CHAPTER 23

Nesting, Emigrations, And Colony Foundation In Two Group-hunting Myrmicine Ants (Hymenoptera: Formicidae: *Pheidologeton)*

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Abstract

The myrmicine ants *Pheidologeton diversus* and *P. silenus* are known to forage by group hunting, as do army ants (Dorylinae and Ecitoninae). Yet there is no evidence that other traits believed to typify army ants, notably nomadism and colony fission, are characteristic of these species. Even large *diversus* colonies probably emigrate on occasion, but some colonies reside at given sites for at least a year. After mating flights, *P. diversus* gynes shed their wings and dig subterranean chambers in which they remain and lay their eggs, supporting the view that nest founding is claustral. Both species usually nest in the ground, with colony size reaching in excess of 100,000 workers in *P. silenus* and at least 250,000 in *P. diversus*. Polygyny occurs in both ants, but many colonies appear to have a single queen.

Introduction

This paper considers aspects of nesting behavior and emigrations in the ants *Pheidologeton diversus* and *P. silenus*. Information on the habitats selected by these ants will also be presented. These species are the only members of the largest of the formicid subfamilies (Myrmicinae) to have been shown to hunt for food in groups (Moffett 1984, 1987). While recruitment to food over a distance is widespread in ants, group hunting is uncommon, having been documented for army ants (Dorylinae and Ecitoninae) and certain ponerine genera (Gotwald 1982, Moffett 1984). The current results indicate that despite convergences of *P. diversus* and *P. silenus* foraging activities to army ants, these species have not adopted other attributes considered wide-

spread or universal in army ants, such as nomadism or colony fission (Gotwald 1982).

Methods

P. diversus ranges in the East Indies from India to south China, Taiwan, the Philippines, and Indonesia. *P. silenus* is restricted to the Malay Peninsula, Sumatra, Java and Borneo. The results given here are based on observations in the course of 28 months of research in 12 countries within the range of both ants. The major focus of behavioral studies on these species concerned foraging, but information pertaining to the subjects covered in this report were obtained whenever possible.

To determine nest structure, colony size, and queen number, 27 *P. diversus* colonies and 7 *P. silenus* colonies were excavated at a variety of localities. Nine *P. diversus* excavations and one *P. silenus* excavation were incomplete, while the others were more thorough, uncovering all but perhaps the most peripheral nest chambers. Colony sizes were determined after certain excavations by counting the number of ants in given fractions of the nest soil.

Several attempts were made to keep *P. diversus* colonies or colony fragments in captivity in 20 gallon aquaria with soil, or in test tubes with a stoppered water source. Workers took little food in captivity and minor workers and larvae died off rapidly. Successful maintenance of *P. diversus* ants will apparently at minimum require greater space for both nesting and foraging.

Emigrations were documented with photographs and by determining the rate of worker and brood flow at set time intervals. Colony stability was studied by documenting the location of given colonies in Singapore for 5 months or more.

Alates were found at street lights and during emergence from nests in Singapore. Dealate gynes were collected at these locations and kept in captivity to observe colony founding behavior.

Additional information on methodology are given as required in the sections that follow.

Results

Habitat selection

P. diversus colonies occur in diverse habitats throughout most of the species' range. The ants can be found in primary and secondary rain forests, fields of rice, rubber, coconut and other crops and even in parks and gardens in some cities. *P. silenus* is common in rain forests, and is not found in very disturbed habitats, except sometimes near the margins of forested habitats. Curiously, *P. diversus* is absent from most forests in Peninsular Malaysia, where this species' range overlaps with that of *P. silenus*. Forested areas where it is found are either marginal habitats or isolated, disturbed habitats lacking *P. silenus*, suggesting the possibility that *P. silenus* displaces *P. diversus* at most relatively undisturbed sites. Unfortunately, no interactions between *P. diversus* and *P. silenus* have been recorded in nature.

