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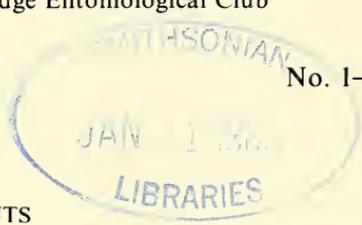
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Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

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Joseph Charles Bequaert

This issue of *Psyche* is dedicated to the memory of Joseph C. Bequaert, who died in his 96th year in Amherst, Massachusetts, on January 12, 1982.

Dr. Bequaert was born in Belgium in 1886 and was educated there, receiving his Dr. Phil. degree in botany in 1908 from the State University in Ghent. The next seven years he spent in the Belgian Congo (now Zaïre), at first as Entomologist on the Belgian Sleeping Sickness Commission and later as head of botanical explorations in the Congo for the Belgian Colonial Government. During those years his main interest shifted from botany to entomology, in which he subsequently did the greater part of his research and teaching. In 1917 he was appointed Research Associate in Congo Zoology at the American Museum of Natural History. Six years later, after becoming a naturalized citizen of the United States, he joined the faculties of the Harvard School of Public Health and the Harvard Medical School, as an assistant professor in medical entomology, and remained there until 1945. He then accepted the position of Curator of Recent Insects in the Museum of Comparative Zoology, succeeding Nathan Banks. In 1951 he was appointed Alexander Agassiz Professor of Zoology, a chair that he held until his retirement in 1956. Most of the remaining 26 years of his life were spent in Tucson, Arizona, where he was associated with the departments of entomology and zoology at the University of Arizona.

He was internationally known for his publications, totalling more than 250, on medical entomology, mollusks, botany, and systematics of several families of insects.

Joe joined the Cambridge Entomological Club in 1923, as soon as he reached the Boston area, and he was very active in the society for the next 33 years. He was president in 1928, 1935-36, and 1942-43; vice-president in 1937, 1941, and 1946; secretary in 1925 and 1926; and treasurer in 1943. He also served on the editorial board of *Psyche* from 1947-1956. He gave many of the scheduled talks at our regular meetings and was chosen as the speaker for the 500th meeting of the Club on December 15, 1931. In recognition of his services and contributions to the activities of the society, he was elected an Honorary Member in 1961.



JOSEPH CHARLES BEQUAERT

PHOTOGRAPH TAKEN IN BELGIAN CONGO, 1934

I first met Joe at the September meeting of the Club in 1923, at which he was nominated for membership. His exuberance and his extraordinary enthusiasm for nearly every aspect of natural history were the most obvious traits of his personality. In 1956 he wrote the following statement of his scientific interests: *ecology of flowers; taxonomy and ecology of Bryophyta; geography and ecology of African plants; relations of Arthropoda to disease; taxonomy and ethology of Diptera and Hymenoptera, particularly Vespidae; malacology; medical entomology.* He was certainly one of the most distinguished and respected entomologists of his generation.

Frank M. Carpenter, editor

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COMMUNICATION, RAIDING BEHAVIOR AND PREY STORAGE IN *CERAPACHYS* (HYMENOPTERA; FORMICIDAE)*

BY BERT HÖLLDOBLER

Department of Organismic and Evolutionary Biology,
MCZ - Laboratories
Harvard University, Cambridge, Mass. 02138 U.S.A.

INTRODUCTION

The former subfamily Cerapachyinae was recently recognized by Brown (1975) as a tribe (Cerapachyini) within the subfamily Ponerinae. All of the cerapachyine ant species investigated feed entirely on ants (see review in Wilson 1958; Brown 1975). During foraging cerapachyine workers engage in mass expeditions during which they raid the nests of the prey species, capturing preferably larvae and pupae, but also occasionally adults and returning them to the raiders' nest.

Although the detailed field observations on cerapachyine foraging raids reported by Wilson (1958) strongly suggest that the raiding expeditions follow chemical trails, this has not yet been experimentally investigated. In fact, almost nothing was hitherto known about the behavioral organization of the raiding expeditions and the underlying communication mechanism. This paper presents the first experimental analysis of the raiding behavior of a cerapachyine ant species.

