which alighted on the outside of



their nest. Through personal experience I believe that A. fulva bites harder and with greater tenacity than other Florida species of Aphaenogaster. A. fulva predation on termites has been reported by various authors. See literature review. At Welaka Van Pelt (1958) saw A. fulva workers carrying live termites in their mandibles. He found A. fulva nesting next to Reticulitermes flavipes colonies. I frequently found A. fulva sharing nest logs with termites. When the logs were broken the ants seized and often stung the termites. Pheidole dentata, living in the same logs with termites, exhibits the same behavior when the logs are broken apart. Under normal conditions very few A. fulva foragers were seen carrying termites. Reed (1958) found A. fulva visiting a dog carcass. Van Pelt (1958) found A. fulva workers attracted to a mixture of peanut butter and oatmeal. Smith (1965) reported an instance of A. fulva feeding on peanut butter in a home.

A. fulva collects seeds and abscised floral parts, particularly those of trees. In North Carolina in May every A. fulva nest I examined contained floral parts. In the laboratory A. fulva took pieces of the mushroom, Russula pusilla. A. fulva was not seen collecting pieces of mushrooms in the field. Greaves and Greaves (1968) infrequently found A. fulva associated with bracket fungi (Polyporaceae and Thelophoraceae) in North Carolina. They felt A. fulva made only chance visits to bracket fungi.

On one occasion three A. fulva workers were seen lingering about waxy fulgorid-like exudations on a tree trunk. No fulgorid was associated with that particular mass of exudations. It was not determined whether the ants were collecting the exudations or perhaps co-workers recently captured the fulgorid. Subsequent observations revealed no

similar behavior. In the laboratory A. fulva workers readily imbibed solutions of sucrose and water in preference to plain water simultaneously proffered them. According to Bhatkar and Whitcomb (1975), this species occasionally visits Homoptera and extrafloral nectaries of Cassia in north Florida. A congregation of more than 30 (diapausing?) cicadellids, adults and last instar nymphs, was found in a rotten log containing an A. fulva colony. The congregation was within 35 cm of the ant nest.

#### Coexistence with other Ants

Those ants commonly traversing or nesting in A. fulva microhabitats are:

Ponerinae- Hypoponera opaciceps

H. opacior

Leptogenys manni

Odontomachus brunneus

Myrmicinae- Aphaenogaster carolinensis

A. carolinensis\*

A. lamellidens

A. tennesseensis

Pheidole dentata

Crematogaster atkinsoni

C. clara

C. vermiculata

Solenopsis geminata

Cyphomyrmex rimosus minutus

Formicinae- Camponotus floridanus

C. castaneus

C. (Myrmentoma) sp.

Paratrechina (Nylanderia) sp.

Remarks on individual species. Not listed above are Solenopsis invicta and Lasius alienus, which may coexist more commonly with A. fulva in the Florida panhandle than they do in the peninsula.

Ponerines are common in A. fulva microhabitats just as they are in the microhabitats of other wood nesting species of Aphaenogaster. Hypoconera spp. often nest in rotten logs containing A. fulva colonies. Odontomachus brunneus is rare or absent from some river swamps in which A. fulva occurs, but is abundant in others. I always found O. brunneus in drier A. fulva microhabitats.

Coexistence among the various Floridian species of Aphaenogaster is discussed in a subsequent section.

In river swamps and cypress domes Pheidole dentata generally nests in logs, stumps, or arboreally, while in drier habitats it nests in the ground. Solenopsis geminata is not as abundant in swamps as in drier areas. Cyphomyrmex rimosus minutus usually nests in logs or stumps in A. fulva microhabitats.

Camponotus floridanus is not as common in river swamps as in slightly drier habitats (e.g. mesic hammocks). In river swamps I often saw C. (Myrmentoma) sp. foragers on trunks of trees in which A. fulva nested. At least two forms (species) of Paratrechina (Nylanderia) occur in A. fulva microhabitats. P. (Nylanderia) sp. often nest in logs containing colonies of A. fulva and occasionally adjacent to the A. fulva nests.

Annual Cycles, Mating Flights, and Colony Size

Alates are in A. fulva colonies in early May in the Gainesville area. Van Pelt (1958) found males in A. fulva nests at the Welaka Reserve from May through July. Mating flights take place from early June to mid-July in Gainesville. I found three alate females in a spider's web on 11 June. In the laboratory alates were found at the windows at approximately six to seven p.m. EDT during the first two weeks of June. In the field flights took place during the same period of the day as in the laboratory.

One colony of A. fulva nesting inside the trunk of a living ash, Fraxinus, was observed from 4 July through 25 July, 1973. The primary nest entrance, a hole about six to seven cm diam, was about 80 cm above the ground. The tree was on a small hummock in the flood plain of a stream. During the course of the observations water frequently rose inundating the hummock except a ring of about 20-30 cm about the base of the tree. The forest canopy was rather continuous but not dense. Workers and alates began massing outside the entrance hole as early as four p.m. EDT. Massing ceased by eight p.m. The periodicity of A. fulva flight activity differs from that of A. treatae which Talbot (1966) reported to fly at midday. No nearby A. fulva colonies staged nuptial flights during the weeks the observed A. fulva was active. During the period of observation alates flew only on four days. Workers and sexuals congregated at the nest entrance. The greatest number of workers massed on the trunk of the nest tree was estimated at slightly over 100. Thundershowers interrupted pre-flight activity on six days. Activity was not resumed following the rain. Temperature ranged from

24 to 30° C. Approximately 60 males and 20 females were the most alates massed on the trunk at one time. A few foragers entered and left the nest during nuptial flight activities. Occasionally females suddenly retreated rapidly to the nest, but the factors eliciting this response are unknown.

The first flight took place on 10 July. At 4:45 p.m. some workers ascended the trunk to as great a height as four m, while large numbers of workers congregated at the nest entrance with the alates. Males were lined up side by side around the nest entrance with a few females interspersed among them. Some males began to mount the females, but were pulled away by workers. At 5:09 a female broke away from the congregation and ran up the sunny side of the trunk to a height of about two m above the ground. She paused nearly a minute waving her antennae. She then fluttered her wings and took flight. Her flight path was nearly vertical for eight to ten m when she was lost from sight in the tree canopy. Thirteen more females flew. Most ran rapidly from the congregation to a height of two to 2.3 m. There they hesitated 30 sec to five min, unattended by workers, and flew upward to the canopy. Seven females flew between 6:25 and 6:35 p.m. By that time many males had migrated upward away from the hole to as great a height as 2.3 m, but none had flown. Ten females had flown before the first male flew at 6:43 p.m. Only three males flew. Males flew upward to the canopy in the same general direction as the females. By 7:30 p.m. nearly all the males had returned to the nest or were carried back by workers. No reproductives were visible by 7:40 p.m. and normal foraging activity had resumed. The following day pre-flight activity was much reduced and no reproductives flew. Subsequent flights

were similar, except that most of the males flew on a day when only two females flew. No more than three females flew on any day after 10 July.

Females and males were collected from the trunk and mixed pairs confined in shell vials for observation of copulatory behavior. Females stroked the males with their legs and antennae, but the males made no ostensible sexual responses. Pairs were confined together till males died. The females were kept in shell vial nests to determine if they would produce worker offspring. None did. One female collected from a laboratory flight raised a colony.

In Florida A. fulva colonies contain as many as an estimated 800 workers.

#### Findings on A. lamellidens

##### Distribution

A. lamellidens, according to Creighton (1950), occurs in "areas of low or moderate elevation throughout the entire southeastern United States from southern Delaware to Florida and west to the Mississippi Valley " (p. 144). More recently Smith (1965) stated A. lamellidens has been found as far north as Illinois and New York. Cole (1940) collected this species at altitudes of 600 to 1000 m in the Great Smoky Mountains.

I collected A. lamellidens in Okaloosa County in the Florida panhandle. It seems to be widespread in peninsular Florida. I have seen specimens from Highlands and St. Lucie Counties and I found it in Marion County. Van Pelt (1958) made a single collection of A. lamellidens at the Welaka Reserve in Putnam County. In the Gainesville region 24

colonies of this ant were found. It may be more common than the number of collections indicate. Its nesting and foraging habits may make A. lamellidens appear scarce. Repeated visits to collecting sites often revealed several more colonies than initially detected. The number of collecting trips to particular sites were fewer the farther the sites were from Gainesville. Therefore the abundance and distribution of this species in south and central Florida may be greater than two collections indicate.

#### Habitats

The arboreal nesting habits of A. lamellidens seem to permit it to occur in a wide variety of wooded habitats. It was found most frequently in mesic and hydric hammocks and river swamps, but rarely in xeric habitats. Several colonies were found in trees around the shores of Newnan's Lake in Alachua County. A. lamellidens nests were found in trees in yards and parklike areas. Carter (1962b) noted a preference for pine forests in the occurrence of A. lamellidens in the North Carolina Piedmont, while on the Coastal Plain he found it largely restricted to well-shaded hardwood forests. I never collected this species in pine woods. Cole (1940) reported A. lamellidens occurs in deeply shaded forests in the Great Smoky Mountains.

With three exceptions all my collections of A. lamellidens were from dead portions of living trees. One exception was an incipient colony collected from a wet rotten log recumbent on the ground. Another exception was a colony nesting in a large dead branch wedged (4.5 m above the ground) among the branches of two live trees. The final exception was a colony nesting in a rotten log. However, one end of

this log was held off the ground by a tree so that the nest was one m above the ground. The trees used as nesting sites were generally oaks or ashes. One colony was discovered in a cypress. Notably unused were pines and sweet gum, Liquidambar styraciflua. Sweet gum is one of the most prevalent trees in habitats where A. lamellidens is commonest, yet no nest of this or any other Aphaenogaster was found in a live sweet gum. No nests of any Aphaenogaster were found in living pines.

Most nest trees I found were more than .5 m dbh. Nests are in dead wood which have been galleried by termites and other insects. One A. lamellidens colony occupying a living tree was nesting adjacent to a colony of the dry-wood termite, Cryptotermes cavifrons Banks. Some nests are in rather dry dead limbs, while others are in damper dead wood surrounded by living tree tissue. The dead wood is often quite hard particularly that adjacent to living tissue. Arboreal nests are 1.7 to ten m above the ground. All nests are at least partially shaded during midday. Nests in the cores of living trees are well protected from extremes of heat or cold (Greaves, 1964, 1965). The frequency with which A. lamellidens nests in living trees may decrease northward, where it is generally found in rotting logs or stumps (Cole, 1940; Carter, 1962b). In Alabama Snow (1958) studied the microhabitat and fauna of a rotten stump containing a nest of A. lamellidens. He found A. lamellidens nesting in the wall of the stump where the moisture content was 30 to 73 percent. It may have been an incipient colony as it consisted of only a queen, 30 workers and brood. In New Jersey Wheeler (1905) found a pair of incipient A. lamellidens colonies nesting in sand. Smith (1965) reported A. lamellidens occasionally infests houses.

The foraging microhabitat of A. lamellidens consists of the trunk



and larger branches of the nest tree and ground around the base of the tree. The trunks and large branches of large trees, particularly oaks, are festooned with vines, resurrection ferns, mosses, lichens, Spanish moss, and other epiphytes.

### Nests

Nests in trunks of living trees are often attenuated along narrow preformed tunnels rather than consolidated in a few large chambers. Some nests are rather superficial, while others penetrate deeply into the heartwood. Often galleries are completely surrounded by living wood. Nests are less diffuse where large compact areas of rotten and galleried wood are available. Nest chambers are variable in size and shape, but usually elongate. The number of nest chambers vary, depending upon the size of the colony and the size and number of preformed cavities in the tree. Pupae and prepupae are often in the more external chambers. Cracks or holes in trunks or limbs used as entrances are partially sealed with wood chips if too large. One mature colony was found in a hard rather dry fallen log. Only a few workers and no pupae were beneath the loose bark. The remainder of the colony was deeper in the log.

### Foraging

A. lamellidens is less a terrestrial forager than any of its Floridian congeners except, perhaps, A. mariae which according to the literature is also rather arboreal. Foragers from arboreal A. lamellidens nests forage terrestrially and on the trunks and large branches of their nest trees. On large trees in which the nest is more than two m

above the ground foragers move about slowly on the trunks, searching in cracks, beneath loose bark and in debris in crotches. Workers from colonies in slender trees (less than about 30 cm dbh) descend the trunks of their nest trees rather directly and forage on the ground. More terrestrial foraging is done by colonies whose nests are less than three m above the ground than by colonies whose nests are higher; unless the nest trees of the higher colonies were slender. I found no foragers more than five m from the base of a nest tree.

