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BIONOMICAL OBSERVATIONS ON MYRMECOPHILOUS BEETLES OF THE GENUS *CREMASTOCHEILUS* (Coleoptera: Scarabaeidae)¹

MONT A. CAZIER² AND MARTIN A. MORTENSON³

Introduction

Information on the bionomics of myrmecophilous scarabs of the genus *Cremastocheilus*, and more especially on their behavior inside ant nests, is scattered and fragmentary. Horn (1886) found *Cremastocheilus* adults in the chambers of *Formica* sp. but made no mention of the depth of these chambers. Hamilton (1888-1889) working with *C. canaliculatus* Kirby found that ant nests under stones rarely yielded more than two beetles but that nests with mounds often contained five or six specimens at a time and if left relatively undisturbed would continue to produce specimens every two or three weeks. These beetles were found near the surface and in nests with mounds no *Cremastocheilus* were found below ground level. Wheeler (1908a p. 74) reported taking 24 specimens of two species, *C. castaneae* Knoch and *C. canaliculatus*, from a single nest of *Formica schaufussi* Mayr. Ritcher (1963, *in litt.*) reports that in Oregon, *Cremastocheilus* occurs only in nests of *Formica*, so far as he is aware, and that 200 or more individuals may be found in a single brushy nest in central Oregon. Mann (1911) reported finding the larvae of *C. pilosicollis* Horn in the nests of *Formica rufa obscuripes* Forel. Wheeler (1908a, p. 76) working in the nests of *Formica microgyna* Wheeler found the adults of *C. wheeleri* (LeConte) and a single cetonine larva that might have been that of *C. wheeleri*. It was buried in the vegetable debris in the nest.

Wheeler (1908a, p. 76) stated: "Nothing is known concerning the development of *Cremastocheilus*. The larval and pupal stages are passed, in all probability, in the ant nests, and from what has been learned of allied forms, like *Cetonia*, we should expect to find the larva in the vegetable debris of the nest." Wheeler (1910) made this statement positive: "The larvae live in the debris of the nests, like the larvae of *Cetonia* and pupate in fragile earthen cocoons (Wheeler, 1908e)." This reference is to his paper entitled "Honey Ants, with a Revision of the American Myrmecocysti" (1908b) in which no reference to *Cremastocheilus* can be found. Furthermore, no reference to *Cremastocheilus* pupae is made in his 1908 paper entitled "Studies on Myrmecophiles. I. *Cremastocheilus*" and therefore no further information is available on this first and only reference to pupae.

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Although the information in the above cited papers is fragmentary, it indicates that there is probably more than a casual or accidental relationship between some *Cremastocheilus* beetles and various ant species. Scattered references to the behavior of these beetles with ants outside the nests also tends to support this assumption. The exact nature of this association is not as yet clear, as was indicated by Cazier and Statham (1962). This latter study dealt with the behavior and habits of *C. stathamae* Cazier and its relationship with the honey ant *Myrmecocystus mimicus* Wheeler outside of the nest entrances. The present study was undertaken to gain information on the behavior and habits of the same scarab species on the inside of the ant nests in the hopes that such information would establish the true relationship. Observations on several other species of *Cremastocheilus* are included for comparative purposes. Between January and April of 1962 the authors excavated and cultured one partial nest of *M. mimicus*, six complete nests of *M. mexicanus* Wesmael and the *C. stathamae* that were found with the latter species.

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Cremastocheilus stathamae Cazier

HABITAT.

The area from which the material was collected was on the eastern foothills of the Chiricahua Mountains, Cochise County, Arizona, two miles northeast of Portal at an elevation of 4,700 feet. Many colonies of both *M. mimicus* and *M. mexicanus* were present in this location in which the dominant perennial shrubs were tar-bush (*Flourensia cernua* DC.), creosote-bush (*Larrea tridentata* [DC.] Coville), mesquite (*Prosopis juliflora* [Swartz] DC.), salt-bush (*Atriplex canescens* [Pursh] Nutt.), white thorn (*Acacia constricta* Benth), catclaw acacia (*Acacia greggii* Gray) and joint-fir (*Ephedra trifurca* Torr.). There were also scattered plants of the perennial herb snake-weed (*Gutierrezia microcephala* [DC.] Gray). The edaphic conditions consisted of a mixture of sand and soil in varying depths overlaying caliche, and the ant nests were found in the open areas among the above-mentioned plant species.

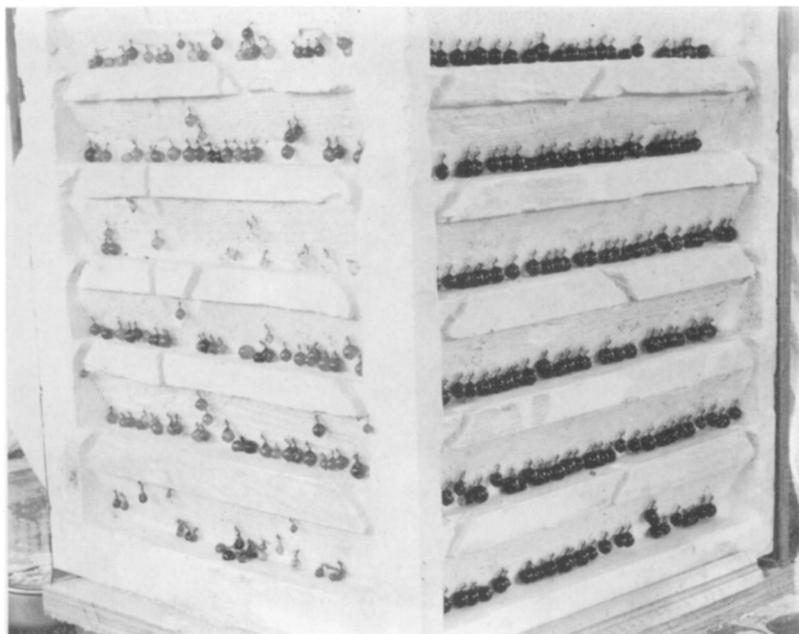


Fig. 1. Two sides of large formicarium, glass removed, showing runways with repletes of *Myrmecocystus mexicanus* installed on sloping rear walls.

PROCEDURE.

Formicaria construction. Before excavating the ant colonies, formicaria of two sizes were constructed of glass and plaster of paris. The large size was 14" square by 16" high and the small one was 10" by 6" high. Because of the weight and expansion of the plaster of paris the large formicaria were formed with wood, with and without attached forms for the runways; the small-sized ones were poured directly into the glass sided forms. The runways were carved out with an electric hand drill. Those on each side were connected with each other and with those on adjacent sides by small holes back of the corners and to the food and loading chambers on top by means of slanting holes. All runways and the entire food and loading chamber on top were covered with glass, the latter by a sliding panel, so that all portions of the formicaria were exposed for observation. One or two holes were drilled down through the top, behind but not connected with the runways, for insertion of water to maintain a moisture balance (Fig. 1).

Excavating. The excavations were started about four feet away from the nest entrances where a hole about two feet square by two feet deep was dug. Working from this hole the earth toward the nest entrance

was carefully removed down to this depth and as the lateral subsurface passageways were encountered they were followed individually to their terminations. Some of these extended on the opposite side of the nest entrance but were easily followed by working into them from the side. Once this two-foot level was reached another one- or two-foot hole was dug at the far end of the trench and the same procedure followed working in toward the nest. As the excavation proceeded, depth measurements were made, the burrows diagramed, and the contents of the passageways and chambers recorded. All the ants, their brood, repletes and the beetles were taken alive and transferred to the formicaria.