MATERIALS AND METHODS

Three colonies of *Cerapachys (?) turneri* (turneri group) (accession #163a, b, c; voucher specimens in Australian National Insect

*Manuscript received by the editor January 22, 1982.

Collection, ANIC, Canberra) were collected from nests in the soil in a sclerophyl scrub pasture near Eungella, North Queensland (Australia). One colony had a single ergatoid queen; the other colonies had two ergatoid queens apiece. Each colony was housed in separate glass tube nests ($8\text{ cm} \times 0.6\text{ cm } \phi$), with water trapped at the bottoms behind cotton plugs. Each nest tube was placed into arenas of varying sizes, depending on the experimental design. Histological studies were conducted according to the procedures described in Hölldobler and Engel 1978. Additional methodological details will be given with the description of the individual experiment, as presented below.

RESULTS

Raiding behavior and paralysis of prey larvae

Species of the genus *Cerapachys* seem to preferably prey on ant species of the myrmicine genus *Pheidole* (Wilson 1958; Brown 1975). When I provided *Cerapachys* with colonies or fragments of colonies of a variety of species of the genera *Iridomyrmex*, *Meranoplus*, *Monomorium*, *Crematogaster*, *Pheidole*, *Stigmacros*, *Polyrhachis*, *Camponotus* (placed in a $65 \times 120\text{ cm}$ arena) they preyed freely only on *Pheidole*. They also accepted *Monomorium* larvae as prey, but only when these insects were directly inserted into the *Cerapachys* nest. When the *Cerapachys* workers encountered workers of the other species, or came close to their nest tubes, they usually showed avoidance behavior. The reaction was very different, however, when individual scouts of *Cerapachys* discovered the nest tube of *Pheidole* (accession #209, voucher specimens in ANIC). The *Cerapachys* worker vigorously vibrated its short antennae and moved slowly into the nest tube, which contained approximately 200 *Pheidole* workers and soldiers and about 150 larvae and pupae. It did not venture very far into the foreign nest but left after a short while and ran, in a somewhat meandering route, back to its own nest, located 70 cm away from the *Pheidole* nest. During homing it appeared frequently to touch the ground with its abdominal tip, as if it were laying a chemical trail or depositing scent spots. Seconds after it had entered the nest of its own colony, its nestmates became very excited. Many grouped around the scout ant, which repeatedly raised its gaster upwards. Within one minute the scout left the nest

again and moved in direction toward the *Pheidole* nest tube. It was closely followed by 17 nestmates. The leading scout ant continued to move with its abdominal tip close to the ground, but intermittently it paused or moved much slower while raising its gaster slightly upwards (Fig. 1). When the *Cerapachys* column arrived at the *Pheidole* nest tube they invaded it and attacked the *Pheidole* workers and soldiers. *Pheidole* fought back but without any effect. The heavily sclerotized and specially protected *Cerapachys* (Fig. 2) were not at all affected by the mandibular grip of the *Pheidole* soldiers, even when they were attacked simultaneously by 3–5 *Pheidole* (Fig. 3). Although *Pheidole* outnumbered the *Cerapachys* invaders more than 10 times, they were rapidly disabled by the obviously very

