Protection of Barteria (Passifloraceae) By Pachysima Ants (Pseudomyrmecinae) in a Nigerian Rain Forest

Daniel H. Janzen

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PROTECTION OF *BARTERIA* (PASSIFLORACEAE) BY *PACHYSIMA* ANTS (PSEUDOMYRMECINAE) IN A NIGERIAN RAIN FOREST[1]

DANIEL H. JANZEN[2]

Department of Biology, University of Chicago, Chicago, Illinois 60637

Abstract. In a Nigerian rain forest, occupation of *Barteria fistulosa* saplings by *Pachysima aethiops* ants results in the plants having more leaves, more branches, more leaves per branch, and less damage to the shoot tips than do unoccupied *Barteria*. At present this difference is the result of insect damage to unprotected *Barteria,* but several traits of the ant colony suggest that in the recent past, large browsing mammals may also have been a threat to *Barteria*. These traits include a few large workers per colony, a deeply painful sting, and the habit of frequently dropping from the *Barteria* crown. *Pachysima* workers attack plants adjacent to their *Barteria* and clean the large *Barteria* leaves of debris and epiphyllae.

Each major tropical landmass has a few obligate ant-plants (myrmecophytes). In the wet tropics of western Africa these are *Barteria* (a small passifloraceous tree) and *Vitex staudtii* (a verbenaceous vine). In the dry tropics of eastern Africa, these are swollen-thorn acacias (Hocking 1970). In 1922, Bequaert summarized the literature on *Barteria* and its pseudomyrmecine ants (*Pachysima*[3] *aethiops* and *P. latifrons*). Just as with the neotropical myrmecophytes *Cecropia* and *Acacia,* at the time of Bequaert's writing it was unclear if the ants on *Barteria* are of significance to the plant. They are.

NATURAL HISTORY

The small trees and shrubs in the genus *Barteria* live in the understory of the rainforests extending from the east side of the Dahomey gap (Moreau 1966: 163) through Nigeria, Cameroun, and into the Congo river basin (Bequaert 1922, Hutchinson and Dalziel 1954). The taxonomy of *Barteria* is somewhat confused, and some species may not be myrmecophytes. The present study is only of *Barteria fistulosa* Mast. in southern Nigeria between Benin City and Sapele (Midwest State); *B. nigritiana* Hook. may occur to the northwest (Hutchinson and Dalziel 1954) but was not found in the study area.

Barteria fistulosa is a locally common small tree up to 15 m tall in the heavily shaded understory of the evergreen or semideciduous rainforest of the Sapoba Forest Reserve (plantations and improved natural forest started 1920–30) about 28 km south of Benin City (6° N). When undisturbed, this forest is much like that described for the Okomu Forest Reserve by Richards (1939) and Jones (1955). At Sapoba, *B. fistulosa* is patchily very abundant along trails and in heavily logged sites where it is selectively avoided by natives clearing brush; its natural population structure appears to be that of widely scattered individuals (0.1–10 trees/ha) under a fully developed forest canopy with local high density in the swampy area lining the Jamieson River. Jones (1955) also found it to be most abundant in "gully margin forest" and secondary forest in clearings in mature forest. In contrast to the neotropical ant-plants *Cecropia* and *Acacia,* it is not an emergent and is not an invader of the early stages of old-field succession. At Sapoba, the fruits are borne in March on trees of 8 m or more in height (10 or more years old). Currently the seeds are dispersed only by birds and small mammals, though duiker (*Sylvicapra*) used to feed heavily on the fruits before their local elimination by hunting (Akpobi Omukoro, personal communication).

