Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

VOL. 127, NO. 7

BEHAVIOR OF *DACETON ARMIGERUM* (LATREILLE), WITH A CLASSIFICATION OF SELF-GROOMING MOVEMENTS IN ANTS

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CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

AUGUST 28, 1962

PUBLICATIONS ISSUED BY OR IN CONNECTION
WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

BULLETIN (octavo) 1863 — The current volume is Vol. 127.

BREVIORA (octavo) 1952 — No. 165 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 40 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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Bull. Mus. Comp. Zool., Harvard Univ., 127(7): 401-422, August, 1962

No. 7 — Behavior of Daceton armigerum *(Latreille), with a classification of self-grooming movements in ants.*

By Edward O. Wilson

INTRODUCTION

The Neotropical ant species *Daceton armigerum* is the only member of its genus and the largest and most primitive representative of the great predaceous tribe Dacetini (Brown and Wilson, 1960). Unlike most dacetines, it is completely arboreal. Further, its worker caste exhibits polymorphism of the greatest magnitude found in the Dacetini and one of the most extreme for ants generally. The combination of these characteristics makes it a strikingly discrete entity within the Neotropical ant fauna.

To date only a few fragments of information on the biology of this significant species have been published. As noted in a recent review of the Dacetini (Brown and Wilson, 1960), it has been collected chiefly from forested localities in the Amazon-Orinoco Basin of South America. A single nest has been found in the trunk of an unidentified tree at Itacoatiara, Brazil (Mann, 1916). On several occasions workers have been discovered foraging during the day. Very limited prey records suggested that the species is generally insectivorous, although the point was far from proven. Until the present study, no nest had been dissected, and details of behavior were unknown.

During field work in Surinam in March, 1961, I made a special attempt to locate and study the species. A single colony was captured and kept under observation in an artificial nest for two months. In April, by a stroke of good luck, a second colony was located in Trinidad, thus yielding the first record of the genus from the West Indies. The Trinidad colony was not recovered from the nest tree, but proved very useful for field studies of foraging behavior.

ECOLOGY

Habitat. Although *Daceton* has been previously considered exclusively a rain-forest dweller, neither of the study colonies came from this environment. One was located in primary swamp forest directly north of the Government Botanical Gardens (Landboewprufstation) at the outskirts of Paramaribo, Surinam. The forest, of uniform facies, extended unbroken from

the edge of the Botanical Gardens to the north coast, seven kilometers away. At the time of the author's visit, at the nadir of the dry season in March, 1961, the floor of the forest was quite dry. But during the wet season the floor is flooded up to a height of one meter. Consequently, it was not surprising to find the insect fauna of the floor extremely sparse in biomass and species. The few ant species abundant there possess well-developed devices for escaping flooding: *Solenopsis geminata* (Fab.) has colonies that are able to cluster in round masses and float out of flooded areas; two species of *Eciton* found swarming on the forest floor are nomadic and probably do not penetrate into this area during the wet season; and, finally, *Monacis bispinosa* (Olivier) nests arboreally but sends long columns of workers, guided by odor trails, onto the floor during the dry season. The truly arboricolous ant fauna, on the other hand, was quite rich, containing species of Pseudomyrmecinae, Cephalotini, as well as *Solenopsis* (*Diplorhoptrum*), *Dolichoderus*, *Azteca*, and *Paratrechina* (*Nylanderia*), as well as *Daceton*.

The second *Daceton* colony was located within one kilometer northeast of Cumuto Village, Trinidad, in the interior of a patch of open, semi-deciduous forest in the Aripo savanna. This locality was ecologically very different from the Paramaribo swamp forest. Also visited during the dry season (in April, 1961), it was notably drier but contained much richer ground and arboreal insect faunas. Arboreal ant species nesting or foraging within the *Daceton* trophophoric field alone included *Neoponera* sp., *Pseudomyrmex acanthobia* Emery, *P.* sp., *Leptothorax spininodis* Mayr, *Paracryptocerus* sp., *Azteca chartifex* Forel, *Camponotus canescens* Mayr, *C. sanctaefidei* Dalla Torre, and one other unidentified *Camponotus*.