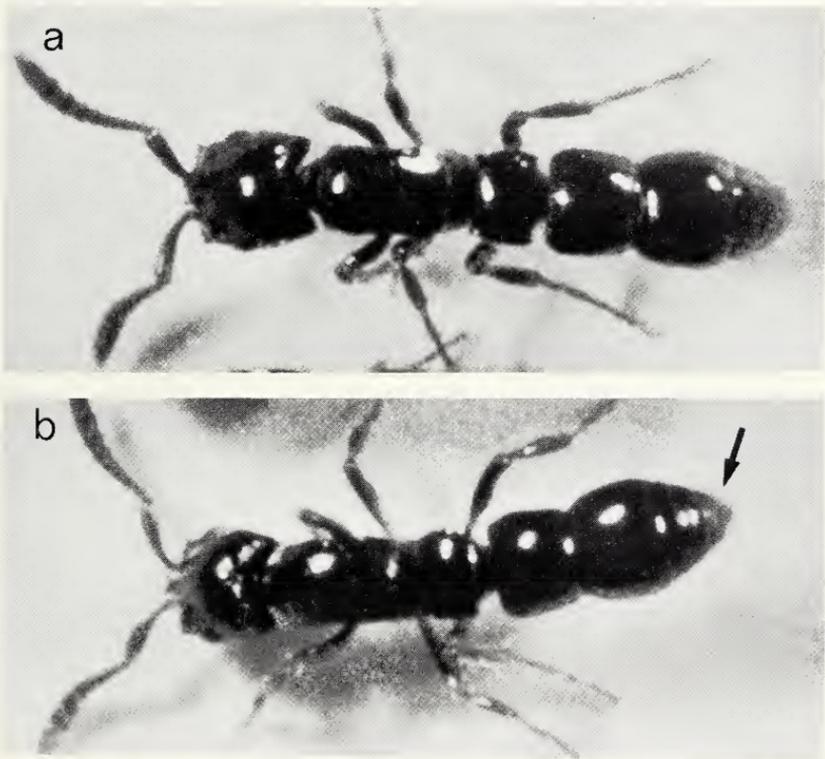


Figure 1. Recruiting *Cerapachys* worker. (a) Worker walking with its abdominal tip close to the ground. (b) Worker raising the gaster upwards; arrow indicates the position of the opening of the pygidial gland.