Myrmecocystus mimicus.

On January 31 and February 1, 1962, a nest of the diurnal *M. mimicus* was excavated to a depth of 43 inches without producing any *Cremastocheilus* or the queen of the colony. The first brood cells were encountered at 27 inches and the first repletes were located in cells with larvae at 37 inches. About 1,000 larvae, 100 major and minor workers, eight full repletes, eight semi-repletes and one deplete were placed in a small formicarium and given a dilute honey solution for food. On February 12, 1962, after the ants seemed to be adjusted to their new surroundings, a male and female *C. stathamae* taken on this date from a nest of *M. mexicanus* were introduced into the food chamber where many of the workers were feeding on the honey solution. The reaction was immediate and violent as the ants left the food to attack the beetles, chewing on the legs and body and dragging them around the food chamber. These same reactions were exhibited by the ants during the following 62 days. A third *C. stathamae* from a *M. mexicanus* colony was introduced on February 15, 1962 and was greeted with the same hostile actions by the *M. mimicus* workers. These observations confirm those made by Wheeler (1908a, p. 72) when he transferred *C. castaneae* from *Formica schaujussi* to *F. integra* nests. These reactions must be the result of the colony odor adhering to the beetles since it has already been shown (Cazier and Statham, 1962) that *C. stathamae* occurs commonly with *M. mimicus*, which haul the beetles in and out of their nests. The longevity of the antagonistic reactions may be due to the fact that the adult beetles feed on the larvae of the ants and the odor might therefore be expected to last for a considerable period.

Myrmecocystus mexicanus.

General observations. Because of our failure to locate *Cremastocheilus* in the *M. mimicus* nest, we excavated a nearby nest of the nocturnal *M. mexicanus* from which no beetles have previously been recorded. Nine specimens of *C. stathamae* were found in this nest and between February 10 and April 8, 1962, six nests of *M. mexicanus* were excavated completely and their entire contents, including the queens, transferred to

formicaria. These nests varied in depth from 30.5 to 92 inches with four of them between 43 and 48 inches. A total of 57 adult *C. stathamae*, 29 males and 28 females, were found at varying depths but no eggs, larvae or pupae could be located. In only two nests were the remains of solid food found and these were the dried pieces of the exoskeletons of five or six weevils (*Eupagoderes*, *Dinocleus* and *Cleonus*) which were scattered in passageways at depths of six to ten inches. The only refuse storage chambers encountered were those packed with infrabuccal pellets. Evidently these ants return the remains of insects to the surface and scatter them over the ground away from the nest entrance. No plant storage was evident in any of the colonies even though numerous empty and available chambers were located at shallow depths. *M. mimicus* and *M. mexicanus* have been observed returning vegetable and animal debris to the surface during the summer months and evidently do not maintain an underground storage for this material. This indicates that at least with these ant species the *Cremastocheilus* larvae could not live in the vegetable debris of the nests as postulated by Wheeler (1908a, p. 76). The only available food for them would be the ant brood (eggs, larvae and pupae) or the repletes, or they might be fed by the workers.

TABLE 1. Number and percentage of *C. stathamae* found at various depths, five-inch increments, in six nests of *M. mexicanus*. Also total depth of nests.

Depth in inches	Nest number						Total No. <i>C. stathamae</i>	Percent of all <i>C. stathamae</i> found
	1	2	3	4	5	6		
1-5		2	2	6	8	3	21	36.8
6-10		1		3		1	5	8.8
11-15		1	1	3			5	8.8
16-20	2	2		1			5	8.8
21-25				5			5	8.8
26-30		4					4	7.0
31-35			1				1	1.8
36-40	5		1				6	10.5
41-45	2	1	1		1		5	8.8
Total Depth of Nests	44	48	44	43	92	30.5		

Depth in nests. From four to 18 *C. stathamae* were found in each nest at depths from one to 44 inches below ground level. In mound building ants Hamilton (1888-1889) found *C. canaliculatus* only in the mound material, not below ground level. In Table 1 it can be seen that the majority (36.8 percent) of the beetles were found within one to five inches of the surface and that none were found below 44 inches even though in two cases the burrows extended below this level, to 48

and 92 inches respectively. In the smallest nest, 30.5 inches, all the beetles were found in the first 10 inches. However, the *C. stathamae* were generally distributed between six and 44 inches, the lowest number being between 31 and 35 inches.



Fig. 2. Adult *Cremastocheilus stathamae* Cazier in burrow with workers.

Location in nests. Their positions within the colonies, relative to nest structure and contents, were variable but included practically every situation. The greatest number (21) were found in empty, terminal cells, with or without workers present. Three were in dead end, empty burrows; five were in similar burrows with workers (Fig. 2); five were in the main vertical burrow; one was at the top of an infrabuccal pellet storage cell; two were in a burrow leading to a replete and worker brood chamber; one was in a cell containing worker brood and weevil remains; two were in cells containing repletes and workers; six were in cells containing worker brood and workers; seven were in chambers containing repletes, worker brood and workers; and four were at or near the bottom of nests in chambers containing repletes, worker and sexual brood, workers and the queens. A total of 39 of the beetles were in burrows or cells in which there were no ant larvae and were located in the first 25 inches of the nests. Eighteen were in chambers below the 21-inch level along with ant brood. Some of the beetles had their anterior ends buried in crevices or small holes in the chambers or burrows, whereas others were found moving about. In no case were any of them being molested by the ants. In all nests excavated the burrows and cells were sufficiently large to permit the entry of the beetles and the presence of such a high percentage of them in the upper portions of the nests might be due to the more crowded conditions lower down and the increased worker activity at these levels. The adult *Cremastocheilus* evidently go for considerable periods without feeding and may enter the lower portions of the nests only when in search of food. In the case

of *C. stathamae* and *M. mexicanus* this would be in search of the ant larvae.

When the contents of the six nests of *M. mexicanus* were transferred to formicaria, the *C. stathamae* in each were kept with them except in colony 7 from which three were used in the tests with *M. mimicus* reported above. The workers allowed the beetles access to all portions of the nests without serious interference although on several occasions single workers would attempt to pull them about by the legs, clypeus or thoracic angles. This indifferent behavior persisted for about 120 days when it was observed that the workers were keeping the beetles up in the loading or feeding chambers most of the time, hauling them back and forth as if trying to expel them from the nests. Had they succeeded, this would have put the beetles out of the nests in June, which corresponds to the time natural breeding was observed in the field. In many cases ants would place the beetles on the refuse piles in the feeding chamber and return them to it whenever they attempted to walk away. In the beginning a few of the beetles burrowed into these refuse heaps, which consisted primarily of dead workers, pupal cases, pieces of plaster of Paris or the remains of other insects, and it was hoped that egg laying would result. Numerous attempts to recover eggs met with failure and it is doubtful that these adults were laying.

Feeding behavior. This was first observed on February 13, or three days after colony 1 was caged, when a beetle was found in the feeding chamber with an ant larva half ingested head first. The larva was still moving, the meconium had been pushed out through the rectum, and a worker was attempting to pull the larva away from the beetle. During the next 120 days many different beetles were seen feeding in the various cultures and with few exceptions the ants paid little or no attention to them. The beetles in turn were cooperative in that they continued feeding while being removed from the formicaria for photographic purposes (Fig. 3). On February 16 a *C. stathamae* was observed as it began to feed on a larva caudal end first. The head end was twisting about and when about one third of its body had disappeared it was discovered by a worker who immediately seized it with its mandibles and attempted to pull it out. Being unsuccessful, the ant investigated the beetle for about 20 seconds, returned to the larva, regurgitated and fed it while it was being ingested. It took the beetle 30 minutes to consume this medium-sized larva. The longest observed period was one hour and 43 minutes but the beetle wasn't being harassed by workers during the process and the larva was a large one. The average time was about 30 minutes, but no definite figures are available because of the difficulty in spotting beetles when they first start feeding.