Nest site and associated arthropods. The Paramaribo colony was nesting in cavities preformed by cerambycid beetle larvae in live branches of a "zwamppanta" tree, *Tabebuia longipes* Baker, a member of the Bignoniaceae (determined by Dr. D. C. Geijskes). The tree had four trunks, each approximately 60 cm. in circumference and apparently arising from a common root stock. Two of the trunks were united to a height of 30 cm. from the ground. The uppermost part of the crown was probably no more than ten meters from the ground and was overshadowed by the crowns of taller trees surrounding it. The *Daceton* colony was distributed in independent beetle-gallery systems in at least three of the *Tabebuia* branches. The sections occupied by the *Daceton* were all within two meters of each other. Not all of the

tree was dissected, but inspection of the few remaining branches left intact showed no further sign of the ants, and it is therefore believed that the entire colony was collected. The first nest branch was 35 mm in diameter; the occupied cavity inside was 6-17 mm in diameter and extended 63 cm. from a node to a cerumen wall built by a colony of small meliponid bees, who filled the remainder of the cavity. A single entrance hole 33 mm from the cerumen wall was oblong, measuring 6 x 8 mm. This portion of the nest contained the mother queen, an alate queen, about 30 workers, and a quantity of brood, mostly eggs. A second nest branch close to the first was 25-30 mm in diameter; its cavity was 7-14 mm in diameter and between two and three meters in length and was reached by a 7 x 16 mm entrance hole; it contained 2 alate queens, about 110 workers, and a quantity of brood of various stages, including a male pupa. The third branch was 25 mm wide; its cavity was 8-12 mm wide and almost exactly one meter in length and was reached by a single slit-like cavity measuring 4 x 14 mm; it contained two callow males, approximately 100 workers, and brood of various stages.

Two of the cavities contained a total of three lepismatids, the only myrmecophiles present. These insects, like other ant-nest lepismatids, were synoeketes, swiftly dodging around their hosts and apparently ignored by them.

A cavity in a fourth branch held decaying fragments of *Daceton* workers. It is not clear whether this was an abandoned nest cavity or merely the refuse pile of some predatory arthropod. Other live branches contained, in addition to portions of the meliponid colony already mentioned, a large, flourishing colony of *Azteca* sp. and, in otherwise empty chambers, two large scolopendrid centipedes.

The nest site of the Trinidad colony was not located with certainty. After most of the smaller trees within the *Daceton* trophophoric area had been cut down and opened without success, numbers of the workers were seen moving up and down the trunk of a large, unidentified tree between 20 and 30 meters in height and 120 cm in circumference two meters from the ground. Since this appeared to be the only remaining tree in the trophophoric field with many workers on it, and the only one in any case large enough to hold a large *Daceton* colony, it was suspected of being the nest tree. The conclusion was confirmed by the fact that workers on the trunk given dead insects moved up the trunk and continued until out of sight near the crown.

Unfortunately, the discovery was made too late to allow time for the tree to be felled and opened.

Colony composition. The Paramaribo colony, as noted, was in a mature state (containing alate queens), so that an estimate of its size is of special interest. After the nest had been dissected, the following numbers of adults were totalled from the live colony in the artificial nest and preserved material: one dealate queen, three alate queens, two males, 270 ± 20 workers. A few workers were left foraging or lost during collection. The total number of workers in the colony, including foragers, probably fell within the limits of 280-320.

No census was made of the Trinidad colony. Nevertheless, casual inspection showed that it was much larger than the Surinam colony. On April 13, 218 workers were collected and preserved on foliage away from the host tree without greatly reducing the foraging population. On April 27, what appeared to be the entire trophophoric field was scanned, and the number of foraging workers was roughly estimated to be in excess of a thousand. In Surinam the ratio of diurnal foragers to nest inhabitants was estimated to lie between 1:10 and 1:5. If the same ratio obtained in the Trinidad colony, the total worker population may have ranged as high as 5,000 or even 10,000. But these latter figures have only the weakest conjectural significance until more *Daceton* colonies are collected.

Foraging area and diet. The *Daceton* workers forage extensively during the day. On April 13 I remained at the Cumuto, Trinidad, locality until dusk, at which time a significant decrease in activity was noted. The nest sites were not visited at night.

Foraging appeared to be limited exclusively to arboreal vegetation but was not devoted preferentially to any part of the vegetation. Workers moved up and down tree trunks, across trees on lianas or at the points of interlacing crown vegetation, onto epiphytes, and out to the very tips of branches, twigs, and leaves. Seedlings only a meter or two in height were visited as well as the tallest trees. At Paramaribo, workers were noted on the trunks of four trees, the more distant approximately 14 meters from the trunk of the nest tree. At Cumuto workers ranged maximally to between 16 and 20 meters from the assumed nest tree. Dead as well as live foliage was visited. At Cumuto, workers were abundant in the crown of a felled "galba" tree, *Calophyllum brasiliense,* from which most of the leaves had already fallen. Evidently, *Daceton* workers do not normally forage on the ground. At neither locality was a single worker seen

there. Workers were followed repeatedly as they neared the ground; some proceeded to the base of the trunk or onto the buttresses, but none went further.