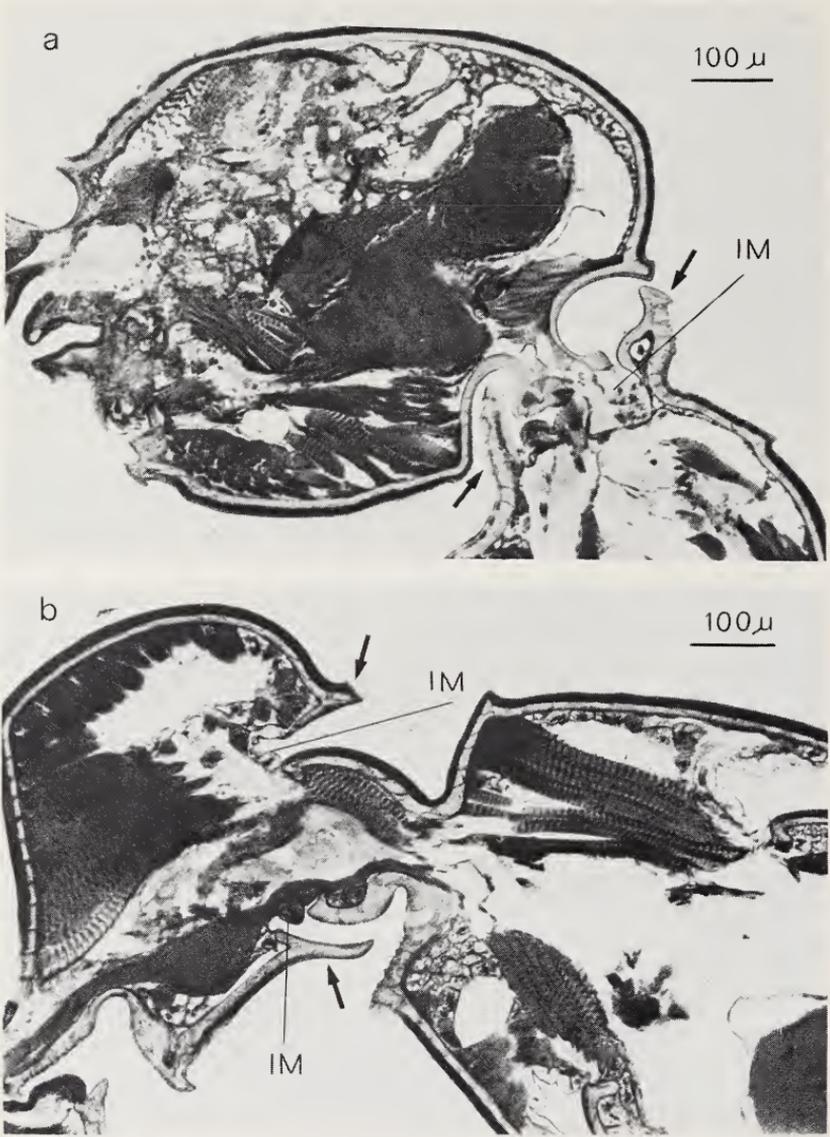


Figure 2. Longitudinal section through the head and part of the thorax (a) and through part of the petiolus and gaster (b) of a *Cerapachys* worker. Arrows indicate cuticle projections over intersegmental membranes (IM).



Figure 3. *Cerapachys* raiding group invading a *Pheidole* nest.

effective stinging attack of the *Cerapachys*, during which the raiders grasped the *Pheidole* with their short mandibles, simultaneously bending their gasters forward, so that in each case the tip, where the sting extrudes, touched the opponent's body. Each sequence usually lasted less than 1 second. Almost immediately after such an attack the *Pheidole* appeared to be immobilized. Only a few *Pheidole* workers escaped from the nest tube into the arena, some of them carrying brood. After approximately 15 minutes almost all *Pheidole* adults in the nest tube were disabled or killed but not a single *Cerapachys* worker was dead or visibly injured. Next the *Cerapachys* began transporting the dead and immobilized *Pheidole* adults to their own nest. After the first workers of the raiding expedition had returned and unloaded the booty they returned to the *Pheidole* nest. Some of them raised the gaster repeatedly upwards, upon which several additional *Cerapachys* workers followed them to the *Pheidole* nest, where they participated in the retrieval of the prey. Only after most of the *Pheidole* adults had been retrieved did the *Cerapachys* begin to transport the *Pheidole* brood. Each larva and pupa was briefly stung before it was picked up and carried to the *Cerapachys* colony. Interestingly, after approximately half the brood had been retrieved, *Cerapachys* nest workers began discarding all the dead and disabled *Pheidole* adults, and the next day only

Pheidole brood was stored in the *Cerapachys* nest. Apparently the booty of this raiding expedition was so abundant that *Cerapachys* preferred to keep only the more valuable and better preservable brood of the prey species, and they discarded the less valuable cadavers of the adult *Pheidole*. In other instances, however, where *Cerapachys* had only adults of prey species available, I observed *Cerapachys* feeding on the gasters of dead *Pheidole* workers and soldiers.

This experiment was conducted on the 25th and 26th of October 1980. At this time there was no *Cerapachys* brood in the colony. On November 10, 1980, I noticed the first large clutch of eggs in the *Cerapachys* nest tube. On December 11, 1980, the colony had many large (presumably last instar) larvae, and another large cluster of eggs (Fig. 4). The colony still contained a very good supply of *Pheidole* larvae (Fig. 4), which did not grow or develop further but which were obviously alive. Under the microscope one could see that the prey larvae slightly moved their mouthparts. Workers, queens and larvae of *Cerapachys* all fed on the *Pheidole* larvae. On December 26, 1980, there were still some prey larvae left. Many of the large *Cerapachys* larvae had pupated; in addition the nest contained many medium sized larvae and another large clutch of eggs. On January 3, 1981, a *Cerapachys* worker was observed leaving the nest tube and venturing out into the arena, for the first time since October 27, 1981. At this time I provided another fragment of a *Pheidole* colony with larval brood in the arena; and on January 5, 1981, *Cerapachys* conducted another raid, very similar in details to that just described. The fact that the captured *Pheidole* larvae were kept alive inside the *Cerapachys* nest chamber for a period of more than two months (but did not pupate or visibly increase in size) strongly suggested that they were sustained in a state of metabolic stasis. Recently Maschwitz et al (1979) provided experimental evidence that the ponerine species *Harpegnathus saltator* and *Leptogenys chinensis* paralyze prey objects by stinging and thereby are able to store prey a limited time. In one case the preserving paralysis effect was observed to last for two weeks, and in no instance did the stung prey object ever recover from the paralysis. Similar observations have been made independently by Traniello (unpublished data) with the ponerine species *Amblyopone pallipes*.