Although some of the larvae were being consumed caudal end first, the great majority were ingested head first. The reason for this appears to be inherent in the behavior of the larvae rather than selectivity on the part of the beetle. When the larvae have been fed and are undisturbed,



Fig. 3. Adult *Cremastocheilus stathamae* Cazier feeding on larva of *Myrmecocystus mexicanus* Wesmael. Posterior end of larva protruding beneath clypeus and between the palpi.

they are lying on their backs with the head bent downward onto the ventral surface. When hungry or being disturbed by workers or *Cremastocheilus* the head is elevated at right angles to the body, the anterior two or three segments of the body are extended upward, and they lean toward the oncoming workers or beetle. Larvae have been observed exploring the mouthpart area of disinterested beetles with their heads, evidently trying to get food and not being able to distinguish between worker ants and beetles. When the beetles are interested in feeding, the anterior portion of the mentum, which completely covers the mouthparts, is lowered, creating an opening between this structure and the clypeal margin. The head is then lowered so that this opening is on the larva or, more commonly, the larva will insert its head into the opening where it is evidently grasped by the beetle's mandibles and maxillae. The palpi can be seen moving in and out laterally and are

evidently synchronized with the opening and closing of the mentum as the larva is drawn slowly into the buccal cavity. When workers attempt to pull the larva out, the palpi cease to move and the mentum is closed on the larva. No cases were seen where worker ants were successful in extracting a larva while it was being ingested. Since the midgut containing the meconium is not connected with the hind gut or rectum in the larvae, its being voided in some cases must have been due to the rupture of intervening tissue through pressures applied by the beetle's mentum.

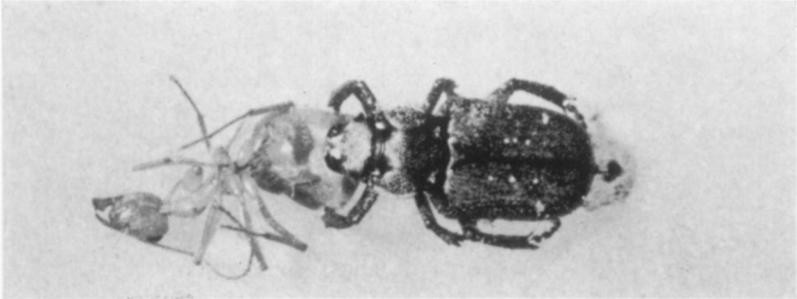


Fig. 4. Adult *Cremastocheilus stathamae* Cazier feeding on liquid or tissue of a deplete (deflated replete).

In only one case was an adult of *C. stathamae* observed feeding on materials other than ant larvae in any of the nests. On February 13, a beetle was found feeding on the juicy, apical portion of the abdomen of a deplete (Fig. 4). When both were removed from the formicarium for photographic purposes, the beetle disengaged itself from the deplete and refused to resume its feeding activities even when replaced in the nest. It was evidently feeding on the sweet solution that covered the apex of the deplete's abdomen. There was no evidence that any of the beetles attacked the repletes either in the natural nests or formicaria, even though they were in close contact with them. Also, they made no attempt to feed on either the ant eggs or pupae in the formicaria although exposed to both. In the colony that was being fed only on other insects, primarily flies and moth caterpillars, no beetles made any attempt to feed on these materials nor were any observed being given regurgitated food by worker ants.

Although most of the larval feeding activities of the adult beetles were treated with indifference by the ants, on two occasions the workers appeared to resent the presence of a beetle. In a cell containing many worker brood, three repletes, three semi-repletes, and a beetle, the workers overnight removed all the brood from this cell, but on the following day when the beetle moved to an adjacent cell containing both brood and repletes no such removal activities took place nor was any attempt

made to evict the beetle. The first brood removal may have been part of the normal shifting of brood from place to place in the formicarium, an activity which consumed much of the time of many workers. On another occasion a small male *C. stathamae* was found trying to ingest a large worker larva, caudal end first, while three workers were busily hauling other brood away from the vicinity and occasionally trying to pull the larva away from the beetle. At the end of 21 minutes the beetle dropped the larva, which was evidently too large for him, and stood over it. It took the three workers 12 minutes to get this larva out from beneath the beetle and carry it away, apparently uninjured.

Horn (1871) was evidently the first to observe the feeding behavior in the adults when he recorded that *C. schauumi* LeConte and *C. angularis* LeConte were frequently found in ant nests and that in one instance they were apparently eating ant pupae. Wheeler (1908a, p. 74) postulated that the adults required no food, since he hadn't seem them eating anything in the nests or being fed by the ants during a three-to seven-weeks observational period. Howden (1960, *in litt.*) found an adult of *C. armatus* Walker feeding on an ant larva.

Comparative feeding behavior. Ritcher (1958) in his "Biology of Scarabaeidae," lists the known food habits of members of the subfamily Cetoniinae as follows: "Larvae on dung, humus, and wood; adults on seed plants." The latter includes the habits of many adult Cetoniinae that feed on plant juices, either sap (Linsley and Cazier, 1963) or juices of ripened or overripe fruit, and those that occur commonly on flowers where they feed on pollen and nectar or the flower parts. Although the saprophagous and phytophagous feeding habits categorize most of the species belonging to the large family Scarabaeidae, to these should be added carnivorous to include the species known to be facultative carnivores as adults and *Cremastocheilus* which, in at least some species, appear to be obligatory in this habit in the adult stage. Buttiker (1955) working in South Africa observed the adults of the cetoniid *Pseudopilophorus plagosus* (Boh.) preying on the scale insect *Coccus hesperidum* L. in a citrus orchard. As many as 27 beetles were found on a single orange tree and all were confined to branches infested with the coccid. Steyn (1960) working on the South African social spider *Stegodyphus mimosarum* Pavesi found adults of *P. plagosus* in the spider nests on seven or eight occasions and proved that they were feeding on the spiders. Since live, active, adult *P. plagosus* were found only inside the silken passages of large *Stegodyphus* nests where there were no insect cadavers he concluded that this cetoniid is araneophagous. Related species belonging to the genus *Pseudopilophorus* have been found in bird nests where both larvae and adults feed on dung. It seems probable therefore that *P. plagosus* may be normally saprophagous but on occasion is also a facultative carnivore (araneophagous and entomophagous).

In the scarab subfamily Dynastinae, tribe Phileurini, Linsley and

Hurd (1959) working on the larval habits of the cerambycid beetle *Plinthocoelium sauveolens plicatum* (LeConte) report that: "In two cases scarab larvae were present in the roots, in one instance associated with the adult scarab, *Phileurus illatus* LeConte, which had worked its way up a burrow in a root and destroyed a larva of *Plinthocoelium*." This appears to be the first and only record on feeding behavior for any species in this tribe and indicates that at least on occasion the adults may be predaceous.