Before the present study, only two records of *Daceton* prey had been published: a tabanid fly and an acridid grasshopper (Brown and Wilson, 1960). In the following list are all of the additional natural prey recorded at Cumuto during the afternoons of April 10, 13, and 27, along with their approximate length: Seven moth larvae (3, 5, 8, 8, and 23 mm; two were not measured); one adult moth; two adult curculionine weevils (both 5 mm); one adult cryptorhynchine weevil (3 mm); one beetle larva (8 mm); one fulgorid (7 mm). All were being carried by single workers, except the 23-mm moth larva which was being hurried along by four workers running together. All of the prey appeared to have been freshly killed, presumably by the *Daceton*. Of all the workers seen running nestward, only a very small fraction, about 1 or 2 per cent, were laden with prey. Foraging workers that were offered freshly killed polybiine wasp workers accepted these readily and carried them homeward. In the artificial nest, the Surinam colony consistently accepted flies (Muscidae, Psychodidae, Sarcophagidae, Tabanidae, Tachinidae, etc.) and usually accepted acridid grasshoppers. On the other hand, they rejected (after killing) a coccinellid beetle, a coccid, several cicadellids, and a honeybee (*Apis*). The significance of this apparent selectiveness, contrasting as it does with the obvious catholicity of prey choice of the wild Trinidad colony, remains to be explained. Workers also commonly consumed brood in the artificial nest; this may have been an abnormal reaction.

It should be noted that while *Daceton* is generally insectivorous, or at least nearly so, the size range of its prey is not very great. For this reason, the two colonies did not have serious competition from other ant species penetrating their trophophoric fields. Only the *Neoponera* at Cumuto could readily capture prey in the size range preferred by *Daceton*, and these ants were represented by a single small colony. The ants that seemed to create maximum interference, on the other hand, were the *Azteca*. At both localities species of this dolichoderine genus were by far the most abundant ants present. They were quite aggressive and were frequently observed attempting to seize the legs of the *Daceton*, especially when the nests were disturbed by the human observer. But the size difference was too great to allow serious interference. The *Daceton* moved through the *Azteca* swarms like elephants through crowds of pygmies.

According to Bodkin (in Crawley, 1916), *Daceton* workers were observed attending coccids in British Guiana. No evidence of nectar or honey-dew gathering was found during the present study. However, workers in the artificial nest fed eagerly on sugar water and exchanged the fluid freely among themselves by regurgitation.

BEHAVIOR

Hunting and nest defense. Daceton workers observed in the field at Cumuto explored the foraging area singly. There was no evidence whatever, either in the field or in laboratory, of trail laying or other special forms of recruitment following discovery of food. In the artificial nest, workers often moved toward areas of excitement, evidently stimulated by other workers when prey were being chased or captured, and this response can be interpreted as a very low level of communication. The ants did not seem to react to movements more than ten millimeters from their heads. The orienting stimuli were at least partly visual, since workers reacted similarly to movement in the area directly outside the transparent walls and cover of the nest. (A description of the type of artificial nest used is given in Wilson, 1962.)

Foraging workers remained nearly constantly in motion, ambling along at a pace proportionate to size that was closer to foraging *Tetramorium* than to the more sluggish higher Dacetini. The mandibles were almost always held partly open, making an angle of between 45° and 90°. Both the surface of the foliage and crevices were explored by antennation. The ants often paused to lift the head slightly and wave the antennae in the air briefly. Resting workers did not appear to be engaged in "ambush hunting." Workers most frequently paused where other workers were resting, and this was typically in crevices and other sheltered places. At such times the mandibles were not held in striking position, nor was there any other aspect of the posture to suggest that the ants were set to ambush prey. A unique feature of *Daceton* morphology is the ability in the worker to swing the head upwards and backwards so that its long axis forms a right angle or less with the remainder of the body. Thus a worker has the capacity to point the head vertically from the surface on which it stands. It has been a point of guarded conjecture among myrmecologists that such a posture might be used in ambushing insects. Yet no such posture was ever seen to be taken during the course of normal foraging.

Nor was such a posture ever assumed during the many captures of insect prey observed in the artificial nest. The adaptive significance of the hinged head may lie in an entirely different behavioral category, that of food exchange (*vide infra*).

Slight disturbance caused the workers promptly to open and lock the mandibles at maximum extension, so that their inner borders formed an angle of approximately 170° (see Figure 1). Foraging workers in the field clearly were very perceptive visually to movement. They wheeled about quickly to face any moving object. If the object was a large one, such as a human hand, the ants darted in reverse, revealing the curious ability to run backward as rapidly as forward. Slight movement, which must