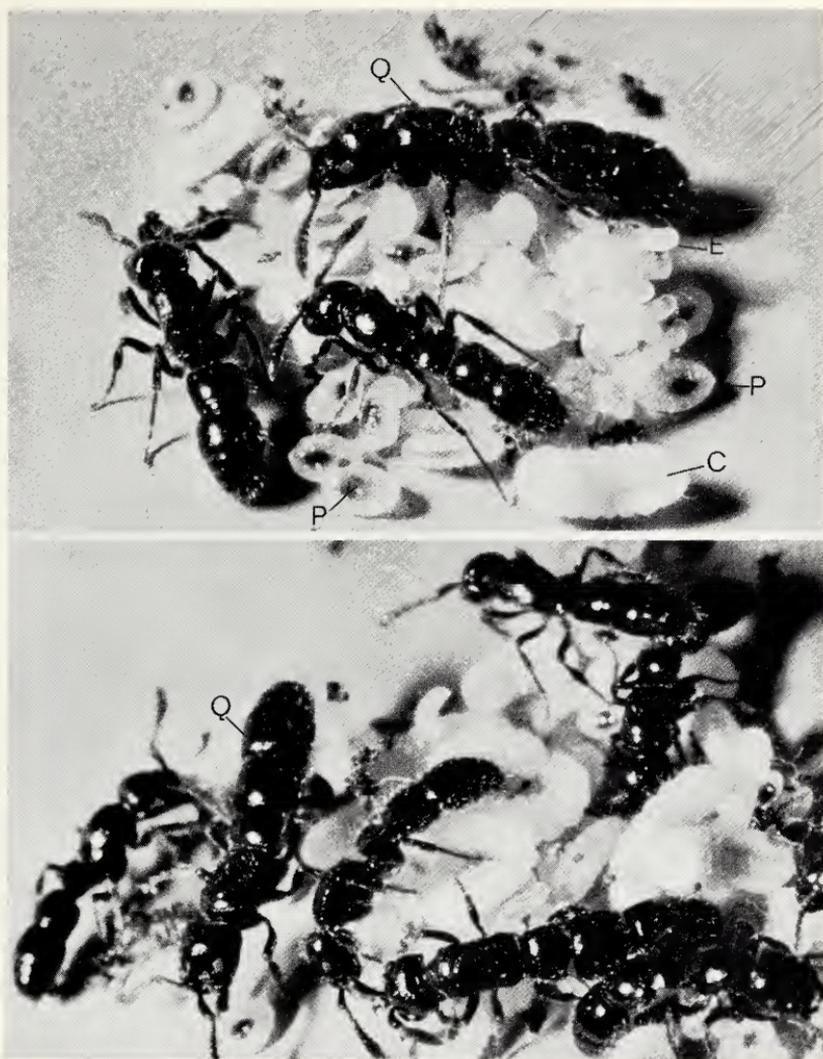


Figure 4. Fractions of a *Cerapachys* colony, with paralyzed prey larvae. Q: ergatoid queens; E: eggs; C: *Cerapachys* larvae; P: *Pheidole* prey larvae.

As just noted, *Cerapachys* workers apparently sting each *Pheidole* larva and pupa during the raid, before they transport the victims to their nest. This appears to be a very stereotyped behavior. For example when I shook a *Cerapachys* colony which contained *Pheidole* larvae out of the nest tube into the arena, so that they had to move back into the nest, *Cerapachys* workers picking up a *Pheidole* larva almost invariably went through the typical stinging motion pattern. They did not do this, however, when they picked up their own larvae. Although stinging behavior did not frequently occur inside the nest, occasionally I observed a *Cerapachys* stinging several larvae while reshuffling a pile.