There is probably intense competition between species of *Pheidologeton* (particularly *P. diversus*) and *Pheidole* ants. Most *Pheidole* species scavenge for a variety of foods such as seeds and insect remains, and thus have a broad dietary overlap with *Pheidologeton*. *Pheidole* is one of the dominant ant genera in most habitats worldwide (Wilson 1976). However, *Pheidole* are usually uncommon at sites of abundant *P. diversus*. For example, *P. diversus* is abundant at the Malacca Zoo and Singapore Botanic Gardens, which harbor rich food sources. *Pheidole* ants occur at these localities but are inconspicuous and comparatively rare, particularly in areas of concentrated *P. diversus* nests. Yet at similar habitats where *P. diversus* is lacking, such as the Jurong Bird Park in Singapore and Botanic Gardens in Bogor, *Pheidole* ants are conspicuous, including species with trails resembling *P. diversus* trunk trails rarely common where *P. diversus* occurs (e.g., *P. megacephala* and *P. plagiaria*). I have repeatedly observed *P. diversus* ants drive various *Pheidole* species from food. It appears likely that competition between species of *Pheidologeton* and *Pheidole* influence the local distributions of both groups.

Nesting behavior and colony size

Most *P. diversus* colonies nest in the ground, often at or near tree bases. One Indian colony and a colony from Luzon (Philippines) nested throughout massive logs in the zorapteran stage of decomposition (Wilson 1959). Some colonies nested within the decayed interiors of standing trees, but in these cases part of the nests usually occurred in the ground at the base of the tree.

The location of a *P. diversus* nest is revealed by the presence of exits leading to one to three middens. Workers often use separate exits to throw out soil, in some cases forming cones or ridges. One or two entrances serve as starting points for stable foraging routes called trunk trails (Moffett 1987). For most colonies all entrances occur within an area of 0.4 m^2 (excluding entrances for trails that run for some distance underground before surfacing). A large colony in Peninsular Malaysia had numerous entrances within an area of between 3.5 and 4.0 m^2.

The bulk of the nest chambers generally lie within 80 cm (usually 50 cm or less) of the surface, although in some cases isolated chambers can be found further below ground. Almost invariably nests have a central 'core area', which houses most of the brood and the queen. Often the core area consists of large cavities of irregular size and shape, which in many cases had clearly been present prior to the arrival of the ants. Cavities can include apparent vertebrate burrows, remnants of termite nests, hollowed dead roots, and even buried bottles and cans. These cavities are often partially filled with a mass of more or less indiscriminately mixed brood lying many layers deep.

Around the core area are numerous smaller chambers typically packed with replete workers (although other ants and some brood are present). These satellite chambers can at times be found as far as 1.5 m from the core area.

P. silenus colonies apparently always nest underground. Excavated nests are similar to those of *P. diversus*, but the core area tends to be ill-defined. Nests are harder to locate than is the case for *P. diversus*, since the conspicuous surface middens typical of *P. diversus* are absent in *P. silenus*.

Limited observations were made on captive *P. diversus* nest samples, particularly from a nest collected in Thailand (colony number 18-83). I observed trophallaxis between minors, and between minors and non-minors (medias + majors) or the queen. The queen, alates, and non-minors were often densely covered with minor workers, which often allogroomed them. As is apparently the case under natural conditions, minor larvae were in large piles, with pupae and clumps of eggs and microlarvae interspersed among them; larger (non-minor) larvae and pupae were often clumped together but not cleanly separated from the minor brood.

Many non-minors were buried within masses of brood, where they remained immobile for hours at a time. These were often, but not invariably, repletes. Minors often stayed immobile also, and many of these stretched themselves between large individuals in the nest (non-minor adults or immatures) so as to link them together. Usually the fore legs held the forward individual and the hind legs were sharply extended to grip the individual behind; the middle legs could grip either individual. Rows of such minors sometimes formed linking two given individuals, in which case most of the ants usually faced the same direction.

Estimates of colony size for three *P. silenus* colonies from Gombak, Malay Peninsula were 64,000, 93,000, and 127,000 workers. A colony of this species from Sarawak (number 37-83) had only about 5,000 to

8,000 workers. *P. diversus* colony number 18-83 from Thailand was estimated to have nearly 110,000 workers; three colonies from Singapore had about 85,000, 183,000, and at least 250,000 workers. Many of the other excavated *P. diversus* colonies were probably within this size range, but some colonies could have been appreciably larger.