Like their congeners A. lamellidens foragers take food items from smaller ants. They also have difficulty capturing larger arthropods. I placed a sluggish sawfly larva (three cm long) in an area where several A. lamellidens workers were foraging. The larva repeatedly repulsed the attacks of one or two (simultaneously) ants by thrashing about until the ants abandoned it. The ants did not return directly to their nest, but resumed foraging. In flood plain areas foragers frequent mud flats and prey upon or scavenge stranded arthropods and other organisms (e.g. small mollusks).

### Feeding

The food taken by A. lamellidens is similar to that of its congeners. The similarity is greatest for those A. lamellidens colonies foraging extensively on the ground. Foragers were seen carrying a variety arthropods; crickets, lepidopterous larvae, soft beetles (e.g. staphylinids) and small spiders. Several times I saw workers carrying psocopterans and also corpses of the arboreal ant, Pseudomyrmex brunneus. I observed A. lamellidens foragers capturing chironomid flies on the trunk of a lakeside cypress on which hundreds of the dipterans were resting.

Petals and seeds (e.g. sweet gum) are collected by A. lamellidens. In the laboratory and in the field A. lamellidens workers took pieces of mushroom, Russula sp., proffered them. However, I saw none visiting mushrooms in natural situations. In the laboratory many more workers drank from a tissue soaked in sugar water than from a tissue soaked in plain water which was simultaneously presented them.

#### Coexistence with other Ants

The following ants were found nesting in or traversing A. lamellidens microhabitats:

Ponerinae-	<u>Hypoponera opaciceps</u>
	<u>Odontomachus brunneus</u>
Pseudomyrmecinae-	<u>Pseudomyrmex brunneus</u>
Myrmicinae-	<u>Aphaenogaster ashmeadi</u>
	<u>A. carolinensis</u>
	<u>A. carolinensis*</u>
	<u>A. fulva</u>
	<u>A. miamiana</u>
	<u>Pheidole dentata</u>
	<u>Crematogaster ashmeadi</u>
	<u>C. atkinsoni</u> Wheeler
	<u>C. clara</u>
	<u>C. vermiculata</u>
	<u>Solenopsis geminata</u>
	<u>S. (Diplorhoptum) spp.</u>
	<u>Cyphomyrmex rimosus minutus</u>

- Formicinae-            Camponotus floridanus  
                           C. (Myrmentoma) sp.  
                           C. (Colobopsis) impressus  
                           Paratrechina (Nylanderia) sp.  
                           Prenolepis imparis

Remarks on individual species. Although nearly all the A. lamellidens nests I found were arboreal, there is reason to believe (see nesting section) that newly mated females start their colonies in terrestrial strata (e.g. rotten logs). While on the trunks of their nest trees A. lamellidens workers interact with relatively few foragers of relatively few other species.

Odontomachus brunneus only rarely nests in rotten parts of living trees and then within one m or so of the ground.

Pseudomyrmex brunneus forages extensively on foliage and slender twigs; areas where A. lamellidens workers were never seen.

Coexistence among the Floridian species of Aphaenogaster is treated in a subsequent section.

On one occasion I found Pheidole dentata and A. lamellidens nesting in the same tree; P. dentata near the base and A. lamellidens at a height of five m. Even when they are not in the same tree arboreal nests of P. dentata are usually within two m of the ground and A. lamellidens higher. I have seen individual A. lamellidens foragers take food items from foragers of Crematogaster ashmeadi and C. vermiculata. However, an Aphaenogaster cannot readily wrest a food item from a Crematogaster as they seem to be able to do from Pheidole minor workers. A dark arboreally nesting species of Solenopsis (Diplorhoptum) was seen foraging on trunks of A. lamellidens nest trees. I never

found this species of S. (Diplorhoptum) nesting adjacent to the nest of A. lamellidens or any larger ant. Cyphomyrmex rimosus minutus occasionally nests in rotten wood at the bases of living trees.

Camponotus (Myrmentoma) sp. often nests in trees containing A. lamellidens colonies. However, I found C. (Myrmentoma) sp. nesting only in rather small dead branches. C. (Myrmentoma) sp. foragers were regularly observed on the trunks of A. lamellidens nest trees. C. (Colobopsis) impressus forages chiefly on foliage and slender twigs. At least two forms (species) of Paratrechina (Nylanderia) occur in A. lamellidens microhabitats.

#### Annual Cycles and Colony Size

Alates of A. lamellidens were found in a field colony in June. D. P. Wojcik collected an alate female on the ground at Ft. Pierce on 12 May, 1973. Males were in a laboratory colony in mid-July. Two field colonies examined in mid-July had no alates present. No mating flights were observed. A small, probably incipient colony, consisting of a queen, ten workers, two worker pupae and a few eggs and larvae, was collected in May. The founding queen may have mated the previous year. The nest was a cell roughly two cm diam. in a saturated fallen log. Colonies may be started in terrestrial situations and later migrate to arboreal sites. Wheeler (1905) discovered founding queens in cells in wet sand. None of the large colonies discovered was collected in toto. Mature arboreal colonies are more populous than those of soil nesting species in Florida. Mature colonies probably contain over 600 workers.

### Development

One larva of A. lamellidens was kept 22 days with two workers and showed very little growth. The duration of the pupal stage is ten to 12 days.

### Findings on A. mariae

#### Description of Male

TL 4.9, HL 0.9, HW 0.8, SL 0.4, AL 1.8 mm. General appearance as in Figure 11. Head shape as in Figure 11; like that of males of A. fulva and more so A. tennesseensis; distinctly wider ventrally than dorsally. Heads of other Floridian congeners tend to be more rectangular in transverse cross section.

Alitrunk as in Figure 11. Scutum, particularly anteriorly, highest along dorsal longitudinal midline and gradually sloping downward laterally. Scutum of A. tennesseensis most similarly shaped, while in other Floridian congeners scutum much more flattened above and more rounded anteriorly and laterally. Dorsum of propodeum with pair of thickened denticles rather than distinct spines as in A. tennesseensis. Metathorax with pair of latero-ventrad rather dorso-ventrally compressed flange-like swellings similar to those in A. tennesseensis, but better developed than other Floridian congeners. Posterior distal tip of each flange-like swelling barely extending past declivious face of propodeum. Viewed dorsally silhouette of alitrunk bullet-like, as in A. tennesseensis, rather than pear-shaped as in other Floridian congeners. Alitrunk with general appearance of being somewhat dorso-ventrally

compressed. However, this description is based on a single specimen which may have been crushed in collection.

Petiole and postpetiole as in Figure 11; most like those of A. tennesseensis and to a lesser extent A. fulva. Petiole laterally compressed, and not as sigmoid in profile as in A. tennesseensis. Postpetiole viewed dorsally about as wide as long; in profile rather globular above. Postpetiole slightly dorso-ventrally flattened compared to A. tennesseensis.

Very heavily sculptured. Mandibles shining, punctate and faintly longitudinally striate. Clypeus punctate and with longitudinal rugae. Remainder of head mostly densely punctate; faint transverse rugae between lateral ocelli and faint longitudinal rugae posterior to compound eyes. Some longitudinal rugae between insertion of mandibles and the anterior of compound eyes. Alitrunk almost entirely punctate dorsally and laterally. Scutum and scutellum distinctly rugose, more so than in A. tennesseensis. Rugae originating along longitudinal midline of anterior half of scutum and running roughly longitudinally the length of the scutum. Anterior half of dorsal longitudinal midline only punctate, more shining than rest of scutum. Rather longitudinal rugae covering much of lateral portions of alitrunk; particularly coarse near metathoracic flange-like swellings. Dorsum of propodeum feebly punctate and shining, especially between denticles. Petiole, postpetiole, and gaster finely punctate.

Pilosity more characteristic of genus than A. tennesseensis. Very dark brown.

### Distribution

According to Creighton (1950) the rare A. mariae is known from scattered records from Mississippi, Ohio, Illinois, and Florida. It has also been found in Connecticut (Wheeler, 1916) and North Carolina (Carter, 1962b). Buren (1944) collected A. mariae in Iowa. Wesson and Wesson (1940) found it several times in Ohio. I have seen what seems to be a male of this species collected in Georgia by Dr. P. S. Callahan (17 November, 1967). A. mariae was described from Florida, but the type locality given by Creighton (1950) is merely "Florida." As A. mariae seems to be a temporary parasite of an Aphaenogaster of the "rudis group," its range probably coincides with that of its host. The closely related A. tennesseensis does not seem to occur very far south in Florida. A. mariae was not collected in this investigation. Van Pelt (1958) did not find this species during his intensive collecting at the Welaka Reserve.

### Habitats

Wesson and Wesson (1940) collected A. mariae in mixed oak woods in Ohio. Carter (1962b) found strays in an oak-hickory-tulip poplar stand in North Carolina.

According to Wesson and Wesson (1940), A. mariae nests arboreally. They found it nesting in dead branches high in living oak trees. Its microhabitat is not entirely arboreal for its host is more terrestrial in its nesting habits. During its parasitic stage it probably lives in rotten logs or beneath stones. A. tennesseensis colonies also seem to migrate into trees after their parasitic stage.



### Foraging

Although Carter (1962b) found strays of this species on vegetation in the North Carolina Piedmont, he provided no further details regarding the location of the ants on the vegetation or what type of vegetation it was. Minimal terrestrial foraging by A. mariae may account for its infrequent collection.

### Annual Cycles

The annual cycle of A. mariae may be similar to that of the other temporary parasite A. tennesseensis. The A. mariae male from the light trap on the tower in Georgia was collected on 17 November, 1967. Mating flights late in the year are often characteristic of parasitic ants. A. tennesseensis is the only other species which has alate forms in the nest in the fall in Florida. In Connecticut Wheeler (1916) found an A. mariae female which had just descended from a mating flight in September.

### Findings on A. tennesseensis

#### Description of Male

TL 4.7, HL 0.8, HW 0.8, SL 0.35, AL 1.75 mm. General appearance as in Figure 11. Head shape as in Figure 11; like that of males of A. fulva and more so A. mariae. Head distinctly wider ventrally than dorsally. Heads of other Floridian congeners tend to be more rectangular in transverse cross section. Viewed frontally head not particularly narrowed posterior to compound eyes.

Alitrunk as in Figure 11. Dorsum of propodeum with pair of laterally flaring rather laterally flattened spines. Metathorax with pair of latero-ventrad rather dorso-ventrally compressed swellings or flanges each narrowing to a point posteriorly. Of Floridian congeners only A. mariae with swellings so well developed and flange-like. Posterior tips of flange-like swellings extend posteriorly beyond declivous face of propodeum. In A. mariae flange-like swellings extend posteriorly scarcely beyond declivous face. Viewed dorsally silhouette of alitrunk more bullet shaped, as in A. mariae, than pear-like as in males of other Floridian congeners.

Petiole and postpetiole as Figure 11; most like those of A. mariae and to a lesser extent those of A. fulva. Petiole laterally compressed and in profile slightly sigmoid. Postpetiole, viewed dorsally, about as wide as long and in profile rather semi-globular above.

Very heavily sculptured. Mandibles shining, punctate and faintly longitudinally striate. Clypeus shining, punctate and laterally with longitudinal rugae. Remainder of head mostly densely punctate; with light at proper angle faint transverse rugae between lateral ocelli and longitudinal rugae posterior to compound eyes visible. Alitrunk almost entirely punctate dorsally and laterally. Scutum and scutellum with faint rugae. Rugae originating along dorsal longitudinal midline on anterior half of scutum and running roughly longitudinally the length of the scutum. Rather longitudinal rugae covering much of the lateral portions of alitrunk, particularly near metathoracic flange-like swellings. Dorsum of propodeum very feebly punctate and shining especially between spines. Petiole, postpetiole, and gaster finely punctate.

Dorsum almost devoid of erect pilosity; except, most noticeably, the distal segments of gaster. Dorsum of first gastric segment with fine appressed hairs. Male of no Floridian congener has so little pilosity. Dark brown with head darkest.