The seedlings are found in even the most heavily shaded understory. When 1–1.5 m tall they produce their first horizontal branches. These branches are 10–20 cm long, hollow, slightly swollen, and entered by *Pachysima* queens which then develop a young colony. A colony is large enough to begin to patrol the young plant surface when there are about 20 workers (based on 43 young trees dissected in this study). At this time all other queens and incipient colonies are actively removed by the colony (as is the case with the "single-queen" species of neotropical obligate acacia ants (Janzen 1966, 1967*a*). The growth to a colony large enough to patrol the tree requires about a year. The colony then steadily grows until the *Barteria* crown stops increasing in size. The tree grows upward at a rate of 50–100 cm per year. The entire colony with its single queen lives in the live hollow branches, depending on scale insects (Kohl 1909, Bequaert 1922) and fungus gardens for food (Fig. 1). As the crown moves upward, the older horizontal branches (80–130 cm in length) are shed, and the ant colony moves gradually upward. *Barteria fistulosa* has an extremely deep tap root and in heavy forest appears to have its greatest rate of

[1] Received October 14, 1971; accepted May 5, 1972.

[2] Present address: Department of Zoology, University of Michigan, Ann Arbor, Michigan 48104.

[3] In the near future *Pachysima* is likely to be synonymized with the widely distributed Old World genus *Tetraponera* (W. L. Brown, Jr., personal communication).