Number of queens

Most *P. diversus* colonies probably have one queen. The only possible instance of multiple functional queens in this species was the discovery of two dealates from a partial excavation of Singapore colony number 32-83. Conceivably other cases of polygyny were overlooked, since many excavations were incomplete, and queens were difficult to find in the masses of excavated soil.

Three large, completely excavated *P. silenus* colonies from Gombak (Malaysia) each had a single queen, and a single queen was also taken during a partial excavation of another large colony from southern Borneo. However, 23 dealates were found in colony number 37-83 from Sarawak, which contained only a few thousand workers. When 17 of these queens were kept in captivity, they clustered together and showed no overt aggressive behavior. During the excavation most of the queens appeared to be located close together within the nest.

Four instances were documented for *P. diversus* of apparent queen rejection by her colony, three in Singapore (colony numbers 49-82, 55-82 and 57-82) and one in northern Sulawesi, Indonesia (colony number 60-83). Each colony was large and apparently thriving. The queens were found near the side of each colonies' major trunk trail, from 0.5 to 3 meters from the nest; the queen at colony 57-82 was in a refuse pile. In each case the queen was pinioned by minor workers, while other minors carried soil to the site and dropped it on her (Figure 1). Two of the queens were slowly dragged further from the trunk trail, and one was nearly dead and virtually abandoned when discovered. When placed on the trunk trail they were dragged off to the side again. The queens were dealate, and all were darkly pigmented and had badly worn mandibles and abraded pilosity suggestive of old age. It is presumed that the queens had been dragged from the nest; expulsion of a gynandromorph by minors from the nest of colony number 63-82 was seen in Singapore. (Rarely minors directed similar aggressive behavior at non-minors on trails, but in this case the ants were often dragged towards the nest; majors introduced from other colonies were dragged along trails in the same way.)

Emigrations: frequency and causes

While it is not difficult to locate emigrations of *P. diversus* colonies in nature, there is no evidence to suggest such emigrations occur frequently or on a regular basis. Six marked *P. diversus* colonies in Singapore were examined periodically for four months, during which time only one emigrated. Returning to the same area one year later, however, I found colonies at only three of the same sites (it was not known whether these were the same colonies). Extended observations on given *P. silenus* colonies have not yet been made, and could yield interesting results.

While the gasters of *P. silenus* (and particularly) *P. diversus* queens are massive, queens do not progress through the alternate physogastric and contracted states typical of army ants (Gotwald 1982). The brood of *P. diversus* are not synchronized, and emigrations differed in the proportions of larvae and pupae (from 9% to 57% pupae in five samples). Thus it seems unlikely that emigrations are triggered by events in brood development.

When emigrations of *P. diversus* did occur it was usually difficult to attribute a cause. For example, Indian colony number 05-82 took in abundant food from a cattle pen up to the time it emigrated, even though the emigration took it into a relatively food-poor area. Colony 49-82 from Singapore took abundant food during a month of study, including on average about 200 gm of seeds given to it in baits during the three days prior to its emigration. Conversely, colonies that were severely disturbed during partial excavations involving removal of large samples of workers and brood did not emigrate in the subsequent weeks.

At least some emigrations may be the result of adverse conditions. Emigrations of *P. diversus* were observed exceptionally often in India, perhaps because conditions during the study in the dry season severely limited food availability. Villagers in India and Thailand have told me that *P. diversus* colonies emigrate into the crowns of palms when flooding occurs during the rainy season. One emigration in Singapore could have been triggered by fights with another colony at food, but similar fights of greater intensity were not followed by emigrations at any other time.

I know of at least six cases in which a given site was occupied by more than one colony. In one case a colony emigrated an unusually short distance of 8 m, then returned to the original site within about two weeks. Frequent re-use of previous nest sites suggests that possible nest sites with cavities suitable for occupancy may often be in limited supply.