#### Distribution

The range of A. tennesseensis, reported by Creighton (1950) is "New England south to the eastern Gulf States and west to Wisconsin, Missouri, and eastern Oklahoma " (p. 151). Smith (1965) stated that the range of this species includes South Dakota and Ontario. He felt it to be more common in the northern part of its range. Gregg (1972) considered A. tennesseensis a constituent of the Carolinian and Alleghenian life-zones. This is peculiar in light of the fact that this species is a temporary social parasite of A. fulva which Gregg does not include in his list of Alleghenian zone ants. Carter (1962b) in North Carolina collected A. tennesseensis only four times. Although this ant was named after its type locality, Dennis (1938) stated that it is not common in Tennessee.

In Florida A. tennesseensis has been found only in the northern tier of counties. Several collections were made at Tall Timbers Research Station in Leon County. It was also collected by Dr. H. V. Weems (7 December, 1957) at Florida Caverns State Park in Jackson County.

#### Habitats

The collections from Tall Timbers Research Station were from mesic hammocks. In North Carolina Carter (1962b) found A. tennesseensis in

mesic woods and once in a grassy pasture land with scattered young pines and decaying stumps. Dennis (1938) and Cole (1940) in Tennessee and Talbot (1934) in Illinois reported that this species generally inhabits mesic woods.

The colonies of A. tennesseensis at Tall Timbers Research Station were usually in living oak trees. One colony was in the trunk of a standing dead tree. Toward the interior of the dead tree the wood was quite hard. Two colonies were found in fallen logs, both of which were of rather hard wood. The nests in trees are at ground level to a height of eight m. Carter (1962b) found A. tennesseensis in rotten logs and stumps. Talbot (1934) remarked that in the Chicago region A. tennesseensis nests in fairly hard logs, which are off the ground, or in the upper parts of logs lying lightly on the ground. In Illinois Wheeler (1910) found mixed colonies of A. tennesseensis and A. fulva beneath stones. In Florida the large oak trees in which this species often dwells have a dense flora of vines, epiphytes and mosses on their larger branches and trunks. All the nests at Tall Timbers Research Station were shaded. Smith (1965) reported that A. tennesseensis occasionally infests homes.

### Nests

The single A. tennesseensis log nest which was dissected consisted of six to eight chambers and connecting galleries. The wood was hard, allowing the workers ample time to move brood to other accessible cavities while the log was being dissected. The nest did not extend into the soil. The chambers and tunnels appear to have been excavated by insects previously inhabiting the log. The chambers were variously

shaped, but most were laterally compressed. Older brood were in outer and inner chambers. Winged reproductives were concentrated in inner chambers, but may have migrated there during dissection. Ants were found 14 cm deep in the log.

The colony in the upright dead trunk was largely concentrated within five cm of the surface. It extended into wood too hard to open with the tools at hand.

### Foraging

The diet of A. tennesseensis consists largely of captured or scavenged arthropods. Most of these organisms are garnered on the ground and are similar to the food items of other species of Aphaenogaster. In the laboratory it took pieces of the mushroom, Russula pusilla, but was not observed collecting pieces of mushroom in the field. I never saw A. tennesseensis tending Homoptera, but in the laboratory workers imbibed sucrose and water solutions rather than plain water presented them. Forel (1901) and Smythe and Coppel (1964, 1973) reported that A. tennesseensis preys upon termites. The attacks they report were on termites whose nests had been broken open and the occupants strewn on the ground. Data on a collection of A. tennesseensis made by Dr. H. V. Weems at Florida Cavern State Park indicate that the ants were feeding on exposed termites. No records of non-fortuitous attacks on termites by A. tennesseensis are known to me. This species was not seen collecting seeds.

Coexistence with other Ants

The following species were found nesting in or traversing A. tennesseensis microhabitats:

Ponerinae-	<u>Hypoponera opaciceps</u>
	<u>H. opacior</u>
	<u>Odontomachus brunneus</u>
Pseudomyrmecinae-	<u>Pseudomyrmex brunneus</u>
Myrmicinae-	<u>Aphaenogaster carolinensis</u>
	<u>A. carolinensis*</u>
	<u>A. fulva</u>
	<u>Pheidole dentata</u>
	<u>Crematogaster ashmeadi</u>
	<u>C. atkinsoni</u>
	<u>C. clara</u>
	<u>S. invicta</u>
	<u>Cyphomyrmex rimosus minutus</u>
Formicinae-	<u>Camponotus floridanus</u>
	<u>C. castaneus</u>
	<u>C. (Myrmentoma) sp.</u>
	<u>C. (Colobopsis) sp.</u>
	<u>Paratrechina (Nylanderia) sp.</u>

Remarks on individual species. Relationships between A. tennesseensis ants with which it coexists are complicated by its role as a temporary social parasite of A. fulva. It is not known if this parasitism is obligatory, but if it is the success of A. tennesseensis in an area is incumbent on the success of A. fulva there. The significance of

migration from terrestrial to arboreal nests by this species is another factor difficult to assess in terms of coexistence with other ants. Since A. tennesseensis was observed at only a single station, the foregoing list is probably not representative.

Pseudomyrmex brunneus and Camponotus (Colobopsis) impressus forage primarily on foliage and slender twigs.

In the hammocks in which I observed A. tennesseensis, Solenopsis invicta has virtually replaced S. geminata. In many hammocks, however, S. geminata still holds its own against its imported congener. S. invicta workers were seen foraging on A. tennesseensis nest trees. Bhatkar (1973) studied confrontation behavior between S. invicta and A. tennesseensis.

#### Annual Cycles and Colony Size

Winged reproductives of A. tennesseensis were in field colonies in August. In the laboratory alate queens began to dealate in late August and early September. Some of these alates persisted into late November. In the laboratory sibling females fought one another, biting legs, antennae, petiolar regions and bases of wings. Workers often took part in attacks on females. Daily for a period of several weeks I found partially dismembered queens dead or trying to escape from the tub containing the Wilson cell. One nest contained over 125 alate females and 68 males, far more females than I found in any other Aphaenogaster colony. Such large numbers of alate females might be an adaptation to the risks of temporarily parasitic way of life, however Talbot (1954) reported A. treatae colonies with more than 130 females. In December I put three dealate A. tennesseensis females (mating status unknown) in

petri dish nests to determine if they were capable of claustral nest foundation. All three females constructed nest cells. They laid eggs intermittently, but they apparently ate them. No larvae developed.

A dealate female, seen running about the nest arena of laboratory colony, was placed in a tray containing a shell vial nest of an incipient A. fulva colony. After about an hour the tennesseensis female entered the nest vial unopposed. Three or four fulva workers examined her and bit her, but she curled up when they attacked. The following day the tennesseensis female was still in the nest vial. However, the A. fulva colony had moved into the other end of the vial. The second day after her entrance into the A. fulva nest the dismembered remains of the A. tennesseensis female were found outside the nest vial. It is not known whether the female was ever mated.

No entire colonies of A. tennesseensis were collected, but mature colonies are estimated to contain at least 600 workers.

#### Development

Although the duration of only two pupae was determined, it was 13 days for both. Thirteen days was the maximum duration for the pupal stage in the other species of Aphaenogaster studied.

#### Findings on A. treatae

#### Distribution

Creighton (1950) stated that A. treatae occurs from southern New England to Florida and the eastern Gulf states, and is sporadically distributed through Ohio to Illinois. I have seen specimens collected



in Iowa by Dr. Buren. Warren and Rouse (1969) recorded A. treatae from Arkansas. Van Pelt (1963) found A. treatae at altitudes in the 700 to 1300 m range in the Blue Ridge Mountains, while Cole (1940) collected it at altitudes of 600 to 1060 m in the Great Smoky Mountains. According to Gregg (1972), A. treatae is a constituent of Merriam's Carolinian life-zone.

A. treatae seems to be somewhat locally distributed in Florida. Nowhere in the state did I find it as abundantly as its close relative A. ashmeadi. It was taken in the Appalachian National Forest in Leon County by Dr. T. J. Walker (16 June, 1958) and Dr. R. E. Woodruff (3 February, 1960). Van Pelt (1958) found A. treatae at the Welaka Conservation Reserve in Putnam County. I found this species only in Alachua and Hamilton Counties. The southernmost Florida record of A. treatae is of some workers collected in a can trap at Winter Haven in Polk County by "M. H. M. and H. L. G." (19 August, 1970). A. treatae is common at some stations in the Gainesville region.

#### Habitats

In Florida A. treatae nests almost exclusively in moderately to well-drained sandy soils. Talbot (1934) in an ecological study of the ants of the Chicago region found A. treatae to be restricted to black oak woods on sand and red and white oak woods on sand. Furthermore, her (1954) population studies of this insect were carried out in sandy fields in Michigan. At the Welaka Reserve Van Pelt (1958) found A. treatae associated only with fine sandy soils. At Tall Timbers Research Station in Leon County, where there has been considerable myrmecological research and collecting in recent years, this species was found but

once. Its apparent scarcity there may be due to the lack of properly drained sandy soils.

In Florida A. treatae is not an open field ant as it is in Michigan (Talbot, 1954). Instead it seems to be associated with minimal shade provided by trees or shrubs. It was never found in deeply shaded macro- or microhabitats. Talbot (1953, 1954) felt that A. rudis replaced A. treatae along the borders of fields and in adjacent woodlands in Michigan. In North Carolina Carter (1962b) reported that A. treatae nested in both field and forest communities and was "most common in and characteristic of grassy, open, young and middle-aged pine stands." Turkey oak - longleaf pine sandhills and scrub oak woodlands are characteristic habitats of A. treatae in the Gainesville region. Populations of A. treatae are greater in the scrub oak woods than the turkey oak sandhills. At the Welaka Reserve Van Pelt (1958) found this species rarely in St. Lucie scrub and occasionally in Leon scrubby flatwoods. The Winter Haven can trap collection was from a sand pine woodland.

The microhabitats of A. treatae are similar to those of A. ashmeadi, but are characterized by less shade and leaf litter. Nest entrances may be at the bases of herbs or clumps of grass. Gregg (1944) said A. treatae could be found nesting in and under logs in the Chicago region, while Carter (1962b) reported it occasionally nested beneath rocks in North Carolina. All the nests of A. treatae, which Cole (1940) found in the Great Smoky Mountains, were beneath stones. In Florida I found no nests associated with logs or stones.

### Nests

A. treatae nests are similar to those of A. ashmeadi. Talbot (1954) described the nests of A. treatae she found in Michigan. The structure of A. treatae nests is quite similar to that of A. ashmeadi nests. Most nests I examined had one or two entrances. One of the entrances is often surmounted by a turret of small twigs, dried plant parts and sometimes arthropod remains. Talbot (1954) found as many as five entrances per nest, but usually only one or two. The nests Talbot described were in a grassy field and each frequently had a superficial chamber among the grass stems. Colonies in Florida are not in particularly grassy microhabitats, but the nests often have a superficial chamber just beneath leaf litter. Pupae and prepupae are usually in the superficial chamber, while the remainder of the brood is in lower chambers. Talbot found the depth of A. treatae nests varied from 22.5 to 100 cm, averaging 75 cm. No nest excavated in this study extended below 75 cm, most were only about 45 cm deep.

### Foraging

A. treatae is similar to A. ashmeadi in its foraging. Like its soil-dwelling congeners A. treatae forages almost exclusively on the ground. Foragers were rarely found in well shaded areas. Talbot (1954) reported that in Michigan A. treatae workers "did not forage during the heat of the day, but were usually most active during the morning and again in the late afternoon when temperature at the ground surface was between 70° F and 90° F "(p. 8). Such pronounced periodicity does not seem to be the rule in Florida. I regularly found foragers in midafternoon

during the summer when ground surface temperatures exceeded 35° C. Only colonies in turkey oak woods tend to remain in the nest during the heat of the day. Foraging is heavier during morning and evening hours in warmer months. If workers return with a food item several foragers leave the nest within one or two min. I once found an A. treatae worker about 15 cm below ground level in a decaying pine stump. Foraging activity is not markedly greater on cloudy days than sunny days. Like its soil-dwelling congeners A. treatae is not very active above ground during the winter. The farthest from her nest any A. treatae forager was found was nearly seven m. Most foraging is within five m of the nest and tends to be in the same microhabitat as the nest.

#### Feeding

A. treatae feeds on the same type items as its congeners, but the food organisms tend to be characteristic of A. treatae microhabitats. I saw an A. treatae worker carrying a termite only once. In the laboratory A. treatae workers attacked termites proffered them. Workers were seen visiting mushrooms, Russula sp. In the laboratory pieces of this mushroom were taken by A. treatae. I never saw this ant tending Homoptera, but in the laboratory workers imbibed sucrose and water solutions rather than plain water as proffered them. Talbot (1954) reported that in Michigan some colonies of A. treatae brought in great numbers of ripening Panicum depauperatum seeds. Only infrequently did I observe A. treatae workers carrying seeds.