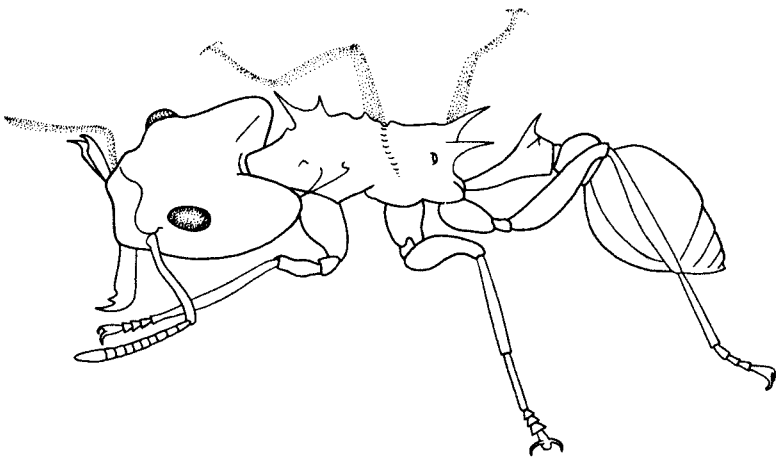

Figure 1. Media worker in stalking posture. Drawn from a single 16-mm frame of a motion picture of the Surinam colony.

be close to the ant, induced a cautious movement toward the object. At such times the mandibles were always locked open, the scapes aligned along the mandibles, and the funiculi pointed straight ahead. If the object were acceptable prey, little time was spent in the approach. In the field the ants walked toward the dead insects offered them (polybiine wasps) deliberately and slowly for periods lasting no more than five seconds, then struck with the mandibles. The stalk resembled that of *Strumigenys louisianae* (Wilson, 1953) but was more abrupt. Sometimes it was eliminated altogether, with the ant briefly antennating the prey before striking. In the artificial nest, living

prey were often chased by the *Daceton*, which seemed to lose perception of them at distances greater than about ten millimeters. The act of chasing for considerable distances sets the hunting behavior of *Daceton* distinctly apart from that of other dacetines studied. It is evidently afforded by the exceptional vision provided by the large eyes of these insects.

The mandibular strike, as in higher dacetines, was convulsive and severe. It drove the sharp apical teeth deeply into the bodies of softer insects and was adequate even to force the points into the softer skin of the author's hand. Following the strike, the prey was lifted slightly from the ground with a barely visible upward movement of the head. Exceptionally long tarsal claws anchored the ant firmly to the bark surface and aided it in holding on to large or vigorous prey. On the field, when prey carried by *Daceton* workers were seized by a pair of forceps and pulled, the ant hung on tenaciously and could be torn loose from the bark only with difficulty; sometimes the prey was pulled asunder in the process. Following the mandibular strike, the ant often made a very short backward run; occasionally it paused for a while, grasping the prey firmly. The sting, when it was administered, involved the same movements already described in *Strumigenys* (cf. Brown and Wilson, 1960). Workers encountering prey being carried by other workers repeated or attempted to repeat the hunting sequence on their own. The result is that large or unusually vigorous insects could be subdued by the attacks of several ants, and sometimes more than one ant cooperated in carrying it home. Workers commonly pulled the prey from the mandibles of other workers, with the result that the largest workers generally ended up with the prey before it got all the way to the nest (see the later section entitled "Division of labor").

While I was collecting the Surinam colony, I was stung twice by large media workers (head width 3 mm), each time in the soft skin between the thumb and forefinger of the left hand. This event perhaps allows me to make the esoteric claim of being the first myrmecologist to be stung by a dacetine ant. The mandibular strike felt like the light jab of a needle, and this was quickly followed by a moderate, very localized burning sensation. An erythema quickly appeared around the point of sting entry, spreading within several minutes to form a circular patch approximately 30 millimeters in diameter. At the same time a welt 5 to 8 mm wide was raised in the center. At maximum development the inflammation caused moderate burning

and itching, very similar to that caused by an allergenic mosquito bite. The effect gradually subsided, and thirty minutes after the sting only a faint erythema remained. The symptoms closely resembled the superficial effects of the sting of certain other myrmicine ants such as fire ants of the genus *Solenopsis*, rather than the deeper, throbbing, fluctuating pain caused by ponerine ant and certain wasp stings.

The nests were defended by aggressive behavior similar in all details to that seen during hunting, save that the ants were more excited and precipitous in their movements. Insects invading the nest but rejected as prey were killed in the same manner as prey, but later were ejected from the nest.

Self-grooming. In describing self-grooming behavior of *Daceton* systematically, attention will be focused on an interesting and promising subject in myrmecology mostly neglected since the time of McCook (1878). Self-grooming involves complex movements which are among the most stereotyped in all the ants' repertory. My own notes on a wide range of genera confirm that self-grooming behavior varies widely within the Formicidae and thus offers excellent new characters for evolutionary studies. It can be further noted that it is not the basic movements themselves that vary greatly, but rather the pattern of their presence or absence. This characteristic provides the excellent opportunity to construct grooming "formulas" for inclusion in taxonomic descriptions. In the short sections to follow are given descriptions of the basic movements used by *Daceton*, plus movements I have observed in other ant groups but not in *Daceton*.