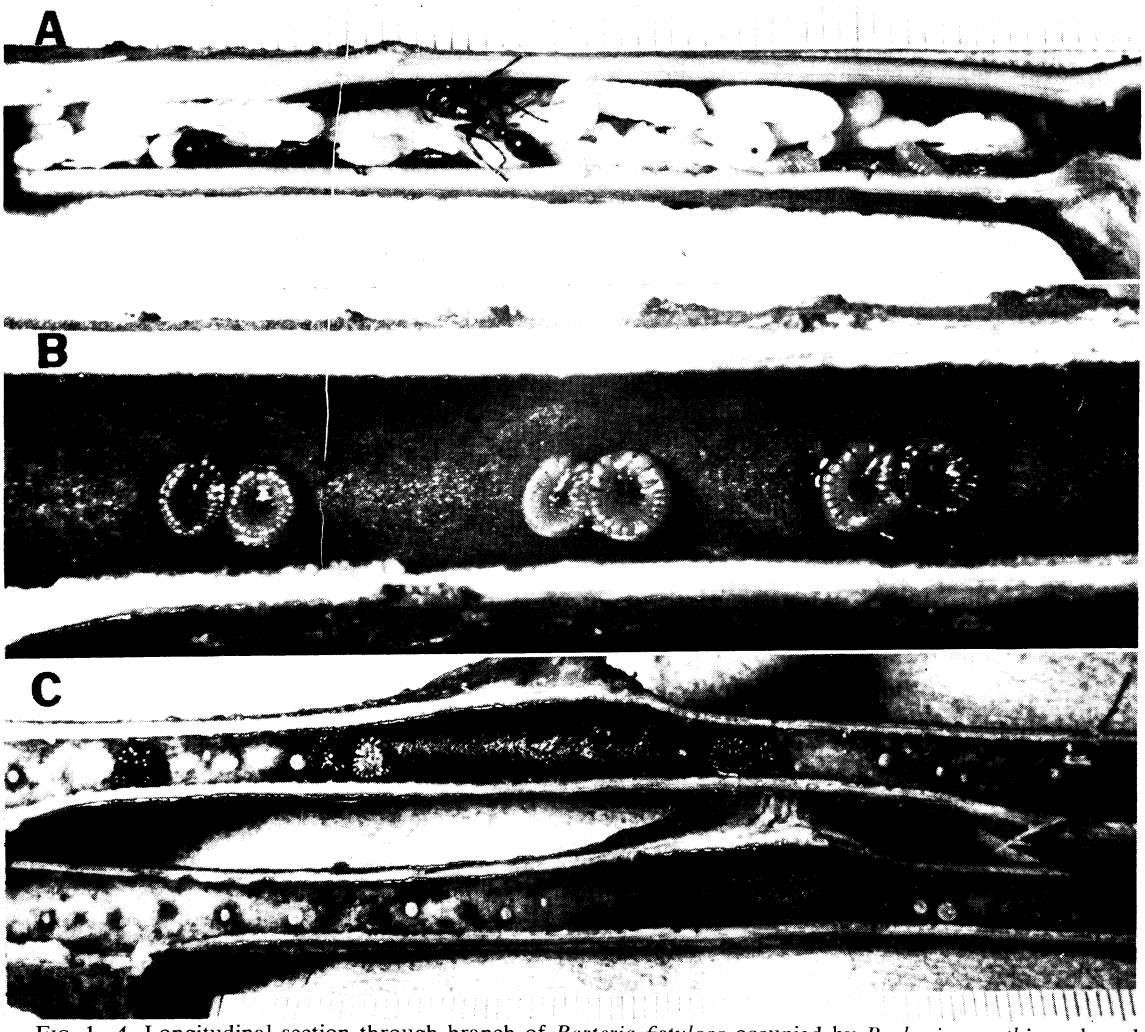

FIG. 1. *A*. Longitudinal section through branch of *Barteria fistulosa* occupied by *Pachysima aethiops;* brood is packed in at the maximum density encountered in a large colony (scale in millimeters). *B*. Scale insects on the inner wall of a living branch of *B. fistulosa;* they are evenly spaced because they are on the evenly spaced pits cut into the stem by the ants. *C*. Fungus patches or "gardens" (dark area in center of upper stem, slightly to right of center of lower stem) in living branches of *B. fistulosa;* scale insects of various ages are also visible (scale in millimeters).

vertical height increase during the dry season when the semideciduous canopy admits the most light (the time of this study, January 1971). The trees die after 15–30 reproductive seasons, at which time their crowns are high enough to be exposed to broken sunlight, but they never reach the general canopy at 35–50 m. Fully grown plants are usually occupied by a colony of 1,000–4,000 worker *Pachysima aethiops* and very rarely by a colony of the slightly smaller *P. latifrons* (cf. Wheeler 1922 for a discussion of the taxonomic status of these ants). All the discussion and data presented here are based on *Barteria* occupied by *P. aethiops,* but *P. latifrons* appears to treat and use the tree in a nearly identical manner. There are about 100 colonies of *P. aethiops* for each *P. latifrons* colony in the Sapoba forest.

The details of internal colony structure, nutrition, and social organization of *Pachysima* will be treated in a paper in preparation.

PROTECTION OF BARTERIA BY "PACHYSIMA"

Insects

Owing to nearly total extinction of vertebrates by hunting in the Sapoba forest, the *Barteria* trees are threatened only by insects at present. Most were not identified but were Lepidoptera larvae, Coleoptera adults, and Orthoptera; their damage was very similar to that done by these same orders of insects to unoccupied swollen-thorn acacias (Janzen 1967*a*) and *Cecropia* trees (unpublished field notes) in Central America. Table 1 describes the more conspicuous herbivore damage to naturally unoccupied young

TABLE 1. Health of *Barteria fistulosa* saplings occupied by *Pachysima aethiops* as contrasted with unoccupied *B. fistulosa* (Sapoba Forest Preserve, Midwest State, Nigeria, January 2–10, 1971)

	Average height (m)	Average no. of leaves	SD	Average no. of branches[b]	SD	Average no. of leaves/branch	SD	Average no. of vines	Central axes: % intact and growing	Central axes: % intact but dormant	Central axes: % with shoot tips chewed off	Lateral branches[c]: % intact and growing	Lateral branches[c]: % intact but dormant	Lateral branches[c]: % with shoot tips chewed off
Tree heavily[a] occupied ($n = 35$)	2.8	60	43	6.2	2.8	8.7	2.8	0	29	63	9	85	15	0
Tree lightly[a] occupied ($n = 6$)	2.7	62	48	6.5	6.3	8.4	3.7	0	17	83	0	66	33	0
Tree unoccupied ($n = 27$)	2.3	13**[d]	10	2.2**[d]	1.9	4.1**[d]	3.5	1.9	15	30	56	30	11	59[e]

[a]A sapling was scored as heavily occupied if worker ants were seen without disturbing foliage during daylight hours. A lightly occupied tree was one that had a colony so small that at least during part of the daylight hours there were no workers visible unless the tree was disturbed.
[b]Only live and occupied branches were counted.
[c]Only the uppermost lateral branch was counted.
[d]This mean is different from that of the pooled occupied trees at the .001 level (t-test). The data from the occupied trees were pooled for this comparison because by inspection they did not differ between the lightly and the heavily occupied trees.
[e]Includes eight totally dead lateral branches.