In the subfamily Troginae, Hayward (1936) reports that the larvae of *Trox suberosus* F. in Argentina are predaceous on the eggs of the grasshopper *Schistocerca paranensis* Burm. Most of the species in this genus, including *T. suberosus*, are known to be primarily saprophagous. In the subfamily Aphodiinae, Howden (1955) has reported that *Aphodius* species will develop in the dung cells buried by other scarabs and that their larvae destroy and may consume the eggs or larvae of the host. He observed five cases in which the immature stages of *Onthophagus* were destroyed by the larvae of *Aphodius lividus* (Oliv.). Most of the members of this and related genera are known to be saprophagous. Additional references to the facultative predaceous habits of Scarabaeidae can be found in Ritche, 1958, pp. 325-326.

From the above it can be seen that carnivorous feeding habits have arisen independently in a number of distinct subfamilies of scarab beetles but that in all known cases it is facultative and evidently a divergence from the normal saprophagous habit. Lacking evidence to the contrary, it appears that at least four species of *Cremastocheilus* (*schaumi*, *angularis*, *armatus* and *stathamae*) are obligatory carnivores, feeding on the larvae and pupae of various ant species. The structure of the beetle's mouthparts and more especially the enlarged mentum, appears to be a limiting factor in food choice but evidently does not prevent larval and liquid ingestion as was observed in *C. stathamae*. The intake of liquid food or water has not been recorded under natural conditions even though several species (*armatus* and *schaumi*) have been found in numbers attracted to damp spots along dirt roads.

Mating habits. On June 16, 1961 the writers, accompanied by Dr. Paul O. Ritche, discovered the natural breeding site of two species, *C. stathamae* and *C. constricticollis* Cazier. The area was immediately adjacent to the location described in this paper under the subheading HABITAT and was about one half mile south of the location described by Cazier and Statham (1962). The site consisted of a dry, earthen, catch basin or tank and the dry, sandy wash leading into it from the adjacent foothill area. Several specimens of *C. stathamae* were observed in midmorning, walking on the sand at the western end of the tank at the entrance to the wash, and additional specimens were walking along the sandy bottom of the steep-sided wash. About 50 feet west of the tank in the bottom of the wash there was a mesquite tree from which several limbs were bent down to the sand and around which small piles

of debris, leaves and twigs, had been washed. Several singles and a greater number of copulating pairs of *C. stathamae* and *C. constricticollis* were found on the slightly moist sand beneath the accumulated debris. None of these specimens were being tended or harassed by ants.

Mating behavior was recorded by Lugger (1891) who noted adults of *C. knochi* LeConte copulating in an open field during the early spring. Wheeler (1908a, p. 76) observed *C. castaneae* Knoch and *C. canaliculatus* Kirby in copulation in the outer galleries of *Formica schaufussi* Mayr nests in April. None of the *C. stathamae* excavated from ant nests between January and early April were in copulation and during the 275–306 days that they were kept under observation in formicaria only one pair mated. Males were occasionally seen riding females but their genitalia were not engaged. The mating occurred on April 1, which is over two months prior to their normal observed mating period outside the ant colonies and was possibly induced by artificial conditions. From this meager information it appears that some species mate within the confines of the ant nests (*castaneae* and *canaliculatus*) whereas others mate outside (*knochii*) or seek out a special environment for such purposes (*stathamae*, *constricticollis*). It seems probable, however, that the location for mating is not strictly fixed in any one species and we suspect that it may occur in several different situations.

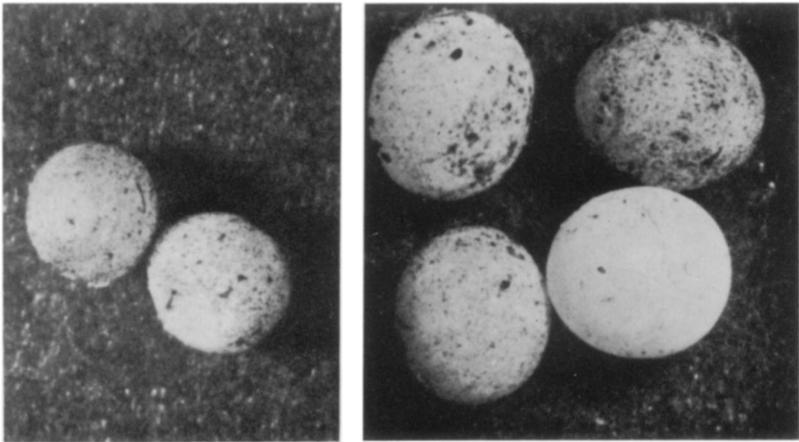


Fig. 5. (Left) Eggs of *Cremastocheilus stathamae* Cazier.

Fig. 6. (Right) Eggs of *Cremastocheilus constricticollis* Cazier.

Egg laying. Two pairs of *C. constricticollis* and five pairs of *C. stathamae* were placed in petri dishes where it was observed that they remained in copulation for several hours and that females mated more than once, at least in confinement. Unfortunately, egg laying took place before the females were segregated and we therefore have no figures on the number laid per individual. Eggs were laid by both species between

July 21 and 26, 1961, or between 35 and 40 days from the time they were collected in copulation. The eggs of both species are nearly round and white in color. Those of *C. stathamae* averaged about 1 mm in diameter while those of the larger *C. constricticollis* averaged about 1.5 mm in diameter (Figs. 5 and 6). Under laboratory conditions all eggs were desiccated from 12 to 15 days after being laid. If these eggs are desposited in the ants' nests there would be no problem in separating them from the ant eggs. In *M. mexicanus* the eggs are elongate, 1 mm \times .5 mm, and amber in color. No eggs of *C. stathamae* were found in any of the ant nests excavated.

Life cycle. The only positive indication we have that *Cremastocheilus* passes its life cycle within ant nests is the record by Mann (1911) who found the larvae of *C. pilosicollis* in the nest of *Formica rufa obscuripes*, the questionable record by Wheeler (1908a, p. 76) who found a single cetoniine larva that might be that of *C. wheeleri* in the nest of *Formica microgyna*, and a recently received record by Windsor (1964, p. 206) who found the larvae and adults of *C. wheeleri* in the nests of *Formica obscuripes* Forel at Manitou Park, Colorado. These observations indicate that at least *C. pilosicollis* and *C. wheeleri* complete their life cycles in *Formica* ant nests where stored plant and animal materials are available for larval food. We know that the adults of 24 species belonging to two genera of North American Cremastocheilini are found in close association with ants belonging to 11 different genera and that they spend a considerable portion of their adult life in the ants' nests. This fact has probably been responsible, in part, for the assumption that all species of Cremastocheilini complete their life cycles in ant nests. The information on *C. stathamae* presented above strongly supports the conclusion that the immature stages of this beetle are not in the nests of *M. mexicanus*, even though the adults are present in numbers.

Ritcher (1958) reports that scarabaeid larvae are known to molt from three to 11 times and that the mature larvae construct a cell in which to pupate. In the Cetoniinae the life cycles are known to vary from one to three years. Under natural conditions we found *C. stathamae* mating outside ant nests on June 16 and these females laid their eggs under artificial conditions between July 21 and 26. Even if we assume that *Cremastocheilus* has a one-year life cycle, we should have found larvae or pupae in the nests excavated between January and April. As stated previously, *M. mexicanus* has no storage chambers for plant or animal materials on which the beetle larvae could feed, which precludes their living in the vegetable debris of the nest as proposed by Wheeler (1908a, p. 76). In order to be successful in the nest of this ant the beetle larvae would either have to be predaceous on the ant brood, or be fed by the workers or by the adult beetle. It seems unlikely that any of these would be the case and we assume that the immature stages of *C. stathamae* are to be found in other situations. In the scarabaeids adult behavior and feeding habits more often than not have no relation-

ship with the larval habitat. An outstanding example of this phenomenon is the scarab *Plusiotis gloriosa* LeConte in which the adults feed and mate on *Juniperus* sp. and the immature stages are found in dead, decaying logs of sycamore (*Platanus wrightii* Wats.). The adult behavior in *Cremastocheilus* may be misleading with respect to where the immature stages are to be found but it will be surprising if more of them are not eventually proven to pass their life cycles in the nests of ants and more especially those that store plant and animal materials.