Self-grooming Movements Used by *Daceton armigerum* Workers

(1) Oral "leg" cleaning. The front tarsi and distal parts of the tibiae are drawn, one after the other, over the lower mouthparts and glossated in the process. This is perhaps the most basic and important self-grooming movement, since it transfers detritus picked up in the strigils of the tibial spurs to the mouthparts, whence it is transferred to the infrabuccal pocket for later discharge as a pellet. All ant species studied by me employ this movement. *Daceton* is unusual in that both front legs are lifted off the ground simultaneously during the movement.

(2) Antenna wiping. The antennae are wiped with the strigils of the fore-tarsal spur. This movement appears to be universal in the Formicidae. As in (1), *Daceton* is unusual in typically holding both front tarsi simultaneously off the ground during the movement.

(3) Normal four-leg wiping. This term might be conveniently applied to the complex movement, apparently universal in ants, in which the body is supported on a tripod consisting of the tip of the gaster and middle and hind legs of one side, while the fore leg of the first side and three legs of the opposite side are wiped together. An aberrant variation is no. 13, four-leg wiping (front-middle) (*vide infra*).

Movements (4) and (5) below can be interpreted as transitional to (3):

(4) Three-leg wiping (front-middle). Similar to four-leg wiping but involving only the two front legs together with the middle leg on one side. Not found in all ant taxa.

(5) Two-front-leg wiping. Involving only the two front legs. Not found in all ant taxa.

(6) Abdominal tip cleaning. The gaster is bent forward between the legs and its tip washed with the lower mouth parts. Found in most, but not all, ant taxa.

(7) Head wiping. The front tarsi are drawn over the sides of the head. An irregular movement not found in all ant taxa. In some other taxa the top of the head is stroked as well.

(8) Abdomen wiping (front legs). The abdomen is bent forward between the legs and the sides stroked briefly and irregularly with the front legs. Accompanies (6). An unusual act for ants generally and seen only twice in the *Daceton* study.

Self-grooming Movements Used by the *Daceton* Queen and Male

The mother queen was observed using movements 1 through 7 above, thus duplicating the worker repertory almost in its entirety. Movement 8 was not seen, but the significance of its omission is uncertain due to its rarity in the worker caste. During a brief observation period males were observed using movements 1 through 5; this is probably not their complete repertory.

Self-grooming Movements Observed in Other Ant Taxa but not in *Daceton*

(9) Abdomen wiping (hind legs). Similar to (8), but the abdomen is held straight and the hind legs are used. The dorsal surface of the gaster may also be stroked. Typical of more primitive taxa.

(10) Metapleuron wiping. The front legs are folded back and rubbed against the metapleura in a sawing motion.

(11) Two-hind-leg wiping. The abdomen is lifted slightly and the two hind legs are stroked together. Typical of some primitive taxa.

(12) Three-leg wiping (hind-middle). In the formicine *Gigantiops destructor* (Fab.) the following unusual movement has been observed: the abdomen is lifted slightly, the hind legs are held rigidly off the ground and pressed together, and one of the middle legs is stroked against the ipsilateral hind leg.

(13) Four-leg wiping (front-middle). In queens of the myrmicine *Erebomyrma urichi* (Wheeler) the two front and two middle legs are sometimes wiped together simultaneously.

Other grooming. As in other ant species, the workers glossated one another, other castes, and the brood frequently. This was the most frequent social act. The mother queen was once observed glossating a callow worker, but she obviously engaged in other-grooming far less commonly than individual workers.

Brood care. Brood in all stages of development were mixed together in irregular piles in the nest. Nurse workers constantly manipulated the brood with their fore tarsi as they washed them, thus alternately burying and bringing to the surface immature individuals. Newly hatched larvae were left for a while with the eggs and were apparently fed by the workers exclusively by regurgitation. The possibility that some larvae, especially young larvae, also fed on queen-laid eggs cannot be excluded on the basis of my own limited observations. No worker was ever seen to lay an egg; it is at least certain that worker-laid "trophic eggs," if they were produced at all, did not play any role of significance in larval and queen nutrition, as they do in some other ant species [e.g., *Pogonomyrmex badius* (Latreille)]. Larger larvae were fed frequently by regurgitation. They were also given fresh pieces of prey placed directly on their heads. Small larvae (but not newly hatched ones) were sometimes placed on top of the prey. The larvae were evidently fed in a manner similar to what Brian (1956) has appropriately termed the "test-servicing" system in the genus *Myrmica*. Workers were sometimes seen to move from larva to larva, extending their glossae in the feeding motion to each, without eliciting a feeding response.