The *Pheidole* larvae are small and tender and the powerful *Cerapachys* sting (Fig. 5) could easily pierce the larva and thereby kill it. Thus the injections of a paralyzing secretion through the sting has to be very subtle in order not to kill, but to preserve the larva. Brown (1975) describes the differentiated pygidium (Fig. 6) with its denticulate margins, being present in all workers and queens of cerapachyine ants. Brown states that "the function of the denticle-bordered pygidial plate is not known from direct observations, but it is assumed to have something to do with helping the insects to force their way through passages and cracks in soil or rotten wood, perhaps in connection with their entry into nests of termites or ant prey species".

Our morphological and histological investigations have revealed that these denticuliform and spinuliform setae on the pygidium of *Cerapachys turneri* and *Sphinctomyrmex steinheili* are sensory setae and comprise probably mechanoreceptors (Fig. 7). It is most likely that during the stinging process these mechanoreceptors signal the gaster tip's touch of the prey larva and the extent of the stings' protrusion is thereby regulated. Many of the nonsocial aculeate *Hymenoptera*, which paralyze prey by stinging, are equipped with mechanoreceptors on the tip of the sting sheath (Oeser 1961, Rathmayer 1962, 1978). We did not detect similar structures on the tip of the sting sheaths of *Cerapachys* or *Sphinctomyrmex*. In additional experiments I further confirmed the suggestion that the prey larvae, captured by *Cerapachys*, are preserved alive. Approximately 30 *Pheidole* larvae collected from a *Pheidole* colony were put without workers in a small test tube, which was kept moist by a wet cotton plug. A second similar test tube contained 30 *Pheidole* larvae which were taken from the *Cerapachys* nest. In two replications the