#### Coexistence with other Ants

Several species of ants share the same nesting or foraging

microhabitats with A. treatae. Among the most common of these are:

- Ponerinae- Hypoponera opaciceps  
Odontomachus brunneus
- Myrmicinae- Aphaenogaster ashmeadi  
A. flemingi  
A. floridana  
Pheidole metallescens  
P. morrisoni  
Crematogaster ashmeadi  
C. clara  
Monomorium viridum  
Solenopsis geminata  
S. (Diplorhoptum) sp.  
Leptothorax pergandei  
Cyphomyrmex rimosus minutus  
Trachymyrmex septentrionalis
- Formicinae- Camponotus floridanus  
C. socius  
Paratrechina (Nylanderia) sp.  
Prenolepis imparis  
Formica pallidefulva

Remarks on individual species. Many of the species occurring in A. treatae microhabitats are the same as those in A. ashmeadi microhabitats. Solenopsis invicta, although not listed above, probably occurs in A. treatae microhabitats in northwest Florida. Monomorium viridum, Iridomyrmex pruinosus, and Conomyrma sp. sometimes coexist with A. treatae in turkey oak woods.

Hypoponera opaciceps and Odontomachus brunneus are not as common in A. treatae microhabitats as in more mesic habitats.

Pheidole morrisi tends to replace P. dentata in turkey oak woods. Both species forage and nest near A. treatae nests in less xeric areas. See Table three. P. morrisi seems to be more nocturnal than P. dentata. Occasionally Solenopsis (Diplorhoptum) sp. nests were found very near A. treatae nests, which suggests the possibility of lestopiosis.

At least two forms (species) of Paratrechina (Nylanderia) occur in A. treatae microhabitats; a yellow nocturnal form in xeric situations and a blackish form more moist microhabitats.

#### Annual Cycles and Colony Size

As early as 13 April, I found female larvae in an A. treatae field colony. On 2 May a male imago and on 11 May an alate female were found. Reproductive forms were found in field colonies as late as 15 July.

In Michigan reproductive pupae are present in A. treatae colonies in early June and most mating flights take place during the first three weeks of July (Talbot, 1954 and 1966). There alates flew in late morning and early afternoon. Talbot found males in one colony as late as 10 August. According to Talbot, flights lasted as long as 25 minutes, but there were many brief flights of less than five minutes. She found flights took place during the interval in which clouds passed over, reducing light to 3800 ft c and ground temperature to 31.7° C. Sometimes after a few days of small flights a long flight emptied all the alates from all the colonies in her study area. The largest flight group from one nest consisted of 15 females and 20 to 30 males, attended by 50 workers.

Talbot (1954) found as many as 199 male and 132 female pupae in one A. treatae colony and 251 male and 71 female pupae in another. No colony I examined in Florida contained nearly as many reproductives. The maximum number of (alate and pupal) females I found in a colony was about 30. Florida colonies seem to be smaller than those in Michigan. Thirty colonies Talbot (1954) examined had an average of 682 workers. No colony excavated in this study had over 400 workers. Most had 200 workers or less. Following mating flights Talbot (1966) found two queens in separate cells alone with small bundles of eggs. In April I found small colonies consisting of a queen and less than 30 workers in shallow nests. Perhaps such colonies represent the previous summer's successfully mated queens.

#### Development

The duration of the egg stage of A. treatae is 19 to 21 days. The pupal stage lasts eight to 12 days. The duration of larval development is only 20 to 23 days.

#### Predators of Aphaenogaster Spp.

Aphaenogaster spp. workers and reproductives fall victim to many general predators of arthropods. Avian predation of Aphaenogaster spp. in Florida was not observed. I examined ants from the stomachs of some Florida woodpeckers, Picidae, for Dr. A. Cruz in ecological study of the birds he plans to publish. No Aphaenogaster species were present among the numerous ants eaten. Some bird or mammal digs into the upper six cm of Aphaenogaster nests, perhaps to feed on the older brood often

present there. I occasionally found Aphaenogaster soil nests thus molested, but the perpetrator was never caught in the act. Various amphibians feed heavily on ants, including Aphaenogaster spp. Fecal samples from two southern toads, Bufo terrestris, contained remains of A. ashmeadi, A. carolinensis, and A. lamellidens; the only Aphaenogaster species in the woodland where the toads were collected. A. lamellidens was represented by only a single worker. One pellet contained five A. ashmeadi workers and eight A. carolinensis workers, while the other pellet had five A. ashmeadi workers and six A. carolinensis workers. Virtually all the identifiable arthropod remains in the pellets were of ants. The pellets contained a greater number of small ants, Paratrechina (Nylanderia) spp. and Pheidole dentata, whose total volume was estimated to be about equal to that of the combined volume of the Aphaenogaster spp. While fewer large ants, Odontomachus brunneus and Camponotus floridanus, were eaten they seemed to comprise a portion of the total fecal volume equal or greater than that of Aphaenogaster. No preference for Aphaenogaster spp. was indicated. The toad fecal contents resembled the surface collections I made around A. ashmeadi nests in that woodland. See Table three collections one and two. Examination of a fecal pellet from a squirrel treefrog, Hyla squirella, from the same woodland disclosed only three A. carolinensis workers. The bulk of the pellet consisted of remains of non-Hymenopterous arthropods. A green anole, Anolis carolinensis carolinensis, captured in the same woodland had no ants in its feces. A gray treefrog, Hyla versicolor, collected from the trunk of a tree containing an A. lamellidens nest had no Aphaenogaster remains in its feces. It had, however, eaten many Crematogaster vermiculata workers. An unidentified



young adult frog captured on a river swamp flood plain abounding with Aphaenogaster spp. foragers had only Crematogaster vermiculata in its feces. Although these samples are very small, toads appear to be important predators of Aphaenogaster spp. workers. The toads defecated within 24 hours of capture, but whether one pellet is excreted daily under natural conditions and represents one day's feeding is not known to me.

Spiders constitute another important group of predators of Aphaenogaster spp. The only records of alate mortality are deaths caused by spiders. Three alate females were found in the web of an unidentified orb web weaving spider. A male and female A. carolinensis and an A. lamellidens worker were found in webs of the Theridiid, Tidarren sisypoides (Walckenaer). Corpses of A. lamellidens workers were also found in the web of an unidentified Theridiid. A worker of A. carolinensis was found in the web of an immature Nephila clavipes (Linnaeus) and another in a web of Leucage venusta (Walckenaer). Workers of A. lamellidens and A. carolinensis were found in abandoned spider webs. On three occasions wolf spiders, Lycosidae, were seen attacking Aphaenogaster foragers (A. ashmeadi, A. carolinensis, and A. lamellidens) returning to their nests with food items. In each instance the ant escaped, losing its burden. In the laboratory a worker of A. floridana was put in a petri dish with a large wolf spider, Lycosa. The spider immediately attacked the ant, killing it almost instantly. However, the spider quickly released the ant and began rubbing its mouthparts and forelegs on the substrate. A lump of cotton saturated with water was placed in the petri dish. The spider drank from the cotton wad for several minutes. Eventually it returned to and

ate the ant. A very large wolf spider was seen standing in the path of two A. flemingi workers returning from an unsuccessful foraging sortie. The first ant encountering the spider bit it on the leg. The spider flicked its leg and the ant continued back to its nest. The process was repeated with the second ant. The jumping spider, Stoidis aurata (Hentz) was observed feeding on A. carolinensis and A. floridana in the field. In the laboratory Edwards et al. (1974) found S. aurata attacked most species of Florida ants, including A. ashmeadi, A. floridana, A. lamellidens, A. tennesseensis, and A. treatae. Two species of spiders, Achaearanea tepidariorum (C. L. Koch) and Pholcus phalangioides (Fuesslin), which infested the laboratory fed heavily on Aphaenogaster spp. workers.

Aside from other ants no insects were seen attacking Aphaenogaster workers or reproductives. Predation on Aphaenogaster spp. by other ants is discussed separately for each species of Aphaenogaster.

#### Myrmecophiles Associated with Aphaenogaster Spp.

A female myrmecophilous cricket, Myrmecophila pergandei Bruner was found in the nest of an A. ashmeadi colony in Gainesville. I recovered another female from the nest of an A. carolinensis\* colony from Tall Timbers Research Station, Leon County. The A. ashmeadi nest was in the soil and the A. carolinensis\* in a rotten log. Both are new host records for M. pergandei. Unfortunately both crickets died before any meaningful observations of their behavior could be made. Wheeler (1910) who described some of their behavior, believed the crickets feed on oily secretions from the ants. According to Wheeler M. pergandei

has been found associated with A. tennesseensis.

Numerous larvae of a ceratopogonid fly were found in a rotten log in which A. carolinensis\* was nesting. The larvae, approximately .5 to two mm long, were most abundant in or near the ant nest. Several fly larvae were in the brood chamber and others in a refuse chamber. Two fly larvae were removed and placed in a petri dish containing moist tissue, an ant pupa, and four red flour beetle pupae. I did not observe the larvae feeding on either the ant or Tribolium pupae. Four days after being placed in the petri dish one larva pupated, two days later the other. An adult emerged from the first fly pupa three days later.

Collembola and mites were found in every Aphaenogaster nest. Mites sometimes irrupted in small laboratory Aphaenogaster colonies. In such colonies ant workers became nearly crippled by numerous phoretic hypopal mites. The Laelaptid mite, Hypoaspis vacua (Michael), was found clinging to the mesonotum of an A. ashmeadi worker collected in Leon County. Mites were observed feeding upon injured ant brood. In Florida Bhatkar and Whitcomb (1975) found the mite Scutacaris sp., Scutacaridae, on Aphaenogaster spp.

## DISCUSSION

### Intragenetic Coexistence

According to Miller (1967), interspecific competition exists when there is "the active demand by ... members of two or more species at the same trophic level ... for a common resource that is actually or potentially limiting " (p. 6). Since the resource requirements of closely related species such as congeners are generally quite similar it might be expected that interspecific competition between coexisting congeners is often intense. Wilson (1971) stated: "In order for species to co-exist, it is necessary that each of them be sufficiently different to reach their equilibrium densities before eliminating their competitors, and the usual way this occurs is through differences in critical dimensions of the 'niche', namely, those parameters of habitat, nest site, diet, foraging periodicity, and other factors capable of limiting populations " (p. 454).

In North Florida nine species of Aphaenogaster are sympatric. This number includes A. mariae, which, although not collected in this study, can be assumed from the literature to occur in north Florida. Both typical and variant forms of A. carolinensis are present in north Florida. As far south as Gainesville, seven species occur. At one station in Gainesville six species nest within 150 m of one another. In south Florida a single species is common and there is only one other

species I am certain is present. With the possible exception of A. lamellidens the eight species of Aphaenogaster studied feed on the same sort of items and are chiefly terrestrial foragers. A model proposed by MacArthur and Pianka (1966) seems to provide some explanation of how so many similar predators utilizing the same type food are able to co-exist. They suggest that the optimal behavior of a predator is to have a broad food and habitat niche, but a low habitat overlap with competitors. According to MacArthur and Pianka, the optimum response of competing predators is to reduce the number of patches of the environment visited rather than the types of food taken. "Resources are distributed in a patchwork in three dimensions in the environment" (MacArthur and Levins, 1964 , p. 603). Although Aphaenogaster spp. are not strictly predators, it is worthwhile to examine the situation of Aphaenogaster spp. in north Florida in terms of MacArthur and Pianka's model.