Cremastocheilus hirsutus Van Dyke

Nothing has previously been known about the habits of this uncommon scarab or of the ant species with which it is associated. The following observations on the adult beetles were made outside the ant nests to get data on seasonal occurrence, relationship of activity to moisture conditions and the possible effect the presence of sexual forms of the ants might have on the worker ants' behavior toward the beetles.

HABITAT. The following observations were made on a study plot located one mile east of Douglas, Cochise County, Arizona. The area was about 300 yards long, north and south, by about 100 yards wide, east and west, extending along a drainage dike which had been scraped up from both sides. All the observations were made on the gently sloping eastern side of the dike where the ground varied from being sandy, sand mixed with soil, heavy loam, or clay with spots of exposed caliche. There were many kinds of annual and perennial herbs in the large open area, which was surrounded on all sides by a rather dense stand of *Larrea tridentata* (DC.) Coville with a scattering of *Prosopis juliflora* (Swartz).

Although a few of the *Pogonomyrmex* nests that were kept under observation were located in this surrounding shrub belt, most of them were in the open area where the ants were operating in competition with the following herbaceous plants in maintaining the clear area around their burrow entrances. The most important of these were: peppergrass (*Lepidium montanum* var. *canescens* [Thell.] C. L. Hitchc.), horse nettle (*Solanum elaeagnifolium* Cav.), hog potato (*Hoffmanseggia densiflora* Benth.), desert marigold (*Baileya multiradiata* Harv. and Gray), and crownbeard (*Verbesina encelioides* var. *exauriculata* R. and G.).

OBSERVATIONS. There were many nests of a number of species of ants on this plot but the most prominent were those of two species of *Pogonomyrmex*, *P. barbatus* (F. Smith) and *P. maricopa* Wheeler. Although daily observations were being made on this plot in connection with other projects, beginning on May 4, 1962, it wasn't until July 4, 1962 that the first specimen of *C. hirsutus* appeared on one of the 47 nests that were being checked from one to three times each day. At 8:30 AM on this date a male *C. hirsutus* was being expelled from a colony of *P. barbatus* by eight workers who had succeeded in dragging

him 5.5 feet from the nest entrance. No further *C. hirsutus* activity was evident at any of the nests until after the first heavy rain soaked the plot on the evening of July 25, 1962.

The morning of July 26 was cool and overcast and surface activity of the ants was greatly reduced; most colonies showed no activity. By midafternoon it was warm, and sexual forms begin to appear at the nest entrances to most colonies. Between 5:36 and 7:25 PM five beetles, three males and two females, were found being expelled from five different *P. barbatus* nests and one female was being pulled away from the nest entrance of *P. maricopa* at 7:15 PM. From three to six workers were involved in each case, the beetles were from two to five feet away from the nest entrance and each colony had winged males and females in the nest entrance.

Although the plot received another soaking rain during the night of July 26, it warmed up earlier on July 27, and between 11:00 AM and noon three *C. hirsutus*, one female and two males, were found being expelled by from six to eight workers of *P. barbatus*. The beetles were found between one and two feet of the nest entrance. One male was found about 15 feet from the nearest nest walking unattended by ants. Between 12:00 and 12:45 PM one male and two females were being evicted from one colony of *P. barbatus*, each beetle had three workers pulling on it and they were from 3.5 feet to six feet away from the nest entrance. Two females were being expelled from two other nests of the same ant species by three and four workers, respectively, who had the beetles 2.5 and four feet away from the nest entrances. On this date nine *C. hirsutus* were being or had been expelled from six different colonies of *P. barbatus*, five of which had winged males and females at the nest entrances when the beetles were found.

On July 28 at 10:18 and 11:35 AM two females were found in two different *P. barbatus* nests, each covered with a ball of 16 workers who were trying to get the beetles out of the nest entrances which were in shallow depressions. Between 11:25 AM and 12:08 PM two more females were being evicted from two different colonies of *P. barbatus* by six and eight workers, respectively, who had them from three to four feet away from the nest entrances. At 6:00 PM a male and female were being expelled from the same *P. barbatus* colony by three and five workers who had them from two to four feet away from the nest entrance. At 11:40 AM three workers of *P. maricopa* were pulling a *C. hirsutus* female into their nest while winged males and females were in the entrance. Of the five *P. barbatus* colonies from which six beetles were being evicted, four had winged sexuals in the entrance.

On July 29 at 11:53 AM and 12:25 PM, two females of *C. hirsutus* were covered with 22 and 12 workers of *P. barbatus* in two different colonies where the workers were trying to get the beetles out of the nest entrances which were in shallow depressions. At 10:37 AM and 12:13 PM two males were being brought out of two different colonies of *P.*

barbatus by four and five workers who had the beetles four and 4.5 feet away from the nest entrances. Winged sexual forms were in evidence at the nest entrances of all four of these colonies. At 6:00 PM a female was found nine feet from a *P. barbatus* colony walking away from it unattended by workers.

Of the 28 specimens, 11 males and 17 females, of *C. hirsutus*, all but one were found in the four-day period following the first soaking fall rain in the area. During this period most of the colonies had winged sexual forms around and in the nest entrances but no concentrated mating flights were observed. As in *C. stathamae* and *M. mimicus* (Cazier and Statham, 1962), many workers were required to get the beetles out of the nests and the number gradually decreased as the beetles were pulled further and further from the nest entrance until at about nine feet all ants had dropped off. During this period only one *C. hirsutus* was seen being brought into a colony.

Cremastocheilus planipes (Horn)

OBSERVATIONS. This species has been recorded previously only in association with *Formica obscuripes* Forel, Wheeler (1908a, p. 70) and Cazier and Statham (1962). We now know that it occurs with two species of *Pogonomyrmex*, *P. barbatus* and *P. maricopa* in the location described above for *C. hirsutus*. On July 20, 1962 at 7:15 PM, a female of *C. planipes* was found being escorted into the nest of *P. barbatus* by three workers. The beetle was headed toward the nest entrance of its own accord with an occasional assist from the three workers who stayed in its immediate vicinity. This was five days before the first fall rains soaked the area and no winged sexual forms were in evidence at the nest entrance. On July 29 at 12:03 PM, 19 workers of *P. maricopa* were trying to get a female beetle out of their nest entrance where both winged males and females were present but were not engaged in the eviction activities. Both specimens of *C. planipes* were involved with ant colonies from which *C. hirsutus* specimens had been or were subsequently expelled.

Cremastocheilus saucia LeConte

Nothing has previously been recorded about the habits of this species or of the ants with which it is associated. Dr. J. G. Watts, University of New Mexico, collected two males on the nest mounds of *Pogonomyrmex occidentalis* Cresson at Ake Ranch, Catron County, October 6, 1961 and at Datil, Catron County, New Mexico, September 19, 1962.