Emigration behavior

In both species emigrations took place over trunk trails used previously for foraging. Emigration behavior in *P. diversus* from the Malay Peninsula was difficult to document because most emigrations followed subterranean trails or surface trails hidden from view by leaf litter or vegetation. Most brood and repletes were transferred at night, apparently sometimes within one night, but usually over at least two or three nights. Worker flow continued on well-protected emigration trails during the day. Repletes moved under their own power and were densely covered with minors. Minor worker immatures were carried by single minors, while larger brood were transported by groups of minors, or sometimes by minors assisted by medias or by unassisted medias. On occasion adult transport of one minor by another was seen (and was also observed rarely along foraging trails).

The two *P. diversus* emigrations followed in most detail occurred in south India, one (colony number 01-82) over a distance of about 62 m, and the other (colony 03-82) over at least 34 m. In both cases most of the routes proceeded over bare ground. In the first case the emigration required at least six nights, with the transport of massive quantities of brood during the first four nights (most repletes emigrated in the first three nights). The second emigration required three nights. In both cases brood transport continued into the morning (at least 0900 hours). Between periods of emigration numerous immatures and repletes were stockpiled under a fallen banana plant, beneath leaves and piles of nuts, and at underground sites along both routes.

During brood transport unburdened ants left the trail to patrol the area within a space 10 to 15 cm from either side of the emigration route. The workers drove away ants and other insects that approached the trail, and killed some of them; even slight disturbances near the trail disrupted emigration activities for up to 15 minutes and caused more ants to join the patrollers. Patrolling ants were most numerous in *P. diversus* emigrations in India. Patrolling occurred during Malayan emigrations where the routes crossed bare ground, but in vegetated or litter-covered ground such ants were less numerous or absent. Patrolling ants included workers of all sizes, but not repletes or teneral ants.

Only one *P. silenus* emigration was documented (colony number 23-83). The transfer of repletes and brood basically required a single night, although the emigration trail remained in use during the subsequent two days, during which time a few immatures were carried. The emigration was watched along a 14 m section of trail on the ground surface. The total length of the emigration route was un-

known, since neither the old or the new nest site was located. The behavior of the emigrating ants was very close to that described for *P. diversus*, except that very few medias assisted minors in carrying brood (a few carried small larvae). There were large numbers of aggressive ants patrolling as far as 40 cm to either side of the route. Non-minor brood, repletes, and teneral majors were most numerous late in the emigration.

The *P. silenus* emigration is the only case in which a queen was observed. The queen appeared at 23:15, when perhaps half the brood had been transferred. She moved quickly and without hesitation, accompanied by a retinue of 500 to 700 unburdened minors. This retinue extended from 5 to 7 cm ahead of her and approximately the same distance behind her. More minors were located up to 1.5 cm out from her sides, so that the column swelled visibly as she passed. While movement on the trail was normally bidirectional, all ants in the retinue moved in the same direction as the queen. Numerous additional minors rode on the queen's body.

Flights of alates

Flights of *P. diversus* alates were recorded at night in May during both 1982 and 1983 in Singapore, when there were heavy rains almost daily. Workers of all sizes swarmed over the ground near nest entrances of colonies with emerging alates; these patrolling ants were unusually sensitive to disturbances. Alates emerged from entrances that had been greatly enlarged: normally entrances were not much wider than needed to permit the largest majors to pass through (<1 cm diameter) but at this time many entrances were 1.5 - 4 cm wide. Numerous medias and majors and some minors repeatedly accumulated around these entrances (Moffett 1987) and then retreated. Increases in these 'guards' took place when alates approached an entrance. when foreign insects (including *P. diversus* alates from other colonies) were dropped within ca 25 cm of an entrance, many of the guard ants at that entrance often came forward to join the patrolling ants in attacking them.

Five *P. diversus* nests were partially excavated on the same day during a period of alate emergence. Numbers of alate adults and pupae in collected samples from each colony were: 43 gynes and 0 males; 1 gyne and 28 males; 5 gynes and 7 males; 8 gynes and 12 males; 0 gynes and 0 males. Thus some colonies seem to specialize predominately on one sex or another, at least at a given time. The fifth colony had no alates or reproductive brood, and was the only colony selected lacking enlarged nest entrances. The larvae and pupae of sexuals and

a mix of worker immatures were found in the colonies harboring alates, and thus a synchronized all-sexual brood was apparently not produced.