Barteria as contrasted with occupied trees of the same height in the same habitat. The occupied saplings had an average of 61 leaves, six living branches, and nine leaves per branch; unoccupied saplings had an average of 13 leaves, two living branches, and four leaves per branch (Fig. 2). The average values for occupied trees are all significantly different from those of unoccupied trees at the .001 level (t-test). Most of the difference in means is the result of cumulative effect of insects having eaten off the shoot apices of the central axis or horizontal branches more frequently on the unoccupied plants than on the occupied ones. For example, we may pool the shoot-tip damage data from the heavily and lightly occupied trees (Table 1) and contrast them with the unoccupied trees. Here, 56% of the shoot tips of the central axes and 59% of the shoot tips on horizontal branches have been badly chewed on the unoccupied saplings, while the comparable figures are only 7% and 0% for the saplings occupied by *P. aethiops*. Mature leaves of unoccupied saplings were much more heavily eaten by insects than were those of occupied plants, which often showed no insect damage. The midribs of leaves and surfaces of the branches had their epidermis extensively eaten by the adults of a species of curculionid beetle. Since this study was done during the dry season, insect densities were probably at their lowest. I suspect that the damage rate to unoccupied *Barteria* is also lowest at this time (as with Mexican unoccupied swollen-thorn acacias, Janzen 1967*a*). On the other hand, *Barteria* is one of the few understory plants growing during the dry season and its shoot tips may therefore be in greater demand by the herbivore community at this time.

In choosing the trees for the contrasts in Table 1, all live saplings that could be found in a 25-ha forest were recorded; to be eligible, a *Barteria* sapling had to be old enough to have at least one horizontal branch but be less than 6 m tall. If the same kind of observations were to be made on swollen-thorn acacias in Central America, the results would have been approximately the same as those that were obtained with more rigorous experimental circumstances (Janzen 1967*a*); I believe that a contrast of experimentally defaunated *Barteria* with naturally occupied trees would give results very similar to those in Table 1. The unoccupied saplings observed at Sapoba lacked ant colonies because queens had not yet been able to establish them, primarily owing to mortality of founding queens. The branches of unoccupied *Barteria* commonly contained dead founding queens. *Pachysima* colonies have a mobility similar to that of *Pseudomyrmex* in *Acacia* or to that of *Azteca* in *Cecropia,* and there is no evidence that unoccupied trees had simply been abandoned by a large ant colony because the tree was in poor health. An aban-