Cremastocheilus (Macropodina) beameri Cazier

The only published note on the habits of any of the three rare species comprising this subgenus is that on *C. beameri* by Cazier (1961) who reported that "On July 14, 1959, Marjorie Statham collected two male

specimens flying about in an open mesquite thicket where the predominant ant nests were of the harvester *Pogonomyrmex barbatus* (F. Smith). While this is not conclusive proof of a more intimate association between the two species, it is indicative of what may eventually be found." The above collection was made one mile west of Portal, Cochise County, Arizona at an elevation of 4,800 feet, the same location in which the following observations were made.

HABITAT. As indicated above the study plot was located in the thorn-shrub area bordering Cave Creek and was at the mouth of Cave Creek Canyon where this type of vegetation fans out from the immediate vicinity of the stream bed. At this point, extending west of Cave Creek, the land rises in two abrupt steps of about 100 feet each, separated by about one half mile from each other by a relatively flat bench which at one time was under cultivation. The first bench, cleared portion, is now covered with grasses and various annual and perennial herbs but is bordered on three sides by thorn-shrub vegetation. The second bench slopes gradually upward and westward toward the foothills of the Chiricahua Mountains but it was in the first half mile that the study area was located.

The primary vegetation on this second bench consisted of an open stand of mesquite (*Prosopis juliflora* [Swartz] DC.), with a few scattered white-thorn (*Acacia constricta* Benth.), creosote-bush (*Larrea tridentata* [DC.] Coville), century plants (*Agave palmeri* Engelm.), prickly-pear (*Opuntia engelmanni* Salm-Dyck), and wait-a-minute (*Mimosa biuncifera* Benth.) Some of the mesquite shrubs were almost trees whereas others formed low multiple plant thickets with many of the branches on or near the ground. The soil was mostly a sandy loam with scattered small gravel on the surface. A few local areas were covered with coarse gravel or rocks and the small drainage channels contained spots of fine sand.

OBSERVATIONS. On July 7, 1963 the entire Portal area received a soaking rain during the day and a light drizzle that lasted until about 4:00 AM on July 8. By 8:30 AM on July 8 there was considerable *Cremastocheilus* activity on a study plot located at the Willy ranch in Portal and between this time and 10:00 AM three specimens of *C. lengi* Cazier, six of *C. constricticollis* Cazier, one of *C. stathamae* Cazier and two of *C. planipes* (Horn) were collected as they were being expelled from nests of *M. mimicus* Wheeler. At 10:00 AM we adjourned to the habitat described above and in which Statham (now Mrs. M. S. Favreau) had collected her specimens of *C. (M.) beameri* in 1959.

Between 10:00 and 12:00 noon, seven specimens of *C. hirsutus* Van Dyke were collected as they were being expelled or taken into nests of *P. barbatus* (F. Smith). One specimen of *C. hirsutus*, 15 specimens of *C. planipes* and one specimen of *C. constricticollis* were collected at the nests of *Novomessor cockerelli* (E. Andre). During this period Arthur Raske collected four specimens of *C. (M.) beameri* as

they were flying around between the mesquite bushes and were not associated with ant nests even though there were a number of large ones in the immediate vicinity. No specimens of this species were seen by the authors at numerous ant nests visited during this two-hour period.

Mating habits. From 1:00 to 5:00 PM on July 8, five females and eight males were collected and kept alive as they were flying into a low mesquite thicket which had branches on and next to the ground and under which there was a layer of loose, damp humus in depths varying between .5 to three inches. On digging into this humus on the south and southwestern sides of the thicket, seven females and 14 males, two pair in copulation, were found beneath the debris. On July 9, four males and three females were taken as they flew into and landed on the edge of three different mesquite thickets in the immediate vicinity. Three specimens were found beneath the humus under one of these thickets and none under the other two. All specimens were kept alive for further examination. From this it can be seen that the mating site and habits of *C. (M.) beameri* are like those reported for *C. stathamae* except that in the latter species the mesquite bush was in a dry, sandy wash.

Egg laying. This has not been observed under natural conditions. On July 8 and 9 eight females were confined in separate petri dishes and each was given one or two males. Mating took place almost immediately and all females mated several times during the following 30 days in confinement. They laid eggs from three to 16 days (average eight days) after the initial mating and each female desposited from 21 to 68 eggs (average 42). Four of the females laid their eggs on two successive days while the other four laid theirs in a single day, including the one that laid the maximum of 68. Most of the eggs were laid singly and scattered around the dishes but one female laid 21 in a large mass. The eggs were opaque white in color, obovate in shape, measuring from 1.25 to 1.35 mm in length and from .50 to 1.00 mm in width. We were unsuccessful in getting any of them to hatch.

The only comparative data are those already given for *C. stathamae* and *C. constricticollis* in which the eggs were laid from 35 to 40 days after confinement as compared to three to 16 days in *C. (M.) beameri*. Both sets of figures, especially the latter with its great variability, are subject to considerable error since we have no idea when these females were first mated, or how many times, before they were collected. However, in *C. stathamae* and *C. constricticollis* the eggs are nearly round whereas in *C. (M.) beameri* they are definitely obovate.

Life cycle. Nothing is known about the life cycle of this species or even where the eggs are laid or the immature stages are to be found. Cazier (1961) postulated that they might be found associated with *Pogonomyrmex barbatus* judging from two collecting records but in the light of what we now know this would appear to be erroneous. During the activity period of *C. (M.) beameri* many nests of *P. barbatus* and

N. cockerelli, openings sufficiently large to accommodate this scarab, were checked many times with negative results. In the same period 24 specimens representing four other species of *Cremastocheilus* were found in association with these two ant species in the same area where the *C. (M.) beameri* were flying. Although this is negative evidence and therefore not conclusive it does indicate that this species is probably not associated with these ant species.

Further evidence, although again not conclusive, was found to support the above opinion. During the same period and in the same location we were gathering information on two other scarab species which were found to breed in woodrat nests (*Neotoma* sp.). Two of these packrat nests were excavated on July 12 and in one the remains of three *C. (M.) beameri* were found in the damp vegetable and excrement debris at the entrance to one of the four nest tunnels. In the other nest we found the larvae of *Euphoria* sp. (fide P. O. Ritcher) and eggs that closely resemble those of *C. (M.) beameri*. These were buried from two to six inches in the wet, sandy, soil beneath the burrow floor and three feet in from its entrance. Unfortunately none of these hatched and we found no live adult *C. (M.) beameri* in the burrows. Both nests were under large *Opuntia engelmanni* plants that were next to or under large, open, mesquite bushes. It is possible that the adults were using the nest debris for mating purposes but at least this is a clue that might profitably be explored further.

DISCUSSION

The several thousand known myrmecophiles in the classes Insecta, Arachnida and Crustacea exhibit many different relationships with ants and may differ in these relationships depending on their developmental stages and on the behavior and existing conditions within an ant colony at any particular moment. Wasmann (1894) proposed four large and inclusive divisions for these myrmecophiles, which groupings were followed by Wheeler (1910) with some modifications. These divisions are as follows:

1. Inimically persecuted intruders, or synechthrans.
2. Indifferently tolerated guests, or synoeketes.
3. True guests, symphiles or myrmecoxenes.
4. Ectoparasites and entoparasites.

Wheeler (1908a, p. 75) concluded that "The cremastochili are not true guests, or symphiles, as Wasmann supposed (1894), but persecuted intruders (Synechthrans) that may eventually become indifferently tolerated guests (Synoeketes)." In 1910, p. 391, Wheeler changed his mind and stated "I am inclined, therefore, to regard the *Cremastocheili* as degenerate symphiles, which are now able to live as indifferently tolerated or even as persecuted synoeketes, because their armor shields them perfectly from the mandibles of the ants." In some ants, such as *Myrmecocystus*, the primary means of defense and attack lies in their

formic acid secretion rather than their mandibles, so it would also be necessary to assume an immunity or protective integument against this acid.