On the macrohabitat level there is a degree of segregation of some congeners from one another. Of the 11 habitats listed in Table one, ten exist in north Florida, the area of greatest Aphaenogaster spp. sympatry in Florida. In each of the habitats at least four species occur. Typically soil-nesting species are restricted to comparatively xeric habitats; those with comparatively well-drained soil. Species which frequently nest in rotten wood are rare or absent in xeric habitats. Thus on a macrohabitat level certain species adapted to extreme habitats can be said to use different patches because they do not coexist in the same macrohabitats. The best example of this is the pair of congeners A. floridana (a xerophile) and A. fulva (rare outside of swamps and moist woodlands). I did not find the following paired species coexisting in the same type habitats:

A. fulva: A. treatae

A. fulva: A. flemingi

A. tennesseensis: A. treatae

A. tennesseensis: A. flemingi

A. tennesseensis: A. floridana

In some habitats one species was characteristically common, while congeners in that habitat were not as prevalent. In turkey oak sandhills and ruderal and sand pine dune areas A. floridana is the common Aphaenogaster, although four congeners also occur in those habitats. A. flemingi is typically more abundant than its congeners in pine flatwoods. The greatest number of Aphaenogaster spp. coexist in habitats, such as xeric hammock scrub oak areas, intermediate between extreme habitats like sandhills and hydric hammocks. Both soil-dwelling and log-nesting species exist in such intermediate habitats. Some species, A. ashmeadi, A. carolinensis, A. treatae, and A. flemingi are characteristic of intermediate habitats, but A. ashmeadi is the only one which is common. A. ashmeadi is one of three species occurring in wide range habitats. It is most conspicuously absent from ruderal areas and moist woodlands. The second species' (A. lamellidens) predilection for nesting in living trees seems to have allowed it to occur in a number of diverse habitats. A. carolinensis sensu lato occurs in a wider range of habitats than its congeners, but as discussed earlier may be a complex of sibling species.

Where several species of Aphaenogaster are present in the same macrohabitat, there often seems to be a segregation of the species into microhabitats (patches) characteristic to each species. In well-drained and intermediate habitats the following specializations exist:

- A. floridana- open patches, no leaf litter, much direct sunlight
- A. treatae- light shade, light leaf litter
- A. flemingi- light shade (mostly from herbs), light leaf litter
- A. ashmeadi- moderate to heavy shade, moderate to heavy leaf litter
- A. carolinensis- rather heavy shade, nests beneath thick shrubs in  
most xeric situations

These species nest and forage primarily in the described microhabitats (patches).

In mesic and hydric hammocks and river swamps, the partitioning of the environment into discrete patches used by particular Aphaenogaster species is not as apparent. An arboreal-nesting species like A. lamellidens would seem to have a foraging patch of its own, particularly when one considers the surface area on the trunks of large nest trees. I am uncertain whether A. tennesseensis overlaps the sort of patches used by A. lamellidens. Observations from the single station where A. tennesseensis was studied indicate its habitat, nesting sites, and foraging strata are like those of A. lamellidens. The patches used by A. tennesseensis may change following its parasitic stage. The pair of A. fulva and A. carolinensis sensu latu is the most difficult to assess in terms of MacArthur and Pianka's model. In river swamps I could not predict which of the two species I would find if I broke open a rotten log or stump. I could not tell the species of a forager on the basis of where it was foraging. Where A. fulva and A. carolinensis occur together I can discern no difference between their patches. The only difference in nesting habits is that A. carolinensis sensu latu nests arboreally slightly more often and sometimes nests up to one m or so higher. The overall distributions of the two species may shed some

light on the situation. North and central Florida is the southern limit of the range of A. fulva. On the other hand the large forms of A. carolinensis sensu latu, which coexist with A. fulva in north Florida, are typically Floridian or Gulf Coast insects. I observed no overt aggression of one species toward the other in natural situations.

An interesting consideration is the utilization by A. carolinensis sensu latu of a wide variety of patches (habitats and microhabitats) in south Florida where only one congener is known to coexist.

Culver (1971) mentioned another optimization which might better permit coexistence of congeners in microhabitats. He suggests that a reduction in the overlap of size of workers may reflect food specialization. The only Aphaenogaster pair to which this might be applicable is A. ashmeadi and the typical A. carolinensis. The foraging areas of two often overlap. See Table three collections one and two. I have no data to support or contradict Culver's premise regarding A. ashmeadi and A. carolinensis. As with the relationship between Pheidole spp. and A. ashmeadi (Table five), size of food item may in some way be related to ability of an ant to successfully garner it in the face of larger stronger species.

#### Consumption of Agaricales

The function and importance of basidiocarps (fruiting bodies) of mushrooms (Agaricales) in the diet of Aphaenogaster spp. remain to be assessed. Field observations indicate that Aphaenogaster spp. are the only ants in north central Florida significantly exploiting free growing mushrooms as a food source. Aphaenogaster spp. were seen regularly



visiting Russula spp. There are more than a dozen species of Russula in Florida. Amanita vaginata is occasionally attacked by A. carolinensis and A. ashmeadi, while Marasmiellus sp. and Clitocybe tabescens are attacked by A. ashmeadi. The four genera of fungi attacked by Aphaenogaster spp. represent three families. The basidiocarps of the mushrooms vary considerably in size from Marasmiellus sp., which is scarcely the size of an Aphaenogaster worker, to the larger species of Russula, which are six cm tall with caps six cm across. All eight species of Aphaenogaster collected in this study took pieces of Russula spp. under laboratory conditions. In the field all but A. fulva, A. lamellidens, and A. tennesseensis were observed visiting or attacking mushrooms. Microscopic examination of mushroom fragments carried by Aphaenogaster foragers revealed no minute mycetophagous organisms upon which the ants might be feeding instead of the actual mushroom tissue or fluids.

It is not unreasonable to suggest that mushrooms provide more than just supplementary nutrients to Aphaenogaster spp. Fungus growing Attine ants, which belong to the same ant family as Aphaenogaster, subsist solely upon the fungi they cultivate. The only other ants observed removing pieces of mushrooms were Pheidole dentata and P. metallescens. At least occasionally, according to an observation by D. P. Wojcik (personal communication), the fungus growing ant, Cyphomyrmex rimosus minutus, attacks mushroom basidiocarps in the fashion Aphaenogaster spp. do. P. morrisoni, P. floridana, and more frequently Solenopsis geminata workers were seen visiting mushrooms. Obviously a dietary specialization, such as feeding on mushrooms, reduces competition between Aphaenogaster spp. and other predatory and scavenging ants. This is illustrated by the following observation. A small island (about seven m by

four m) in a river swamp contained a large colony of S. geminata, which foraged throughout the island, and one or more colonies of A. carolinensis\*. S. geminata dominated at meat baits set out on the island. Despite the presence of S. geminata foragers in every square meter of the island, only A. carolinensis\* workers visited Russula mushrooms. Unmolested, the A. carolinensis\* workers chewed off pieces of the mushrooms and carried them nestward.

Several authorities have speculated on the evolutionary origin of fungus growing by Attine ants. Von Ihering (1894), as cited in Wilson, 1971, suggested that the Attines originated from harvesting ants with slovenly habits. In this regard he mentioned the genera Pogonomyrmex, Pheidole, Lasius, and significantly Aphaenogaster. He thought collected plant material might become moldy in humid ant nests. The ants while eating the plant material would eat some of the fungi, and perhaps prefer the fungi. Forel (1902), as cited in Wilson, 1971, believed that proto-Attines lived in rotten wood and gradually acquired a taste for fungi they found growing on the excrement of wood boring insects. Weber (1973) proposed that the proto-Attines might have started feeding on fungi growing on their own feces. According to Wilson (1971), the genus Cyphomyrmex has generally been considered as exhibiting the most primitive characteristics among the Attini.

Investigation of the mushroom harvesting activities of Aphaenogaster and Pheidole might provide new insight into the evolution of fungus cultivation by ants. Aphaenogaster spp. are rather generalized ants of the same subfamily as the Attini. Certain aspects of their behavior, such as larval feeding, are considered primitive. Perhaps the Attines could have evolved from a generalized ancestor along the

lines of an Aphaenogaster rather than one similar to Cyphomyrmex. The Attine genus Apterostigma resembles Aphaenogaster morphologically. No less an authority than Wheeler (1910) remarked on the resemblance of Apterostigma to Aphaenogaster. Furthermore, several aspects of Apterostigma biology and behavior are considered rather primitive. Forel (1902) believed the feeding habits of Apterostigma approximated those of his aforementioned hypothetical Attine. Some Cyphomyrmex spp., the putative primitive Attines, feed on fungi imperfecti, while, according to Weber (1973), the other Attines feed or are assumed to feed on Basidiomycetes. If the proto-Attine resembled an Aphaenogaster, it would have fed on a variety of Basidiomycetes. Not only would it have already had a "taste" for fungi, but it would be introducing fungi into a humid nest where there were refuse and storage heaps of animal and plant matter. Fungi might readily grow on the substrate of stored or discarded animal and plant matter. Thus, the same fungi which the ants collected in the field would then be growing within the confines of their nest. The steps from that point to present fungus cultivation by ants would be the same as those postulated by other authors. The question of why and how ants started feeding on fungi remains unanswered. Furthermore, many questions remain unanswered regarding the evolution of the Attines, particularly so in light of the marked morphological dissimilarity between the Attines and all other ants. Somewhat pertinent to this subject is the report by Goetsch (1942) on the leaf cutting behavior of the European Aphaenogaster testaceopilosa. However, the Attines are strictly a New World tribe.



Table 2. Nesting strata of Florida Aphaenogaster species. Incipient colonies not included; see species discussion for details.

	soil	leaf mold	logs, stumps, cypress knees	arboreal, height above ground 2m	2m
<u>ashmeadi</u>	3	0	1	0	0
<u>carolinensis</u>	2	3	2	1	0
<u>carolinensis*</u>	2	0	3	2	0
<u>flemingi</u>	3	0	x	0	0
<u>floridana</u>	3	0	0	0	0
<u>fulva</u>	2	0	3	2	0
<u>lamellidens</u>	0	0	1	2	3
<u>mariae</u>	x	0	0	0	x
<u>tennesseensis</u>	x	0	2	3	2
<u>treatae</u>	3	0	0	0	0

Frequency of occurrence based on number of colonies of particular species found in given stratum in relation to total number of colonies of that species found.

0 = Not found in given stratum in this study.

1 = Rarely found in given stratum in this study.

2 = Occasionally found in given stratum in this study.

3 = Commonly found in given stratum in this study.

x = In literature as occurring in given stratum, but not found there in this study.

Table 3. Ant foragers collected in one hr within a two m radius of nests of Aphaenogaster species.

Foraging Species	<u>A. ashmeadi</u>				<u>A. flemingi</u>		<u>A. floridana</u>		<u>A. treatae</u>	
	Collection no.				Coll. no.		Coll. no.		Coll. no.	
	1	2	3	4	1	2	1	2	1	2
<u>Hypoponera opaciceps</u>			1							2
<u>Odontomachus brunneus</u>	5	8			5	1		3		
<u>Pseudomyrmex pallidus</u>					3			1		
<u>Ps. brunneus</u>		2								
<u>Pogonomyrmex badius</u>										2
<u>Aphaenogaster ashmeadi</u>	18	14	3	26			1			
<u>A. carolinensis</u>	2	1								
<u>A. flemingi</u>					13	6				
<u>A. floridana</u>								2		
<u>A. treatae</u>									15	11
<u>Pheidole crassicornis</u> Emery										10
<u>P. dentata</u>	65	83	9	36	10	2	4	22	4	1
<u>P. floridana</u>	5	2		2						
<u>P. metallescens</u>			27	58	30	66			44	17
<u>P. metallescens splendidula</u>							61	54		

Table 3 - continued

Foraging Species	<u>A. ashmeadi</u>				<u>A. flemingi</u>		<u>A. floridana</u>		<u>A. treatae</u>	
	Collection no.				Coll. no.		Coll. no.		Coll. no.	
	1	2	3	4	1	2	1	2	1	2
<u>P. morrisi</u>				6	1		1		1	
<u>Cardiocondyla</u> <u>nuda minutior</u>				6						
<u>C. sp.</u>				6						
<u>Crematogaster</u> <u>ashmeadi</u>									4	1
<u>C. clara</u>					2	2				2
<u>Solenopsis</u> <u>geminata</u>			30	5	25	59			42	1
<u>Solenopsis</u> ( <u>Diplo-</u> <u>rhopstum</u> ) sp.	1	1								
<u>Leptothorax</u> <u>pergandei</u>			4		1		3	2	6	1
<u>L. texanus</u>			4		10	3				7
<u>Trichoscapa</u> <u>membranifera</u>					4					
<u>Cyphomyrmex</u> <u>rimosus</u> <u>minutus</u>	5		2		2	1			3	5
<u>Trachymyrmex</u> <u>septen-</u> <u>trionalis</u>	17	6	5		6	2	2	1	5	1
<u>Iridomyrmex</u> <u>pruinus</u>							36			
<u>Conomyrma</u> <u>flavopecta</u>			1	3			3	5		
<u>Brachymyrmex</u> <u>depilis</u>	2	1	2			1				

Table 3 - continued

Foraging Species	<u>A. ashmeadi</u>				<u>A. flemingi</u>		<u>A. floridana</u>		<u>A. treatae</u>	
	Collection no.				Coll. no.		Coll. no.		Coll. no.	
	1	2	3	4	1	2	1	2	1	2
<u>Camponotus</u> <u>floridanus</u>		1				1				
<u>Camponotus</u> <u>socius</u>						1		1	2	4
<u>Paratrechina</u> <u>(Nylanderia)</u> sp. A	96	39	2							
<u>P. (Nylan-</u> <u>deria) sp. B</u>				7	10	15			10	3
<u>Formica</u> <u>Prenolepis</u> <u>imparis</u>				25						
<u>Formica</u> <u>pallidefulva</u>				5						



Table 4. Size, nesting, foraging and food similarities between Aphaenogaster spp. and other ant species nesting in or traversing their microhabitats. For Florida only.