In one colony monitored continuously from 2130 to 2400, three gynes left the nest at well-spaced intervals, climbing the trunk of the tree where the colony was based. Initially these were covered with minor workers, but the minors climbed off as they ascended the trunk. The first gyne flew away when it reached a height of about 50 cm; the other two were collected.

Alates came to street lights in Singapore. Some males moved about rapidly on the ground under the lights. others were found in clumps of up to 30. These stayed quiescent even when numbers of *Oecophylla smaragdina* workers dragged adjacent males away, but attempted to fly when disturbed directly.

Three balls of 2 to 4 males around single alate gynes were found beneath street lights. In one case, one of the males was copulating with the gyne. Another gyne was found mating with a solitary male. Other alate gynes were kept in containers with a water source for 1 to 3 days with one or more males, but mating was never observed in captivity (under these conditions males lived for at most two days).

Colony founding

No incipient colonies of *P. diversus* or *P. silenus* were located in nature. Attempts at finding such colonies included the placement of baits of vegetable oil or honey at 117 sites in the Singapore Botanic Gardens, which is rich in *P. diversus*. Some baits were put on islands in the Gardens lacking large *P. diversus* colonies. Baits were checked two to eight times a day for two to four days, but all *P. diversus* feeding at them were clearly members of large colonies. Yet the evidence presented below suggests *P. diversus* shows the claustral mode of colony foundation typical of most ants.

P. diversus gynes which were dealate when collected under lights or which became dealate after being kept with males were maintained in plastic containers. These held either a 3 cm layer of soil, or a test tube with stoppered water source. Of a total of 16 gynes, eight died within four days. Five gynes given test tubes apparently never left their tubes (except for one case of about thirty minutes), almost invariably staying in the portion of the tube covered with red cellophane. All laid eggs, with the number of eggs rising to about 50 to 250. In addition, three gynes provided with soil quickly dug chambers with small openings to the surface, in which they stayed. At least two of

these laid eggs. Unfortunately, all of the gynes died after three to nine weeks, and none was ever observed with larvae.

Unlike dealate queens taken during nest excavations and kept without workers, the freshly dealate gynes consistently refused to feed on vegetable oil or sugar. They maintained a characteristic posture. Their gasters were held vertically and most or all of the eggs were stuck together in a mass that was attached to the gaster on the fifth or sixth sternum (Figure 2). Most of the gaster is hairy, including the forth sternum. However, the fifth and sixth sterna are bare, which presumably aids egg adhesion. Sometimes the eggs came loose from the gaster and fell to the floor of the gyne's chamber. Typically the gyne soon picked up the mass with her mandibles or between her foretarsi and repositioned it on the gaster surface. A freshly laid egg or other loose egg was added to the gaster in the same manner.

The gynes had to raise themselves high on their legs to keep the gaster oriented vertically or slung beneath the alitrunk (Figure 2). This made movement awkward. Gynes were usually quiescent, but they could walk short distances and sometimes carried soil or tufts of cotton.

In one case two gynes were kept in the same container. Both moved into the test tube provided. There was no sign of aggression between these gynes, even though they were often in physical contact. Usually there was one major egg mass, which was held at various times by both gynes. Isolated eggs were also picked up, apparently indiscriminately, by either gyne. It is possible, however, that one gyne was laying most or all of the eggs; this gyne held the major egg mass perhaps 80% of the time.

Alate gynes taken from nests or at lights consistently had crops greatly expanded with an oily (Sudan Black positive) fluid of the same orange-yellow color found in the crops of worker repletes. The remainder of the gaster was invariably packed with fat bodies. In comparison, two dealate queens taken during nest excavations had nearly empty crops and few fat bodies.