Brood transport poses a special problem for the *Daceton* workers because the sharp apical teeth of their predatory mandibles might easily break the skin of immature forms, especially the larger larvae. It may be noted in passing that the workers of

the related genus *Acanthognathus* have the same problem and a novel device for solving it: a pair of small teeth near the base of the mandibles are used to grip and carry brood, thus bypassing the apical teeth (Mann, 1922; later confirmed by W. L. Brown, *in litt.*, 1961). The *Daceton* also have a peculiar solution. When highly excited, as when the nest was first broken open, they used the apical teeth and were able to transport brood rapidly in this manner. But in leisurely emigration from one chamber to another in the artificial nest, workers almost invariably moved brood by tucking it under the head with the front legs and wrestling it backward!

Queen and male care. The mother queen and males were apparently fed exclusively by worker regurgitation. In two months of observation the queen was never seen to feed directly on prey, although it was constantly available.

When first captured and transferred to the artificial nest, the queen was closely attended by crowds of workers. As many as 14 touched her simultaneously, directing their heads to her body. When she moved she was invariably followed by a retinue of one to eight workers. Attending workers typically extended their lower mouthparts far enough to allow the maxillary and labial palps to play over the queen's body surface. One worker, always one of the majors or large medias, assumed the posture of "footman" during the queen's movements: it followed directly behind her, its front legs and fore part of its body resting on her gaster and the middle and hind legs and rear part of the body running awkwardly behind. Later, as the colony declined, the queen received increasingly less attention and finally lost her retinue altogether, including the remarkable "footman."

Regurgitation. Transfer of liquid food by regurgitation was a very common event in the captive Surinam colony. When the colony contained approximately 200 workers, one could find one or two pairs, or 1 to 2 per cent of the worker population, engaged in regurgitation most of the time. On several occasions when sugar water was given after being withheld for two or three days, the percentage of simultaneous regurgitating workers increased conspicuously, to as high as 10 per cent. Mature workers regurgitated more to callow workers and larger workers to minimae than vice versa, at least at first, but otherwise there was no visible structure with reference to castes in the exchange pattern. Minors gave freely to minors, majors to majors, majors to minors, minors to majors, etc., in what seemed to be every

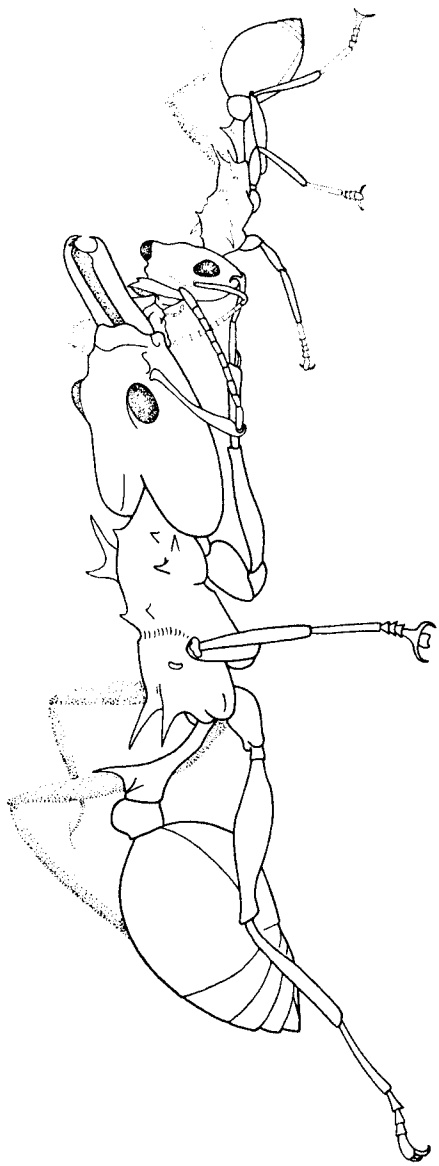

Figure 2. Minor worker regurgitating to large media. The recipient grasps the head of the donor with its fore tarsi, while both individuals slowly antennate the vicinity of the passing ingluvium. In this case the head of the donor is tilted upward in the posture peculiar to *Daceton*. Drawn from a single 16-mm frame of a motion picture of the Surinam colony.

possible combination. After they had received sugar water in this manner, the callows and minimas confined too closely to the brood area to feed directly on the food, donated it readily among themselves and to others. There may, however, have been differences in the frequencies of exchange too subtle to detect without extensive measurements.

During liquid exchange both partners held the mandibles closed or nearly so. The donor usually held its body straight or leaned slightly to one side. Its head and thorax were tilted upward, and the head was often turned more radically upward to form as much as a right angle with the thorax. In a minority of cases, the donor placed its front tarsi on the head of the recipient, and it usually antennated the head of the recipient rapidly during the exchange. The recipient typically twisted its body more strongly than the donor, sometimes as much as 45° from the ground level. If its body was held straight, it usually turned the head up to a right angle with the thorax to touch mouthparts with the donor in the same position. Thus the unique head-lifting posture of *Daceton* workers appears to be used chiefly to facilitate food exchange. During transmission the recipient almost always placed its front tarsi on the head of the donor and antennated its head rapidly. Occasionally two workers received simultaneously from the same donor, forming with it a "tripod" of bodies. (See Figure 2).