Species	Approx. size (mm)	Nesting	Foraging	Feeding
<u>Platythyrea punctata</u>	6-7	l,a	g,t	p
<u>Hypoponera opaciceps</u>	3	l,s	g	p
<u>H. opacior</u>	3	l,s	g	p
<u>Leptogenys manni</u>	7	l,s	g	p
<u>Odontomachus brunneus</u>	8-9	l,s	g	p,h (Bhat. & Whit.,1975)
<u>Pseudomyrmex brunneus</u>	3-4	a	f,t	p,h (Nielsson et al.,1971)
<u>P. mexicanus</u>	7	a	f,t	p,h (Carroll, 1970)
<u>P. pallidus</u>	3-4	a	f,t	p,h
<u>Pogonomyrmex badius</u>	5-8	s	g	seed harvester
<u>APHAENOGASTER</u>				
<u>ASHMEADI</u>	6-7	s	g	p
<u>A. CAROLINENSIS</u>	4-6	l,s	g	p,h (Bhatkar & Whit., 1975)
<u>A. CAROLINENSIS*</u>	5-7	l,s,a	g,t	p
<u>A. FLEMINGI</u>	6-7	s	g	p
<u>A. FLORIDANA</u>	6-7	s	g	p
<u>A. FULVA</u>	5-6	l,s,a	g,t	p
<u>A. LAMELLIDENS</u>	6-7	l,a	t,g	p

Explanation of letters:

- a = arboreal, including herbaceous
- f = foliage
- fg = extensive foraging on foliage and ground
- g = ground primarily
- h = associated with Homoptera/extrafloral nectaries
- l = logs, stumps, decaying cypress knees
- p = predator/scavenger
- s = soil
- t = tree trunks and larger lower branches

Table 4 - continued

Species	Approx. size (mm)	Nesting	Foraging	Feeding
<u>A. TENNESSEENSIS</u>	5-6	1,a	g,t	p
<u>A. TREATAE</u>	6-7	s	g	p
<u>Pheidole dentata</u>	2-3	1,s,a	fg,t	p,h (Nielsson et al., 1971)
<u>P. floridana</u>	2	1,s,a	fg,t	p,h (Carroll, 1970)
<u>P. metallescens</u>	2	s	fg	p,h
<u>P. metallescens splendidula</u>	2	s	fg	p,h
<u>P. morrisi</u>	2-3	s	fg	p,h (Nielsson et al., 1971)
<u>Cardiocondyla</u> spp.	2	s,1,a	fg,t	p,h
<u>Crematogaster ashmeadi</u>	3	1,a	fg,t	p,h (Nielsson et al., 1971)
<u>C. atkinsoni</u>	3	1,a	fg,t	p,h ( " )
<u>C. clara</u>	3	1,a	fg,t	p,h
<u>C. vermiculata</u>	3	1,a	fg,t	p,h
<u>Monomorium floricola</u>	1-2	1,a	fg,t	p,h
<u>M. viridum</u>	1-2	s,1,a	fg,t	p,h
<u>Xenomyrmex stollii</u>	1-2	1,a	f,t	p,h
<u>Solenopsis geminata</u>	2-5	s,1	fg,t	p,h (Nielsson et al., 1971)
<u>S. invicta</u>	2-5	s,1	fg,t	p,h ( " )
<u>S. (Diplorhoptum) spp.</u>	1-2	s,1,a	g,t	p,h ( " )
<u>Leptothorax pergandei</u>	3	s,1	g	p?
<u>L. texanus</u>	2	s,1	g	p?

Table 4 - continued

Species	Approx. size (mm)	Nesting	Foraging	Feeding
<u>Tetramorium guineense</u>	3	s,l,a	fg,t	p,h (Carroll, 1970)
<u>Cyphomyrmex rimosus</u> <u>minutus</u>	3	s,l	g	fungus grower
<u>Trachymyrmex</u> <u>septentrionalis</u>	3	s	g	" "
<u>Iridomyrmex pruinosus</u>	2	s,l	fg,t	p,h (Nielsson <u>et al.</u> ,1971)
<u>Conomyrma</u> spp.	3-4	s	fg,t	p,h ( " )
<u>Tapinoma</u> <u>melanocephalum</u>	1-2	l,a	fg,t	p,h (Carroll, 1970)
<u>Brachymyrmex depilis</u>	1-2	s,l	fg	p,h (Whitcomb <u>et al.</u> ,1972a)
<u>Camponotus castaneus</u>	6-10	s,l	fg,t	p,h
<u>C. floridanus</u>	6-10	s,l	fg,t	p,h (Nielsson <u>et al.</u> ,1971)
<u>C. socius</u>	7-11	s	fg,t	p,h
<u>C. (Myrmentoma) sp.</u>	5-7	a	fg,t	p,h
<u>C. (Colobopsis)</u> <u>impressus</u>	3-5	a	f,t	p,h (Nielsson <u>et al.</u> ,1971)
<u>Paratrechina</u> <u>(Nylanderia) spp.</u>	2-3	s,l	fg,t	p,h ( " )
<u>Prenolepis imparis</u>	3	s	fg,t	p,h ( " )
<u>Lasius alienus</u>	3	s,l	fg,t	p,h
<u>Formica archboldi</u>	6-7	s	fg,t	p,h
<u>F. pallidefulva</u>	6-8	s	fg,t	p,h

Table 5. Success of A. ashmeadi and ants neighboring an A. Ashmeadi nest in finding and removing dead house fly (Musca domestica) baits various distances and angles from the A. ashmeadi nest entrance.

Species	Number of times first attacking bait at distance in cm from entrance						Total Number of times first ant attacking bait
	0	15	21.2	30.0	33.5	42.4	
<u>Pheidole metallescens</u>		1		2	4	2	9
<u>APHAENOGASTER ASHMEADI</u>	1	2	1	1	2	1	8
<u>Pheidole dentata</u>		1	2		2	1	6
<u>Hypoponera opaciceps</u>			1				1
<u>Solenopsis geminata</u>				1			1

Species	Number of times first attacking bait	Number of times able to remove bait to nest	Returned nest with bait taken from other ants
<u>Pheidole metallescens</u>	5	1	<u>A. ashmeadi</u> (4 times)
<u>P. dentata</u>	4	0	" (4 times)
<u>A. ASHMEADI</u>	2	2	0

Species	Number of times first attacking fly head	Number of times able to remove it to nest	
<u>P. metallescens</u>	5	1	<u>A. ashmeadi</u> (1 time) <u>P. dentata</u> (3 times)
<u>P. dentata</u>	2	2	0

Other ants nesting or foraging within a 42.4 cm radius of A. ashmeadi nest entrance

<u>Pheidole morrisi</u>	<u>Conomyrma flavopecta</u>
<u>Pheidole floridana</u>	<u>Prenolepis imparis</u>
<u>Cardiocondyla sp.</u>	<u>Formica pallidefulva</u>
<u>Trachymyrmex septentrionalis</u>	

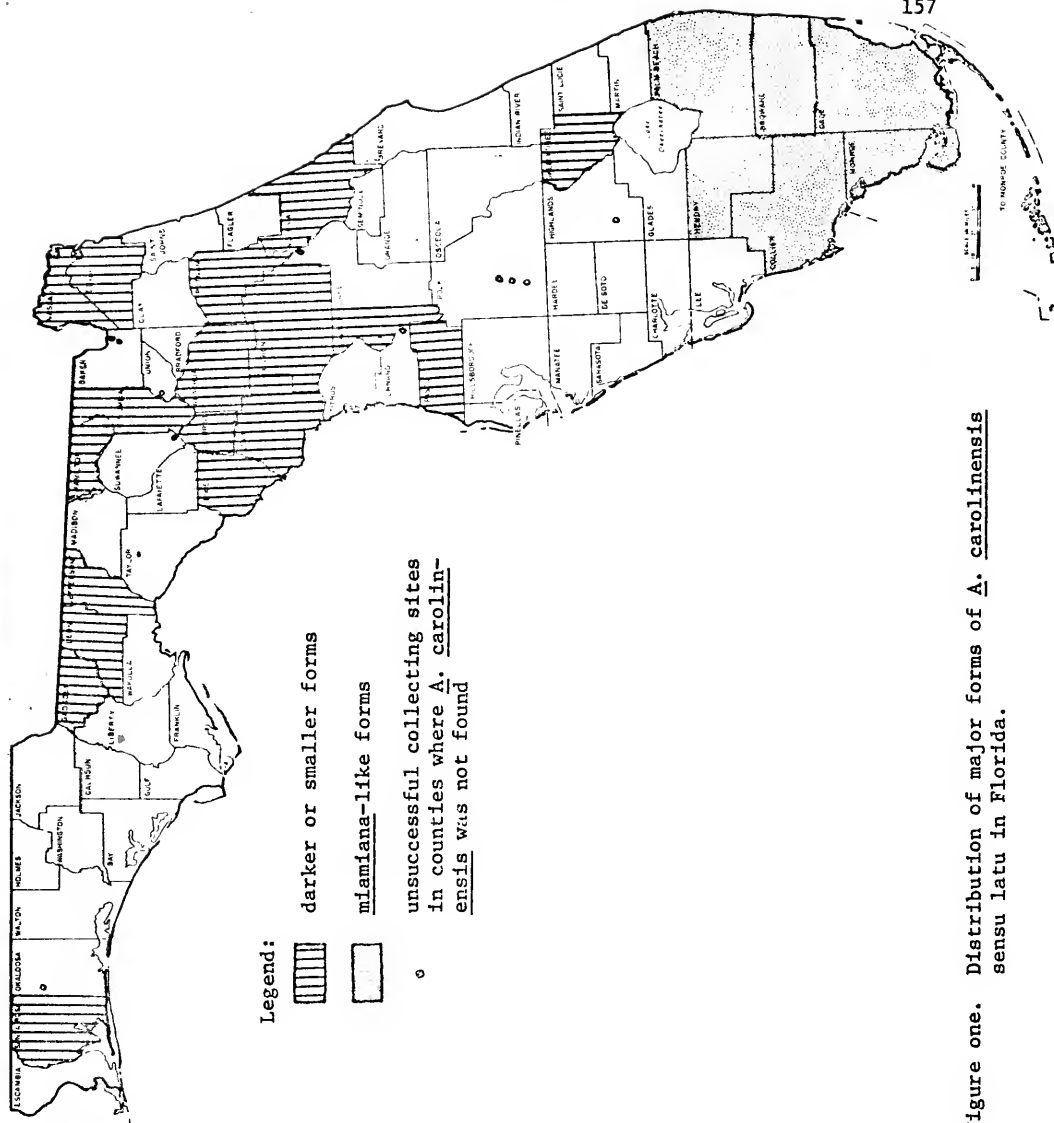


Figure one. Distribution of major forms of *A. carolinensis* sensu lato in Florida.

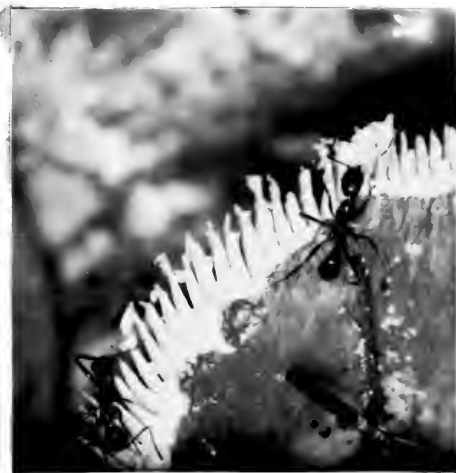


Figure two. Workers of A. ashmeadi removing pieces of cap of fruiting body of the mushroom Russula pusilla.