Discussion

How far have *P. diversus* and *P. silenus* gone in their convergences with army ants (Dorylinae and Ecitoninae) in terms of behavioral attributes other than raiding activities? The answer seems to be very little. As discussed below, most aspects of nesting behavior in these species do not appear to have been altered greatly from that typical of many other myrmicine groups.

The nests (or bivouacs) of army ants are generally more or less temporary, and indeed in a minority of species (Gotwald 1982) a functional cycle has developed with distinct nomadic phases in which colony emigrations occur in a predictable fashion (Schneirla 1971). Nomadism probably evolved in response to the eventual depletion of food in the vicinity of the nests of these efficient predators (Wilson 1971). Some army ants, however, can stay at one location for months at a time; e.g., certain species of *Labidus* (Ihering 1912, Borgmeier 1955) and *Anomma* (Raignier and Boven 1955, and W.H. Gotwald, Jr., pers comm). The emigration frequency in most ants is probably often much lower than in many army ants.

Certain features of both *P. diversus* and *P. silenus* are suggestive of species prepared to shift their nest sites as needed. The partial reliance of many colonies on available cavities presumably reduces the need for nest construction and often gives nests a 'temporary' appearance. *Pheidologeton* queens, like those of army ants, have robust waists and large gasters, and strong legs that permit rapid locomotion during nest changes. The well-developed retinue accompanying the emigrating queen of *P. silenus* is also reminiscent of army ants (Rettenmeyer et al 1978). Indeed enough *P. diversus* emigrations have been observed to suggest most if not all full-grown colonies emigrate occasionally. Yet, probably colonies often remain at given sites for a year or more, and thus have nests more stable than have been documented for any army ant. Further long-term studies are needed on both *Pheidologeton* species to clarify how often and why colonies emigrate.

At least a minority of *P. diversus* and *P. silenus* colonies are polygynous (although the existence of functional polygyny, i.e, the occurrence of more than one egg-laying queen, remains to be determined with certainty). Hölldobler and Wilson (1977) hypothesize that polygyny has arisen primarily in species occupying either short-lived nest sites or long-lived, patchily-distributed sites. Neither description seems to apply to *Pheidologeton*. Perhaps polygyny represents a form of protection against colony fragmentation during nest emigrations, as Rettenmeyer and Watkins (1978) proposed for the only known polygynous army ant, *Neivamyrmex carolinensis*. More probably polygyny in *P. diversus* and *P. silenus* could result from pleometrosis (nest founding by multiple queens) with subsequent reduction to a single queen in most cases. This would explain worker attacks on old queens observed in *P. diversus*; similar behavior has been documented in species with pleometrosis (Hölldobler and Wilson 1977, Fletcher and Ross 1985). Two young *P. diversus* queens kept together in captivity remained near each other and tended the same eggs. Such pleometro-

sis, if it occurs in nature, would accelerate early colony growth. Rapid growth could be crucial, since both species depend on the coordinated action of worker groups during foraging.

The colonies of army ants reproduce through colony fission (Gotwald 1982), a method of colony founding often termed swarming (Hölldobler and Wilson 1977). There is no evidence for swarming in either *P. diversus* or *P. silenus*. Both species produce alate gynes. Documentation of flights of *P. diversus* gynes and the occurrence of groups of *P. diversus* males on the ground suggests this species shows the male aggregation syndrome typical of most ants with independent colony foundation (Hölldobler and Bartz 1985).

Successful brood rearing did not occur in my captive gynes. Yet evidence for claustral nest-founding includes the food reserves carried by alates, the chambers dug by gynes upon shedding their wings, and the stereotyped behaviors gynes use in attaching eggs to their gasters. The function of holding brood on the gaster surface is uncertain, but at minimum it probably reduces incidences of lost or trampled brood, and permits the queen to keep her brood relatively clean. It is clearly not a very effective method of transporting brood.

Mr. G.H. Lowe, an amateur myrmecologist from Australia, has kindly provided information on *P. diversus* confirming the claustral mode of colony founding. At Niki Sonkurai in Thailand he found a solitary queen in a cavity 25 mm in diameter within moss on a tree stump. The queen had a round mass of eggs with her about the size of a pea. He later induced a freshly mated queen to enter a plaster nest chamber, and this queen successfully reared two workers within 28 days. Mr. Lowe described the queen as holding the ball of eggs between her foretarsi on the upturned gaster (which was slung beneath the alitrunk). The brood stayed on her gaster during much of its development.