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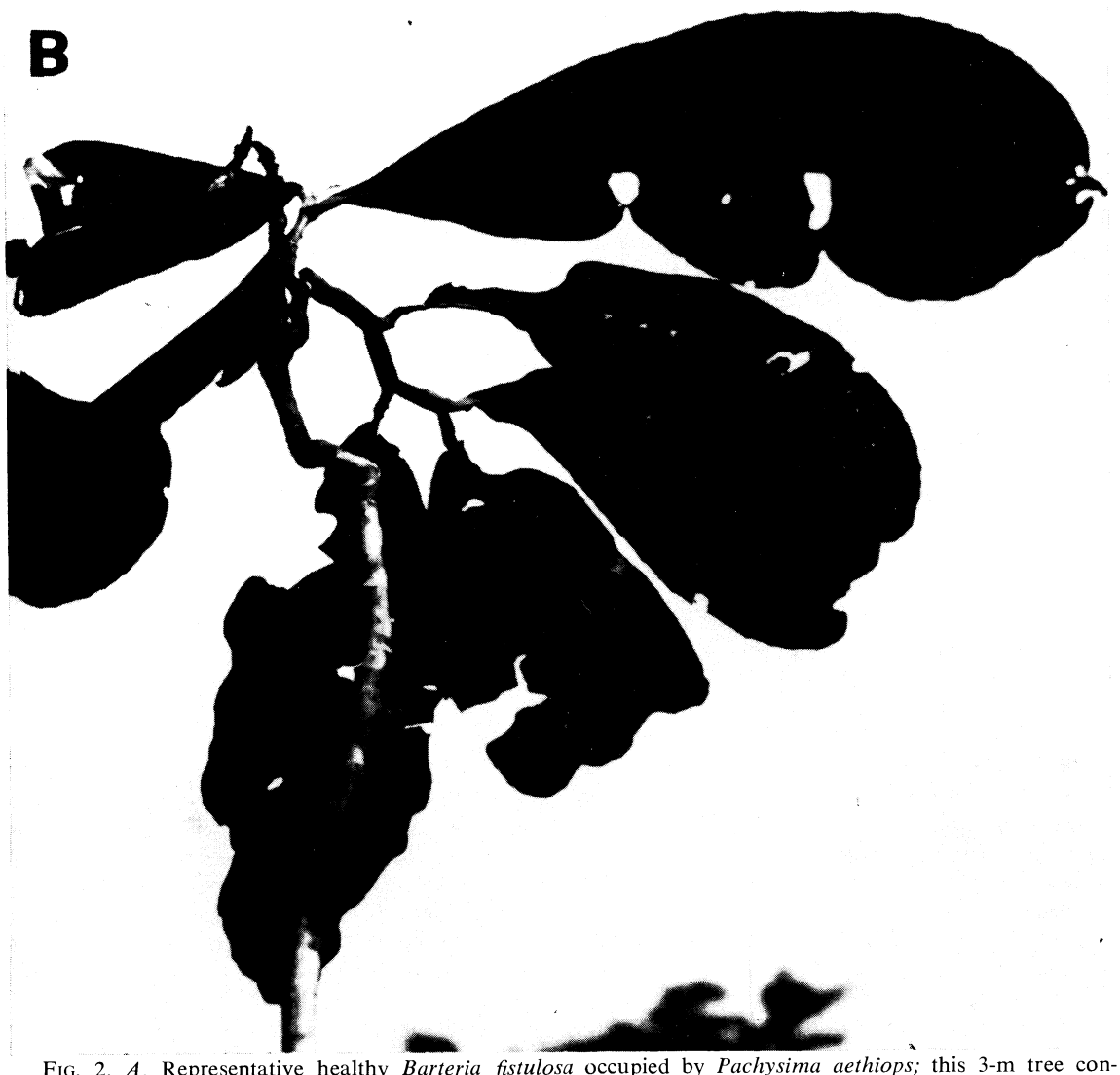

FIG. 2. *A*. Representative healthy *Barteria fistulosa* occupied by *Pachysima aethiops;* this 3-m tree contained 1,802 worker ants (for scale, the longest leaves are about 25 cm in length). *B*. A representative unoccupied *B. fistulosa* crown; this 2.5-m tree was the same age as the occupied plant in *A* above.

doned tree is easily recognized by the characteristic entrance holes cut in the branches by the worker ants.

Jones (1955) and Kohl (1909) noted that *Barteria* tends to be highly aggregated in brushy areas. While this aggregation may be in part due to microscale patchiness of suitable germination sites, it is much more likely to be the result of established *Pachysima* colonies expanding to occupy and protect nearby *Barteria* seedlings that would otherwise have perished before a colony could become established in them from a founding queen. The same phenomenon is common with neotropical swollen-thorn acacias (Janzen 1967*a*).

Mammals

There is no evidence to suggest that browsing mammals were of major importance in the coevolution of neotropical ant–plant mutualisms (Janzen 1966, 1967*a*, 1967*b*, 1969*a*, 1969*b*). In contrast, several indirect lines of evidence suggest that large mammals were important in the coevolution of the *Barteria-Pachysima* mutualism.