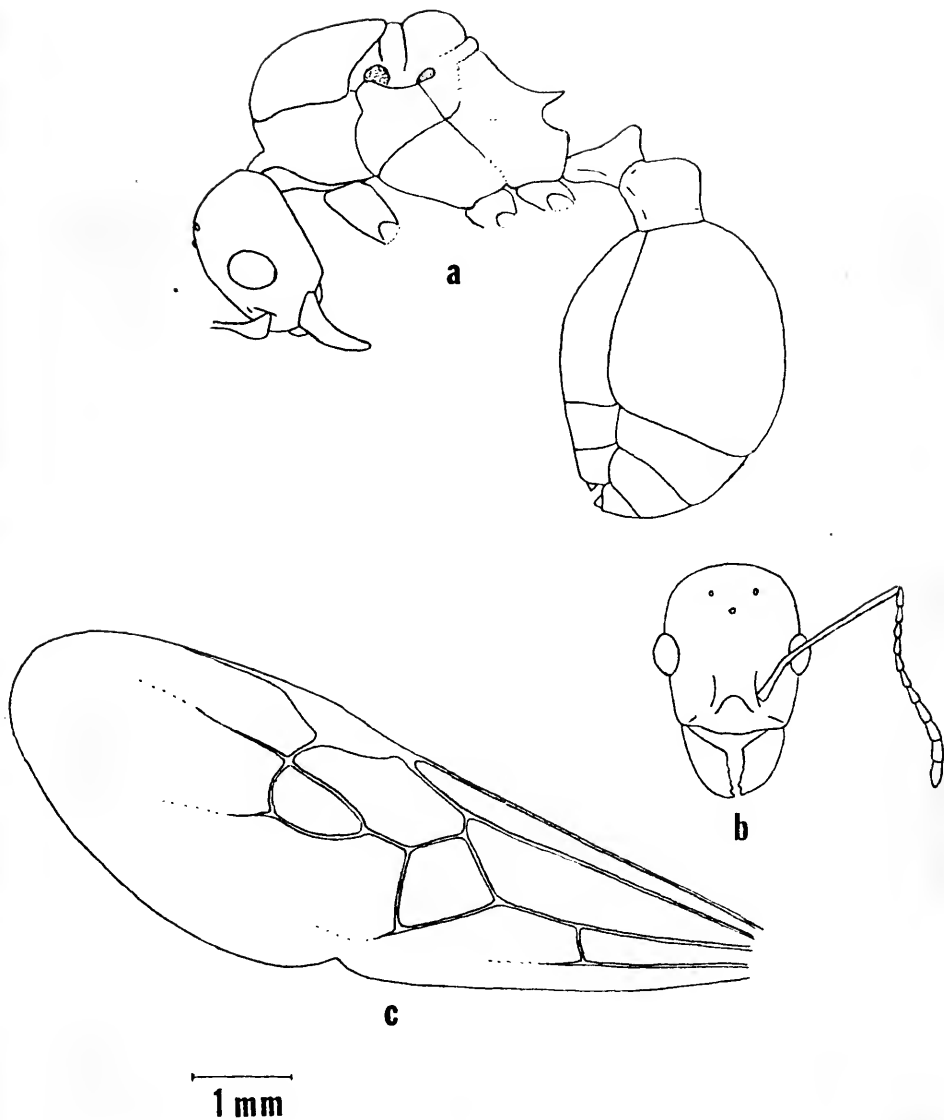


Figure three. Female of A. ashmeadi. Note flattened lobe on base of antenna.

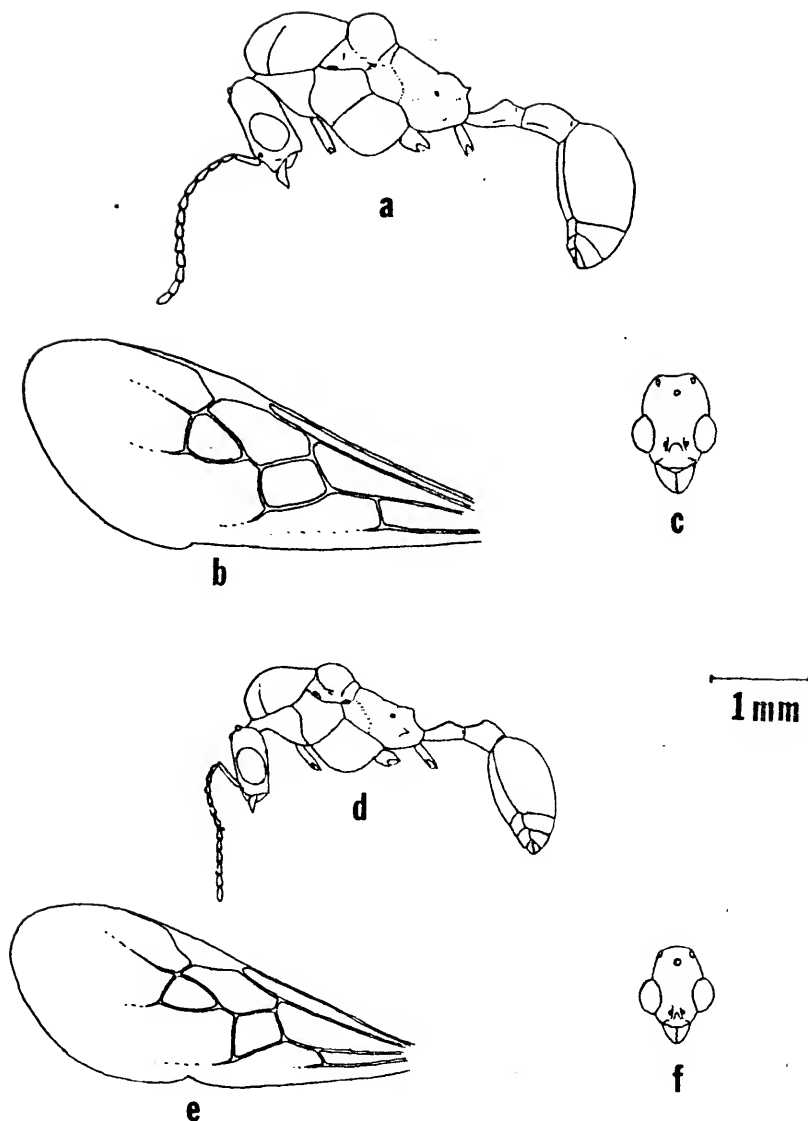
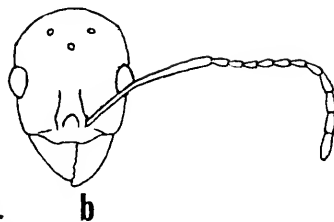
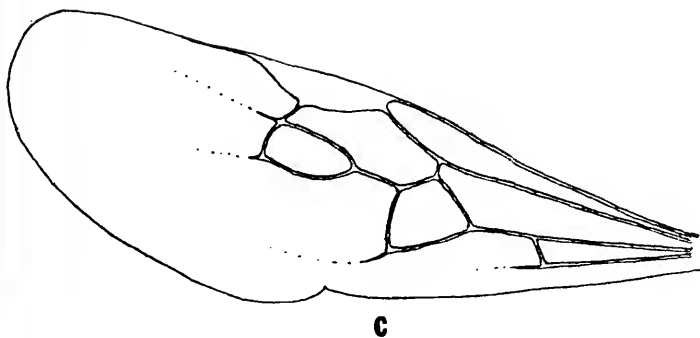
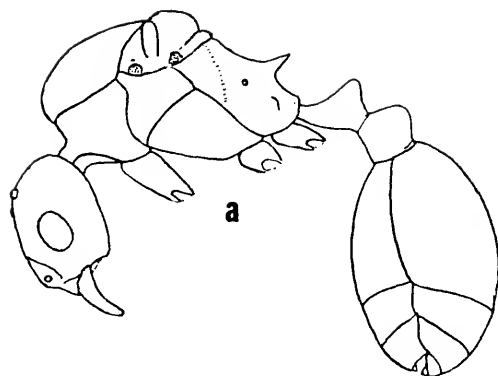


Figure four. Male of *A. ashmeadi* (a,b,c) and male of *A. carolinensis* (d,e,f). Propodeal spines of *A. carolinensis* males sometimes longer than in specimen depicted.





1 mm

Figure five. Female of *A. carolinensis*.

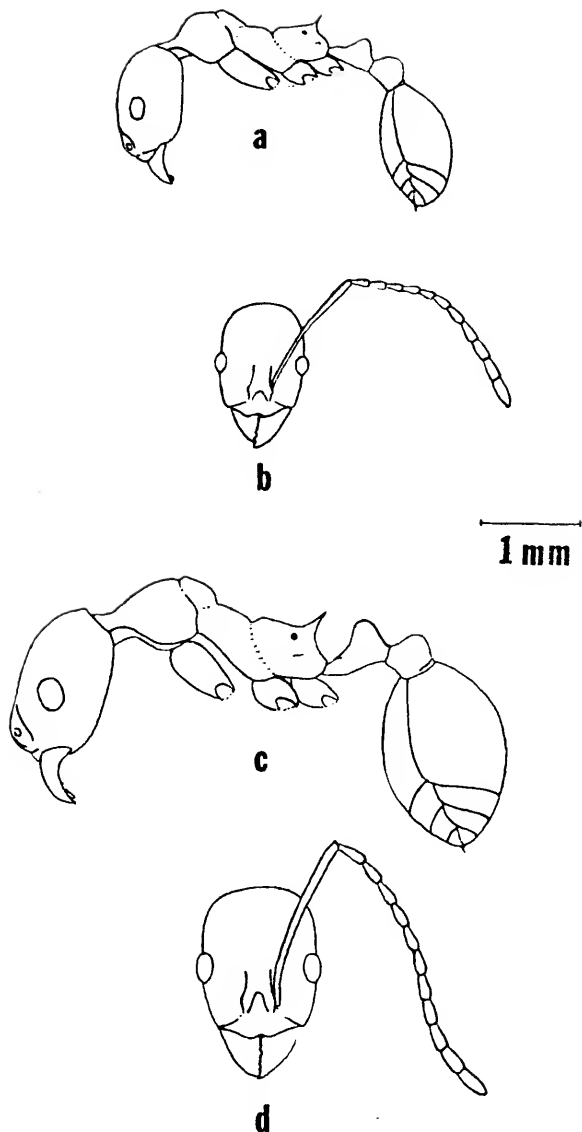


Figure six. Worker of miamiana-like form (c,d) of A. carolinensis from Key Largo and worker of north Florida form (a,b) more closely resembling typical A. carolinensis from North Carolina. Note proportionally larger compound eyes and wider head of miamiana-like form.

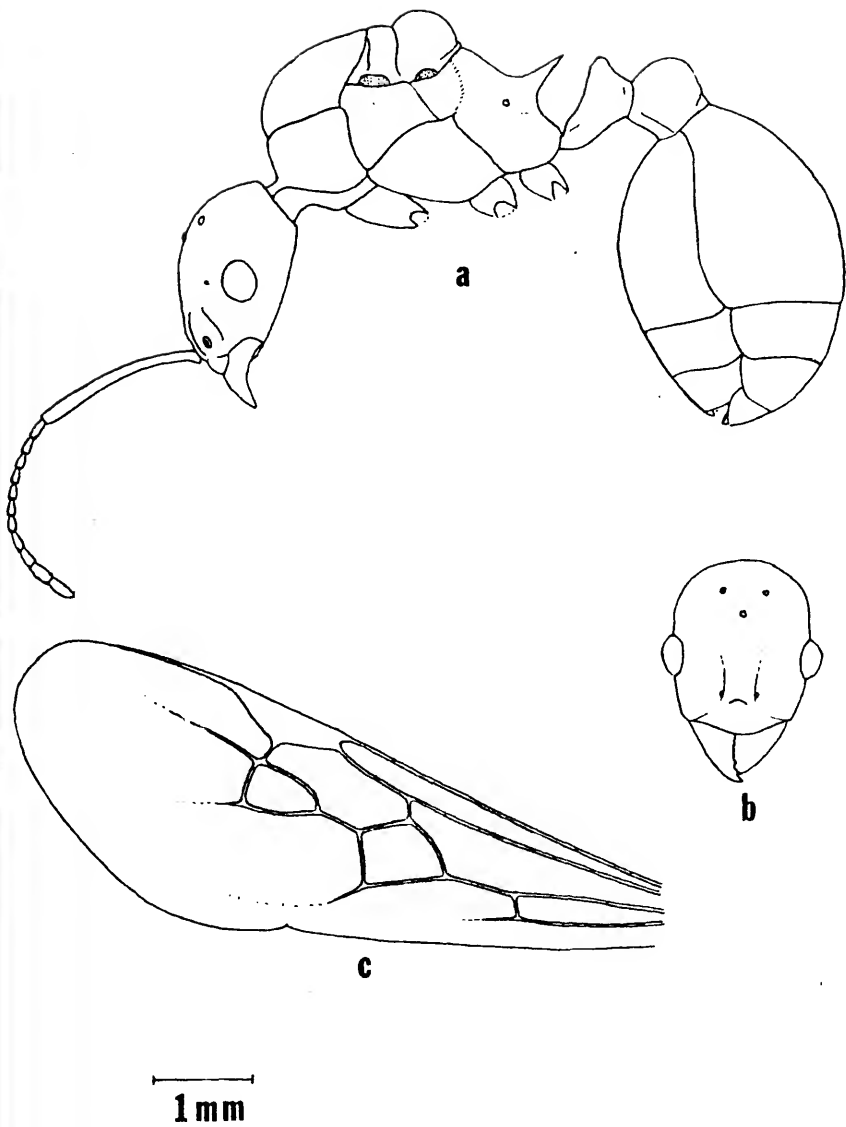


Figure seven. Female of *A. flemingi*. Note long propodeal spine (a).