Adult transport. The carrying of adults by other adults was conspicuously absent. In numerous emigrations observed following dissection of the Surinam nest and later in the artificial nests, all adult members moved on their own. Only once was a worker observed carrying a newly eclosed callow worker over a brood pile in the artificial nest. It treated its burden much like a pupa, gripping it awkwardly by the thorax and legs. Even true brood was rarely lifted with the mandibles (see under "Brood care").

Egg-laying. The mother queen was observed once in the act of oviposition. She held her body straight. When first observed the egg was already one-third extruded; then it was totally retracted; finally, about 30 seconds later, it was totally extruded and stuck onto the nest ceiling, where the queen hung suspended. Immediately after the egg was detached, the queen walked slowly away, paying no further attention to it. The egg was soon thereafter approached by a minima worker, who commenced washing it and pulling at it with its front tarsi.

Division of labor. The total range of head width of workers in the Surinam colony was 1.2-4.6 mm. The head width of living workers in the artificial nest could be measured with reasonable certainty to the nearest two-tenths of a millimeter. For convenience, workers were classified according to the nearest millimeter of head width, thus dividing them into four arbitrary classes: "minor," including the smallest "minimas," (1 mm), "small media" (2 mm), "large media" (3 mm), "major" (4 mm). Only one individual was found with head width as great as 4.6 mm and thus was classified as 4 mm. The method afforded little information about the size frequency distribution but was most useful in detecting the major features of polyethism. The results of the study are given in Table 1. Except for the small foraging sample, which was collected in the field, all of the measurements on the Surinam colony were made in the artificial nest between April 2 and April 10. All of the measurements on the Trinidad colony were made in the field, on April 13 and April 27.

TABLE 1

Division of labor among workers of *Daceton armigerum*

	Head width (mm)				Total no. of observations
	1	2	3	4	
Surinam colony:					
Total population (in artificial nest, April 5)[1]	13	60	20	9	102
Disposing of corpses and refuse[2]	0	19	12	2	33
Dismembering and feeding on fresh prey in nest[2]	0	14	25	5	44
Feeding larvae by regurgitation[2]	8	15[3]	3[3]	1[3]	27
Attending egg-microlarva pile[2]	24	3	0	0	27
Foraging in the field[1]	0	0	4	10	14
Trinidad colony:					
Foraging in the field[1]	1	91	77	12	181
Resting in way-station[1]	0	8	19	10	37
Carrying prey[1]	0	1	1	10	12

1Numbers refer to separate, individual workers.
2Numbers refer to separate behavioral acts, without regard to the number of workers engaged.
3Consisting mostly of callows; see text.

These data allow some interesting conclusions. The *Daceton* polyethism appears to approach most closely that of the formicine *Oecophylla longinoda* (Weber, 1949), but contains some unique features of its own. The smallest workers (head width 1.2-1.4 mm) remained constantly close to the brood and, despite their small numbers, were the principal custodians of the egg-microlarva pile and contributed heavily to the feeding of the larvae. They were assisted in the latter task by the callows of larger size classes. Thus, of the 15 times that small medias (head width 2 mm) were observed regurgitating to larvae, callows were involved in 7 cases, while of the larger castes only callows were seen engaged in this task. On one occasion a minor worker was seen cleaning a shed skin from a larva. Minor workers also freely regurgitated sugar water to other workers after they had received it by regurgitation themselves (see under "Regurgitation"). The minor workers were evidently limited to this simple repertory. They took virtually no part in hunting and dismembering of prey, refuse disposal, or nest defense. They seldom joined the queen's retinue.

Polyethism among the larger size classes (head width 2-4 mm) was less marked. Although measurements were not made, all seemed to partake equally in nest defense and in attending the queen. Large medias and majors (3-4 mm) were seemingly more prone to dismember and feed directly on fresh prey and more prone to serve as the queen's "footman" (see under "Queen and male care"), but distinctly less prone to feed larvae by regurgitation. Since the nest population of the Trinidad colony was not sampled, and the foraging sample of the Surinam colony was too small, it cannot be determined whether the medias or majors tend to forage more. But the Trinidad sample is sufficient in itself to reveal some finer polyethism with reference to the category of foraging behavior. A sample of workers, collected as they rested in a crevice of a tree trunk far removed from the nest, contained a significantly higher proportion of majors and larger medias than the sample of other foraging workers. Further, a strikingly high proportion of major workers occurred in the sample collected while carrying prey. The latter effect is perhaps due to the fact, mentioned previously, that workers constantly try to pull prey away from each other on the homeward journey. Very likely the major workers usually win in these struggles and arrive at the nest carrying prey which, in most cases, they have not captured themselves.