1) A native community of large browsing mammals was present to provide selective pressure. Various species of Bovidae and elephants used to occupy *Barteria* habitats in the Sapoba region; forest antelopes were hunted there as late as 1940 (Akpobi Omukoro, personal communication). Local inhab-

itants agree that these animals "never" browsed *Barteria* foliage and attribute this avoidance to the ants. In other western African forests, elephants create disturbed habitats where *Barteria* grows well, but they do not feed on *Barteria* (P. W. Richards, personal communication). Shoot tips of *Barteria* are not bitter to my taste and were readily eaten by small rodents when left on the tabletops at Sapoba. Despite the demonstration that cows and brocket deer (*Mazama americana*) are deterred by *Pseudomyrmex* obligate acacia-ants living in neotropical acacias (Janzen 1967*a*), the former animal is introduced and the latter is not tall enough to threaten growing swollen-thorn acacias. The neotropics does not appear to have a large enough contemporary community of appropriate large browsing mammals to maintain the selective pressure for specific traits in the ant–plant interaction.

2) The behavior of *Pachysima* workers includes some characteristics that should be very efficient in deterring large mammals. When working under occupied *Barteria*, I became very preoccupied about being stung by *Pachysima*, something that has not happened with neotropical myrmecophyte ants. First, within a few minutes, one or two *Pachysima* workers found me either by falling from the tree or walking up from the ground; there is literally a slow rain of ants from a heavily occupied *Barteria*. The rate of fall increases somewhat, but not dramatically, when the colony is disturbed. Neotropical myrmecophyte ants also fall from the tree, but much more rarely. Second, if unmolested, the *Pachysima* workers do not immediately bite and sting, but rather walk about until a patch of bare skin is found and then attack. Neotropical myrmecophyte ants tend to attack any foreign object immediately (such as clothing or hair) and are thus much less effective against people and presumably other large animals. Third, on the surface of the plant, *Pachysima* workers are clumsy and do not accurately locate small moving objects such as insects. However, they have no difficulty locating large objects touching the foliage. Acacia-ants, on the other hand, are very agile and accurately attack small insects after approaching within a few centimeters. Fourth, once they have found bare skin and grabbed on to bite and sting, they are very difficult to remove. Neotropical myrmecophyte ants can be easily brushed off. When disturbed, *Pachysima* ants are so adept at holding on to surfaces that they are very difficult to aspirate from the surface of the tree.

Local inhabitants have a strong avoidance reaction to *Barteria* trees, as evidenced by failing to cut them when clearing brush, and by the observation that the leaves and bark have a superstitious use as a medicine that has the power to act at a distance or can ward off a spell by casting it back on the person generating it (Dalziel 1948:50–51). Wheeler (1922) attributes the following statement to Kohl: "It was customary in his part of the country to punish unfaithful wives by tying them to plants inhabited by the '*Sima*' " (= *Pachysima*).

3) The sting of *Pachysima* appears modified in the direction of deterring mammals rather than insects. Once they have settled down to sting, they stay at one site pumping in venom, rather than running from site to site as do neotropical myrmecophyte ants (*Azteca* in *Cecropia* do not even have a sting). The pain from a *Pseudomyrmex* sting is almost instantaneous, sharp but of short duration, and seems to affect only the body surface. The pain from a *Pachysima* sting is not felt for several seconds after the sting has been deeply inserted. It is a deep throbbing pain, seeming to come from the muscles. It lasts for 1–2 days, during which time the muscle is sore and stiff. In short, *Pseudomyrmex* and *Azteca* ants are an effective deterrent against easily frightened insects with little memory (Janzen 1967*a*), while *Pachysima* ants appear most effective at producing a long-lasting memory in a persistent mammal. While hundreds of stings of *Pseudomyrmex* can be tolerated if there is a compelling reason to invade the tree, 1–5 *Pachysima* stings were enough to drive me away from a tree, leaving me very reluctant to return.