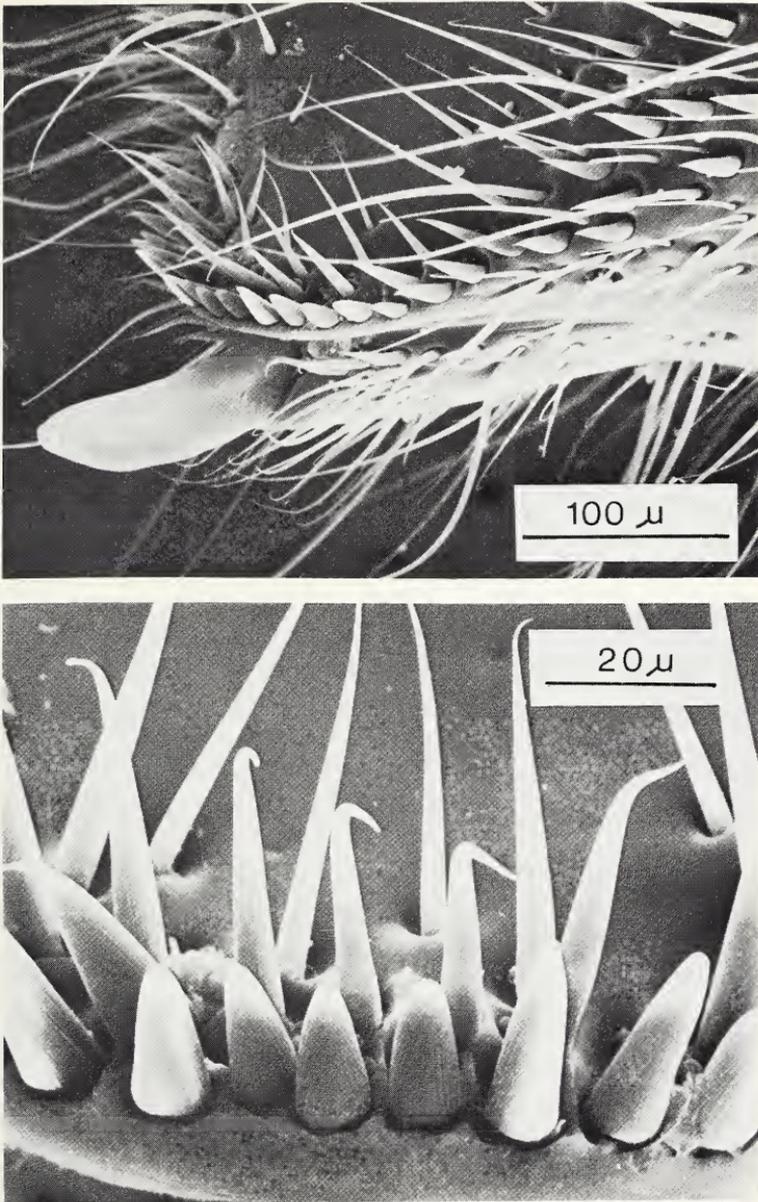


Figure 5. (a) SEM picture of the abdominal tip of a *Cerapachys* worker. The picture shows the partly extruded sting, surrounded by the sensory setae at the pygidium, and last exposed sternite. (b) Close-up of the two kinds of setae at the pygidium.

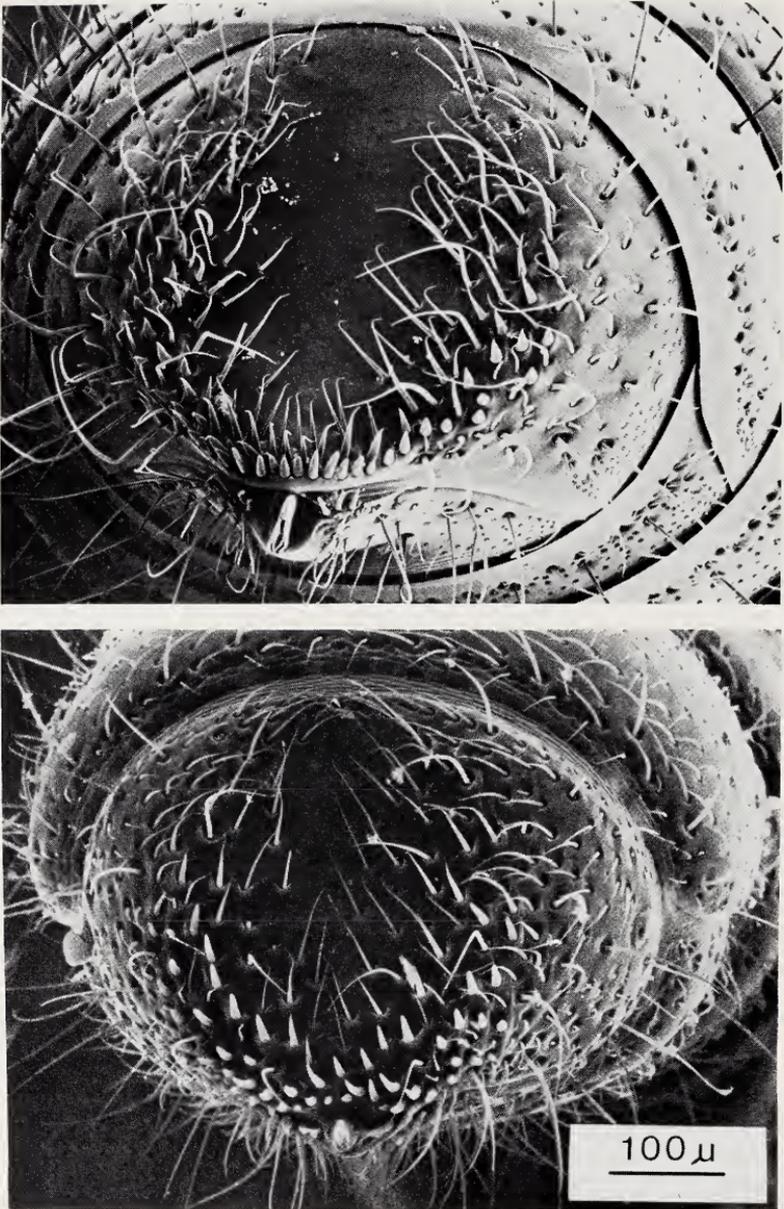


Figure 6. SEM picture of frontal view of pygidium of a *Cerapachys* worker (a), and a worker of *Sphinctomyrmex steinheili* (b). Note the arrangement of the two kinds of setae on the truncated pygidial plate of both species.