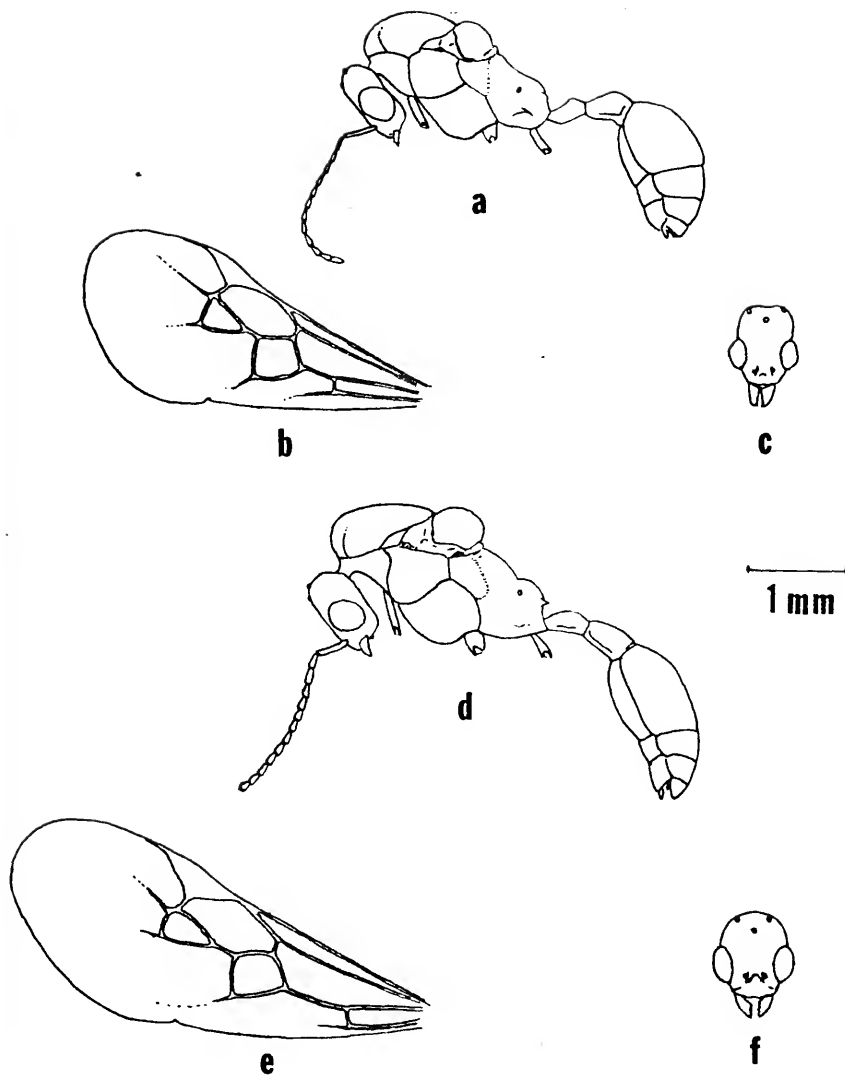


Figure eight. Male of A. flemingi (a,b,c) and male of A. floridana (d,e,f). Note propodeal spine on A. floridana (d); workers of A. floridana lack propodeal spines.

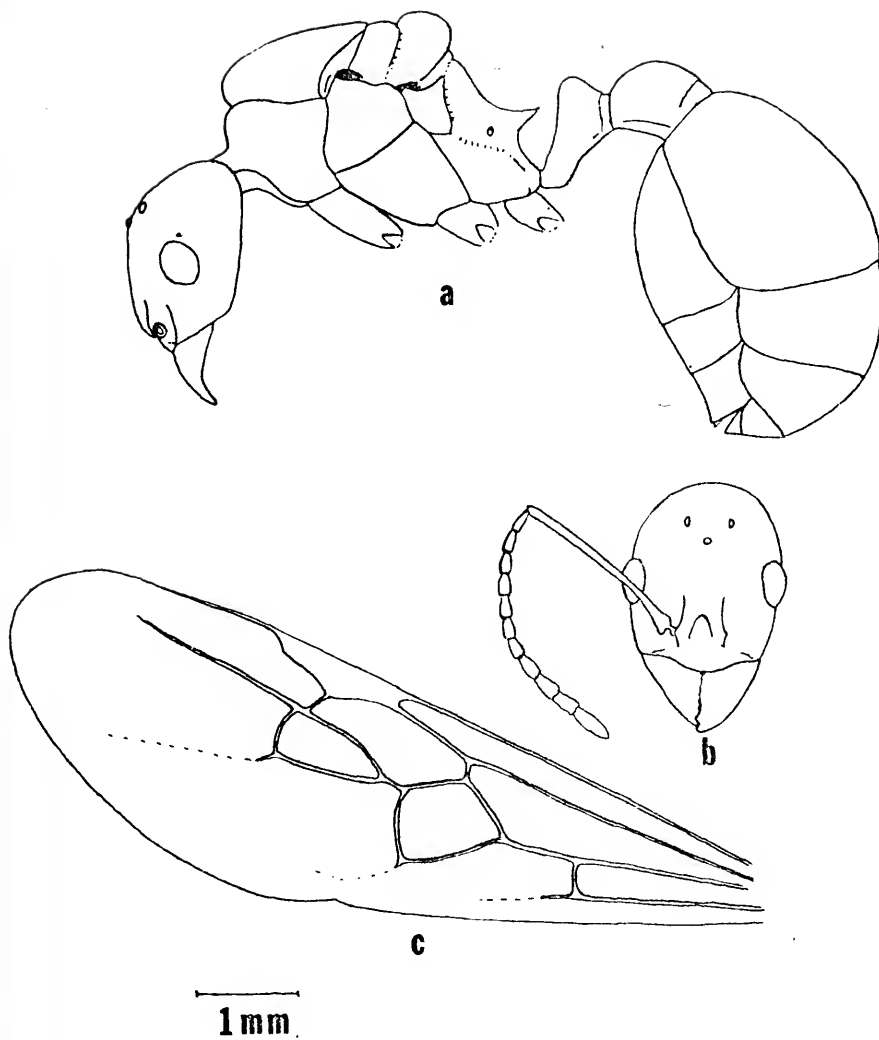


Figure nine. Female of A. floridana. Workers of this species lack propodeal spines present in female (a).



Figure ten. Nest entrance of an A. floridana colony. Note debris surrounding entrance.

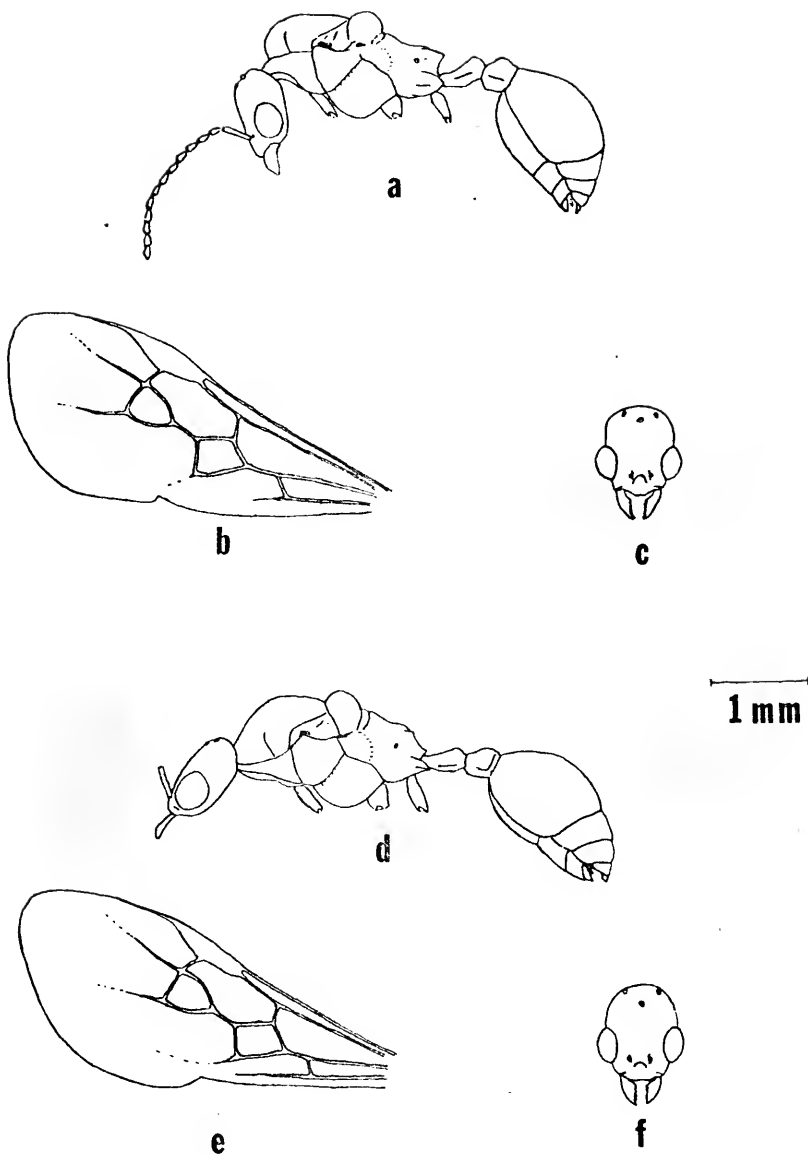


Figure 11. Male of *A. tennesseensis* (a,b,c) and male of *A. mariae* (d,e,f). Males of both species notable for having wide heads, short postpetioles and well-developed latero-ventrad protuberances on alitrunk.



a



b

Figure 12. (a) Three species of Aphaenogaster were found nesting in the pictured portion of turkey oak woodland; A. floridana in the open sand in the foreground, A. treatae in the moderately littered area near the center of the picture and A. ashmeadi beneath the dense wax myrtle bush in the upper right.  
(b) A. ashmeadi, A. flemingi, A. floridana and A. treatae were found nesting in this second growth woodland.



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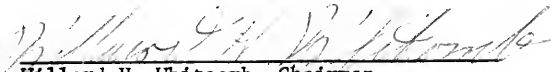
#### BIOGRAPHICAL SKETCH

John F. Carroll was born August 14, 1945, in Poughkeepsie, New York. He attended public grammar school in Poughkeepsie. In June, 1963, he graduated from Our Lady of Lourdes High School, Poughkeepsie.


He attended St. Bernardine of Siena College, Loudonville, New York, from 1963 to 1967. He received a BA in English in June, 1967.

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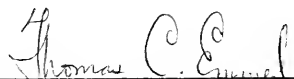
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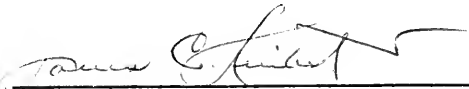
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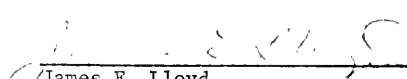
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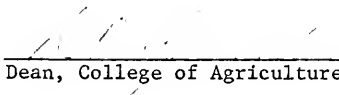
  
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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