Mixing of colonies. It was discovered that foraging workers from the Trinidad colony could be introduced successfully into the captive Surinam colony. Fighting was rare and brief and resulted in no injuries.

DISCUSSION: THE PHYLOGENETIC POSITION OF *DACETON*

The new information on *Daceton armigerum* invites a second look at its evolutionary position. Like most "primitive" or linking taxa, *Daceton* exhibits a mosaic of primitive, intermediate, and specialized characters. Brown (1949) has pointed out that certain morphological characters, such as the antennal and palpal formulas, sculpturing, and pilosity, are quite generalized with reference to the Myrmicinae as a whole. The epigaeic foraging behavior is primitive for ants generally and certainly for the Dacetini, most of the higher members of which are conspicuously modified for cryptobiotic life (Brown and Wilson, 1960).

The hunting behavior is intermediate in development between the generalized myrmicine pattern and the peculiar higher dacetine pattern; that is, the mandibular strike is typically dacetine while the hurried approach and chasing behavior resemble more that of other myrmicine groups. Frequent regurgitation to larvae and other adults is a generalized characteristic, but the vertical head posture often assumed in regurgitation between adults is a unique development. The broad insect diet is primitive, as is the ready acceptance of sugar water and the rapidity with which it is distributed by regurgitation. *Daceton* is peculiar among the lower dacetines in its extreme adaptation to arboreal life, and in this regard it has probably deviated from the mainstream of early dacetine evolution. The extreme polymorphism and elaborate polyethism are probably also deviations.

The method of transporting brood with the forelegs is unusual, but higher dacetines have a similar tendency to use the forelegs skillfully. The absence of adult transport is unusual, although the behavior is shown by at least some higher dacetines. Details of self-grooming behavior are not sufficiently well known in other ant taxa to allow an evaluation of *Daceton* in this regard.

In conclusion, it is gratifying to be able to record that *Daceton* possesses some ecological and behavioral characteristics that are wholly primitive with respect to the rest of the Dacetini, just as was predicted in our earlier studies of dacetine evolution.

But there also exist a surprising number of striking specializations. One is tempted, in reliance on the convenient evolutionits's cliché, to place *Daceton* well down on the tribal tree but off to one side of the main stem. In our continuing search for the elusive dacetine prototype, we are forced now to turn to *Acanthognathus*, the little-known Neotropical genus most closely related to *Daceton*. This taxon, which is monomorphic and terrestrial, may prove on closer examination to form a more plausible link between the higher Dacetini and the remainder of the Myrmicinae.

SUMMARY

Biological notes are given on two colonies of *Daceton armigerum*, one from Paramaribo, Surinam, and the other from Cumuto, Trinidad. The latter comprises the first record of the genus from the West Indies. The nests were located in living trees in swamp forest (Surinam) and savanna forest (Trinidad). The Surinam nest was further determined to consist of abandoned beetle burrows in live branches. Estimates of colony size and composition are given. The workers preyed on a wide variety of insects 3-23 mm in length. Hunting and defensive behavior resembled that of *Strumigenys*, except that vision played an important role in orientation and the stalk was more hurried. Nest behavior of the Surinam colony is described in detail. A classification of the movements of self-grooming in *Daceton* and other ants is given. The workers exchanged liquid food freely among themselves by regurgitation; larvae were fed directly with pieces of prey and liquid food by regurgitation. Brood was normally transported about the nest by means of a peculiar wrestling movement involving the head and fore legs. Associated with the extreme polymorphism of the worker caste was an elaborate polyethism most closely resembling that of *Oecophylla* but with features peculiar to *Daceton*.

The combination of generalized myrmicine characters in morphology and behavior with a number of striking specializations suggest that *Daceton armigerum* is a relatively very primitive member of the Dacetini but already well diverted from the mainstream of early tribal evolution.

ACKNOWLEDGMENTS

I am indebted to Mr. Harry Beatty, Dr. P. H. van Doesburg, and Dr. D. C. Geijskes for their invaluable aid in locating the Surinam colony. In fact, it was Mr. Beatty, a professional collector for the Chicago Natural History Museum, who succeeded in discovering foraging workers after I had searched fruitlessly for the species around Paramaribo for two weeks. Dr. Geijskes' assistant, Mr. Stefanus Ligorie, gave important help in dissecting the nest. I am further grateful for the assistance of Dr. A. D. Blest, Mr. Thomas Collett, and Mr. Eric Edler in locating and studying the Trinidad colony. The field study was supported in part by a grant from the National Science Foundation.

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