4) The apportionment of ant colony biomass into worker ants reflects the emphasis on defense against mammals. An average large "single-queen" *Pseudomyrmex* colony contains 8,000–15,000 worker ants (e.g., *P. ferruginea*, Janzen 1967*a*). The dry weight of each worker is in the area of 1.2 mg (*Pseudomyrmex belti* from Costa Rica) to 0.5 mg (*P. nigrocincta* from Costa Rica). The species with smaller workers have larger numbers of workers in colonies of equal age than do those with larger workers (weight data are based on specimens dried in the field and not preserved first in alcohol). A large *Pachysima aethiops* colony has 1,000–4,000 worker ants, each weighing about 7 mg (dry weight). A mature colony of each of these two pseudomyrmecine ant groups is thus sustaining about the same amount of worker dry weight, but *Pachysima* makes a few relatively dangerous individuals while *Pseudomyrmex* makes a large number of mildly irritating individuals. The same may be said of the large colonies of small *Azteca* in *Cecropia* trees.

Associated with the small number of workers in *Pachysima* colony, a maximum of 8–12 workers patrol the actively growing shoot tips and this number declines to 1–3 at night. The mature leaves may have no workers on them at night and average less than one ant per leaf during the daylight hours. The comparable numbers are much higher on neotropical myrmecophytes; maxima on the main shoot tips may be 30–50 workers and there may be as many as three