Since these major divisions of the myrmecophiles were based primarily on other groups and were proposed at a time when little was known about *Cremastocheilus*, it is not too surprising that we have found it difficult if not impossible to fit this genus into any of the divisions without proposing modifications in their definitions and limitations. Rather than doing this, we feel that it will be better to attempt an interpretation of the seemingly complex behavior patterns which have been observed and which, in some instances, appear to be antagonistic to each other. Our observations include those on *Cremastocheilus stathamae*, *C. constricticollis*, and *C. lengi* with the ants *Myrmecocystus mimicus*, *M. mexicanus* and *Novomessor cockerelli*. *C. mentalis* with the ants *Novomessor albisetosus*, *Pogonomyrmex maricopa*, *P. barbatus* and *Dorymyrmex pyramicus*. *C. hirsutus* and *C. planipes* with the ants *Pogonomyrmex barbatus* and *P. maricopa*. *Genuchinus ineptus* with the ants *Crematogaster coarctata* and *Liometopum occidentale luctuosum*.

The beetles may enter the ant colonies of their own volition or are found by the ants during their foraging activities and either pulled or guided into the nests as legitimate prey. All the above listed ant species collect both dead and live animal booty, either whole or in parts, and return it to the nest. It would be impossible for the smaller ant species to get a beetle to its nest were it not for the fact that the beetle is also motivated toward gaining access to an ant colony. A single *M. mimicus* worker attached to the clypeus of a beetle many times its own size will guide or act as a rudder for a *C. stathamae* traveling at the rate of about one foot a minute toward the nest (Cazier and Statham, 1962, p. 138). Other live beetle booty of smaller size than the *C. stathamae* required the attention of numerous workers to get it into the nest because of its resistance. A single *Novomessor cockerelli*, a much larger ant, will pick this same species up off the ground and carry it into its nest. *Novomessor albisetosa* was seen doing the same thing to *C. mentalis*, a larger species of *Cremastocheilus* (Cazier, 1961, p. 7). *C. mentalis* will dig its way, with the help of the ants, into the nests of *Dorymyrmex pyramicus*, an ant so small that 11 of them were unable to move a beetle (Cazier, 1961, pp. 7 and 8). Individuals of *C. hirsutus* and *C. planipes* were found being guided into the nests of *P. barbatus* and *P. maricopa* by three workers each.

We are sure that at least the above listed species of *Cremastocheilus* make every effort to gain access to the ant nests and we suspect that they are motivated in this behavior by at least two factors:

1. *Food*. We now know that the adults of *C. stathamae* are predaceous on the larvae of *M. mexicanus* and occasionally phytosuccivorous on stored solutions in dead repletes of this same species.

2. *Protection.* These beetles overwinter as adults and are well protected from the elements and perhaps their natural enemies while inside the nests.

We suspect that the beetle's activities and motivation to gain access to the nests is supplemented by its trichomes which increase its chances of being found by the ants. Although some writers have attached or postulated a gustatory significance to these organs, the writers have after hundreds of observations been unable to concur. Ants have been observed grasping the beetles by the thoracic angles, under which the trichomes are located, but in no cases have they been observed trying to lick them or to bring the hypopharynx into contact with the hairs. The thoracic angles, legs and clypeal margin are the only areas on the beetles onto which the ants can get a firm hold with their mandibles for pulling or directing the beetles and they spend less time on these angles than they do on the legs and clypeus. Furthermore, Wasmann has shown that these trichomes are located on the integument at points or in depressions where clusters of unicellular glands open and that they function in rapidly diffusing some aromatic secretion. He further concludes that the secretion is not liquid but volatile or etherial, perhaps a fatty ether. Ordinarily the beetle is slow moving and in most instances does not land immediately adjacent to or on the ant nests. The possession of glands secreting an aromatic, perhaps attractive, scent would greatly increase the beetles' chances of being detected by the ants and taken or guided into their nests as desirable items of food. Evidence that the trichomes, if they function as suspected, are of secondary importance or serve no necessary function exists in the related *Genuchinus ineptus* which lacks them and yet lives with two different genera of wood-inhabiting ants that we know of.

Once inside the nests the *Cremastocheilus* may receive preferential treatment because of the odors emanating from the trichomes or more likely their armament saves them from the same fate that attends other live booty. Our observations show that most of the time the beetles are treated with indifference in the nests, which would probably not be the case if the ants were able to "milk" the trichomes of a desirable secretion. They are allowed access to all parts of the nest down to a depth of 44 inches (*C. stathamae* in *M. mexicanus*) but the majority are found from one to five inches from the surface. The passageways in *M. mexicanus* are sufficiently large to permit the beetles easy access to the chambers containing ant brood upon which they feed. Even during feeding the mouthparts of the beetle are protected from the ants by the trapdoor-like action of the mentum which opens narrowly along its front margin, allowing the entrance of the larva, and closing on it when workers try to interfere. In most cases the ants paid no attention to the cannibalistic activities of the beetles; when they did, although concerned with trying to pull the larva out rather than to dispose of the beetle, their efforts were unsuccessful.

As stated previously, the movements of *Cremastocheilus*, under ordinary circumstances, are slow and sluggish and this may in part account for their being ignored by the ants. On being disturbed, the beetles insert their heads into cracks or depressions in the burrows where it would be impossible for a single ant to dislodge one. The beetles probably spend most of their time in the upper portions of the nests, in empty side tunnels and chambers, in order to avoid most of the worker activity which takes place in the brood chambers, lower down. When hungry, the beetles undoubtedly move down to the brood chambers, feed, and then perhaps return to burrows near the surface. This presupposes of course that the ants are behaving "normally" and are not engaged in hauling foreign objects or their sexual forms out of the nest. Cazier and Statham (1962) found that no specimens of *C. stathamae* were being expelled from the nests of *M. mimicus* during periods of clean-out activity or reduced ant activity caused by unfavorable climatic conditions.

The writers have observed *C. hirsutus* and *C. planipes* being taken both in and out of the nests of *Pogonomyrmex barbatus* and *P. maricopa* during the same period and Cazier and Statham (1962) recorded the same behavior for *C. stathamae* in the nests of *M. mimicus*. However, beetles being expelled from the nests are forcibly ejected by from six to 22 workers and resist being moved until the ants have escorted them from four to nine feet away from the nest entrance. When released at this point, which coincides in general to the distance to which refuse is hauled, the beetle usually walks or flies away but may return to the same colony under his own power or by being escorted back by a worker who was not involved in the eviction activities. Cazier and Statham (1962) were unable to account for this reversal in behavior and it wasn't until March and July of 1962 that the present writers made observations that appear to make possible a reasonable explanation.

From observations on *M. mexicanus* in formicaria we know that the workers become very excited when the winged sexual forms appear in the nests and that they are pulled or escorted toward the top of the nest by the workers. Field observations on *M. mimicus*, *Pogonomyrmex barbatus* and *P. maricopa* have shown the same type of worker excitement around the nest entrance just prior to and during the emergence of the winged sexuals from the nests. Wheeler (1910, p. 183) states, "It is certain that the workers forcibly detain the impatient sexes in the nests till the propitious hour arrives." We now know that in *M. mimicus* both winged males and females are present in the subsurface burrows (one to three inches), along with *C. stathamae*, as early as March 9 even though their nuptial flights occur in late July and early August after the first rains. This would mean a holding period of more than five months during which time sexual forms and their accompanying workers would be in close contact with the beetles who prefer these shallow burrows and cells. We have already shown that *C. hirsutus* and

C. planipes are evicted primarily from the nests along with the winged sexuals following the first fall rains and that such activities continue for about four days. Two specimens were being taken into nests but we don't know whether they would have been allowed to stay.