The behavior of nascent *P. diversus* and *P. silenus* colonies remains an intriguing unsolved problem. Do ants in small colonies work together in miniature versions of the raiding activities typical of larger colonies, or are they more independent in their foraging activities? The ants in worker samples from large nests often appeared to be more independent, but whether this indicated a fundamental shift in strategy or was a result of a breakdown in colony organization under captive conditions is not known.

Summary

1. *P. diversus* occupies a range of disturbed and undisturbed habitats, while *P. silenus* is restricted to forested habitats. *P. silenus* appears to exclude *P. diversus* from most forests where the range of these species overlap. Evidence is presented that competitive interactions between *P. diversus* (and possibly other *Pheidologeton*) and many *Pheidole* species could affect the local distributions of both groups.

2. Colonies of both *Pheidologeton* species often make at least partial use of previously available subterranean cavities for nesting. These are often located near the central part of the nest harboring the queen(s).

3. Three *P. silenus* colonies ranged from 60,000 to 120,000 workers, and another colony had 5,000 to 8,000 workers. Size estimates for *P. diversus* colonies ranged from 80,000 to 250,000 workers. No small *P. diversus* colonies were located.

4. Most colonies of both species apparently have one queen. One *P. diversus* colony had two queens, and a small *P. silenus* colony had 23 queens. Four cases of the expulsion of old queens from *P. diversus* nests were documented, indicating reduction in queen number (or perhaps queen replacement) can occur.

5. Probably all *P. diversus* colonies occasionally emigrate, but emigrations are not frequent enough to justify calling this ant 'nomadic'. Most likely many colonies often stay in place for at least a year, and conceivably much longer. Available evidence suggests emigrations are not predictably related to food availability or brood development.

6. Flights of alates occur, and at least the species *P. diversus* apparently shows the male aggregation syndrome (Hölldobler and Bartz 1985) typical of many other myrmicines.

7. Nest founding in *P. diversus* is claustral. Young queens attach the brood to their gasters.

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Figure 1. Pheidologeton diversus queen being pinned down by minor workers to the side of the trunk trail of colony number 49-82 in Singapore.

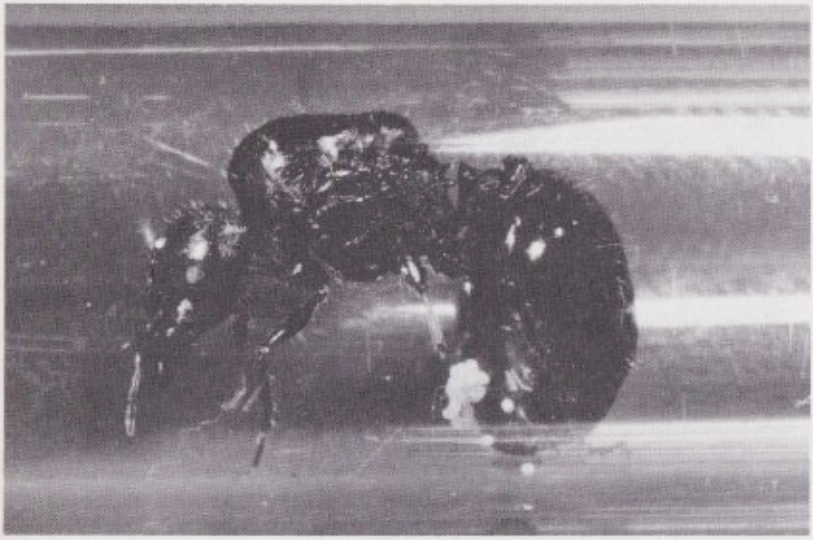

Figure 2. Young Singaporean *Pheidologeton diversus* queen in an artificial nest. Note the egg mass attached to the underside of her gaster.