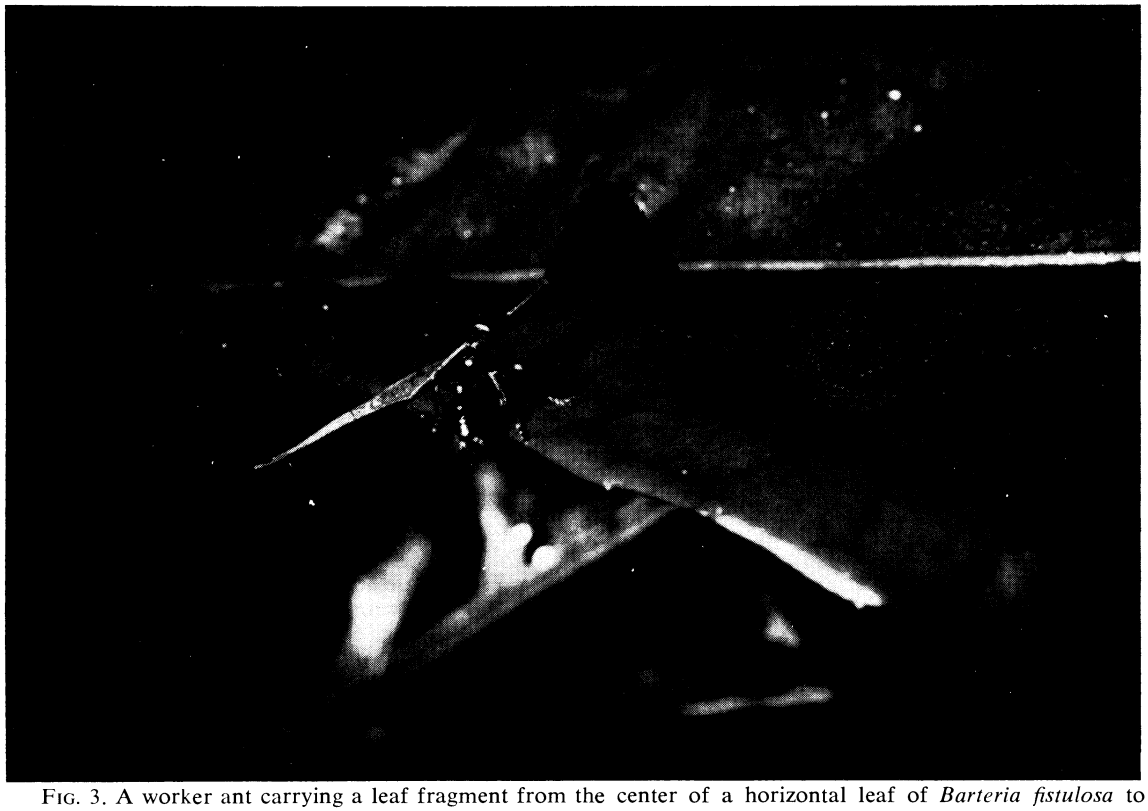

FIG. 3. A worker ant carrying a leaf fragment from the center of a horizontal leaf of *Barteria fistulosa* to the edge, after which it turned around and dropped it off.

ants per mature leaf during the daytime. There is often little or no decline in numbers of workers at night on actively growing shoot tips of swollen-thorn acacias. When a large animal contacts a *Barteria* tree, there is likely to be at least one ant close enough for an attack to occur immediately; this is not the case for an insect landing on the tree. On numerous occasions insects were observed sitting motionless for many hours on a *Barteria* leaf without being encountered by a *Pachysima* worker. This would not happen on a heavily occupied neotropical swollen-thorn acacia.

5) *Pachysima* workers release a strong fetid-smelling chemical when disturbed that does not produce a visible alarm reaction by the colony. A chemical with a similar odor is released by workers of a large, black, ponerine ant, *Paltothyreus tarsatus,* that forages solitarily on the ground in *Barteria* habitats; presumably this is a warning or even a noxious odor to animals that forage at night. It seems a reasonable hypothesis that *Pachysima* workers release this odor for a similar reason. Neotropical myrmecophyte ants also have a distinctive odor, but it clearly serves as an alarm odor for other members of the colony, though horses, cows, and burrows will learn to use it as a cue to the presence of an ant-plant (Janzen 1967*a*). If in fact *Pachysima* can be viewed as a skunk of the ant world, then it is likely that browsing mammals have been important in its evolution for a long time.

Plants

As with neotropical myrmecophyte ants (Janzen 1969*a*), *Pachysima* workers produce a 2- to 3-m-diameter bare area around the base of their *Barteria* tree (Kohl 1909, Bequaert 1922). This is done by repeatedly chewing off the growing and mature foliage of plants below the tree or growing into the *Barteria* crown from the side. The latter activity is reflected in the total absence of vines from the occupied saplings but an average of 1.9 vines on the unoccupied saplings (Table 1). As with neotropical swollen-thorn acacias, the horizontal branches of *Barteria* make excellent standards for vines when the plant is unoccupied. The destruction of the vegetation around the *Barteria* tree was originally interpreted by Bequaert as being "of use to the ants in their hunts for other insects, making the capture of their prey so much easier and quicker." He also pointed out that "*Barteria* too may be benefited, since it is saved competition with more vigorous species of trees or shrubs." However, Bequaert was a supporter of the concept that the relationship between ants and their myrmecophytes was neither coevolved

nor mutualistic, and therefore did not view the ants' behavior as adaptive for the ant colony as well as for the plant. There is little doubt that this antiplant activity has been selected for through its adaptive significance to the ant via lowered competition for the *Barteria* plant. My own observations strongly support Kohl's (1909) that *Pachysima* does not forage off the tree except to attack plants, and obtains all its nutrients from the Homoptera and other organisms tended inside the hollow branches.

An unappreciated aspect of *Pachysima* antiplant activities is that the ants are diligent in cleaning the 5- to 20-cm broad *Barteria* leaves which are nearly horizontal in orientation. Unoccupied *Barteria* trees have a much heavier load of epiphyllae and debris fallen from the general canopy than do occupied trees; the ants literally pick up plant matter, carry it to the edge of the leaf, and drop it over the side (Fig. 3). This cleaning behavior is identical to that of *Pseudomyrmex* and *Azteca* ants on neotropical *Acacia* and *Cecropia* trees.

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This study is dedicated to all the unfaithful wives who were tied to *Barteria* trees.

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