It would appear that during the prenuptial flight period most of the winged sexuals and many excited workers are present in the upper portions of the nest where the *Cremastocheilus* are most abundant. When conditions outside the nest are correct for the nuptial flight, these excited workers drive the winged sexuals up to the nest entrance along with other foreign objects, which would include the reluctant *Cremastocheilus*. Meeting resistance, the excited workers would tend to gang up on the beetle especially when and if it clogged a burrow. Once outside the nest entrance the number of workers involved diminishes as the beetle is taken further and further away until all have dropped off in the vicinity of where nest debris would normally be deposited. During these nuptial flight activities many workers carry on their routine foraging duties and if one of these happened onto a beetle that had been evicted she would take it back into the nest with the beetle's cooperation. The beetle didn't want to leave in the first place. Beetles evicted at other times may be victims of a carry-over of this excited behavior or they may have become obstructions in burrows. The longer period for such activities noted in *M. mimicus* may be due to the presence of winged sexual forms in the nests over longer periods of time. It is also possible that some of these beetles may have been from colonies of other ant species and were evicted because of their foreign odor. We have already described the antagonistic reactions of *M. mimicus* to *C. stathamae* that were taken out of an *M. mexicanus* colony.

Most of the *C. stathamae* that were brought out and released by *M. mimicus* flew almost immediately and may have gone in search of a mating site. This would mean that the bulk of the mating would take place after the first fall rains, a phenomenon we have not observed. We observed mating in the field on June 16, before the fall rains, and if the preceding statements are true then the outside breeding season should last from at least June to September, depending on ant activity. Wheeler (1908a, p. 76) observed mating in the outer galleries of nests in April and we observed copulation in formicaria in the same month, which might indicate either a much longer mating period or different mating periods depending on the location of the beetles.

With the information at hand we propose that the adults of at least some species of *Cremastocheilus* are obligatory predators or occasional modified phytosuccivores, who at times are welcomed by the ants, treated indifferently at other times, and periodically subjected to persecution by eviction. We have found no evidence that they contribute anything to the ant in exchange for their food, lodging and protection. Furthermore, we doubt that *C. stathamae* lays its eggs in the nests of at least *Myrmecocystus* since we found no larvae or pupae in the nests excavated

at a time when one or the other should have been present. The limited observations made on adults of *C. (M.) beameri* indicate that this species, and possibly this subgenus, may not be myrmecophilous.

SUMMARY

Between January 31 and April 8, 1962, one partial nest of the diurnal *M. mimicus*, six complete nests of the nocturnal *M. mexicanus* and 57 adult *C. stathamae* (29 males, 28 females) that were found with the latter ant species were cultured in formicaria. Field observations were made at the time the nests were dug and laboratory observations continued over a period of from 275 to 306 days. The following are contributions toward our better understanding of the relationship between the ants and their myrmecophilous scarab guests.

1. Adults of the diurnal scarab *Cremastocheilus stathamae* are winter residents in the nests of the nocturnal honey ant *Myrmecocystus mexicanus*. From four to 18 were found in each nest at depths of one to 44 inches below ground level and in practically every situation present in the colonies. Unfortunately we have no information on the nocturnal behavior of *M. mexicanus* in relation to the normally diurnal *C. stathamae*.

2. *M. mexicanus* nests have no winter storage cells or chambers for debris, which precludes the possibility of the larvae of *C. stathamae* developing in such a situation, at least with this ant. No eggs, larvae or pupae of *C. stathamae* were found in any of the nests and we suspect that they will be found in other situations.

3. *C. stathamae* adults were treated with indifference by the worker ants both in the nests and formicaria. However, when scarabs taken in nests of *M. mexicanus* were introduced into a nest of *M. mimicus* they were met with violent opposition which lasted for at least 62 days. This reaction on the part of *M. mimicus* workers is probably evoked in response to olfactory stimulation by the *M. mexicanus* colony odor adhering to the beetle.

4. Adult *C. stathamae* feed on the larvae of *M. mexicanus* and this appears to be the first obligatory predator known in the family Scarabaeidae. Only one specimen of the scarab was seen feeding on the liquid of a defunct deplete. None were observed feeding on ant eggs, pupae, repletes, or workers, although all were available. No vegetable or other palatable animal food was present in any colony and no workers were observed regurgitating to the scarabs.

5. Adults of *Cremastocheilus* have been seen mating in the galleries of ants by Wheeler (1908a, p. 76) and we observed one mating in a formicaria. However, the preferred breeding site of *C. stathamae*, *C. stricticollis* and *C. (M.) beameri* appears to be under damp debris beneath mesquite trees and thickets where they were unmolested by ants. In captivity they remain in copulation for several hours and the females mate more than once.

6. Nothing is known about normal egg laying in *Cremastocheilus* but under artificial conditions females of *C. stathamae* and *C. constricticollis* laid eggs between 35 and 40 days after being found in copulation. The eggs are white and nearly round; those of *C. stathamae* averaged 1 mm in diameter, those of *C. constricticollis* about 1.5 mm in diameter. In *C. (M.) beameri* the eggs were laid from three to 16 (average eight) days after confinement, they are white, obovate in shape and measured from 1.25 to 1.35 mm in length and from .50 to 1.00 mm in width.

7. Adults of *C. hirsutus* and *C. planipes* are now known to occur with *Pogonomyrmex barbatus* and *P. maricopa* in a location one mile east of Douglas, Cochise County, Arizona. Those of *C. saucia* were found on mounds of *P. occidentalis* in Catron County, New Mexico.

8. Of the 30 specimens of *C. hirsutus* and *C. planipes* only two were seen prior to the first fall rain that soaked the area. The remaining 28 were taken during the four days following this rain and in most cases winged sexual forms of the ants were present in the nest entrances. Only two of the 30 specimens were being taken into nests during this period.

9. A single species of ant, a single nest, sometimes has more than one species of *Cremastocheilus*. A single species of *Cremastocheilus (mentalis)* inhabits the nests of at least four species of ants belonging to three different genera. This lack of specificity would tend to support the conclusion that the beetles are considered to be booty by the ants.

10. From all indications the adults of *C. (M.) beameri* are not associated with ants and the immature forms may eventually be found in packrat (*Neotoma* sp.) nests.

11. *Cremastocheilus stathamae* appears to be an obligatory predator on the larvae of *Myrmecocystus mexicanus* and on occasion a modified phytosuccivor on the plant secretions stored in the repletes of this species.

12. In the four arbitrary divisions of myrmecophiles recognized by Wheeler (1910), the adults of several species of *Cremastocheilus* appear to exhibit behavior patterns at various times that would place them in all of these as follows:

A. *Synechthrans*. They appear to be inimically persecuted intruders at certain times when they are forcibly ejected from the nests.

B. *Synoeketes*. During most of the time in the nests, especially during the winter months, the adults are treated as indifferently tolerated guests even while eating ant larvae.

C. *Symphiles*. When the adult beetles are being brought into the nest they are amicably treated by the ants and assisted by them in gaining access to the nest. A *Cremastocheilus* being brought in does not receive the same treatment as other live booty and when ejected is alive and apparently healthy.

D. *Ectoparasites* and *Entoparasites*. Several species are now known to be predaceous on ant larvae and pupae.

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