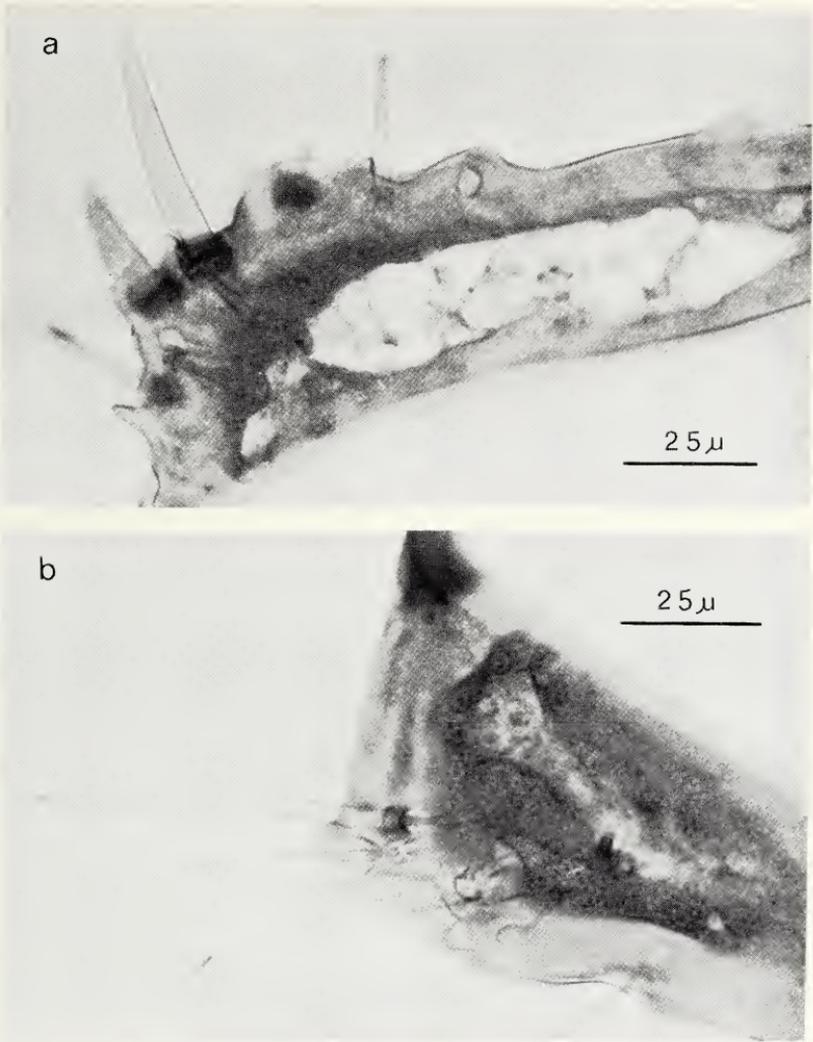


Figure 7. Longitudinal section through pygidial plate (a) and last exposed sternite (b) of a *Cerapachys* worker. The structure and innervation of the setae suggest that they function as mechano receptors.

larvae taken directly from the *Pheidole* colony were all dead after two weeks. On the other hand all of the larvae from the *Cerapachys* colony were obviously still alive after two weeks, many of them moving their mouthparts slightly. These findings clearly demonstrate that *Cerapachys* can store living prey larvae for a considerable period of time. This food storage system appears to enable *Cerapachys* to stay inside their nest for longer intervals. They evidently do not conduct raids as long as a good food supply is present. The following experiments were designed to test this hypothesis.

One day after the *Cerapachys* colony B had conducted a raid on *Pheidole* all prey larvae were removed. As a control I manipulated colony A in the same way, but the prey larvae were immediately returned to colony A. A few days later I observed scouts of colony B in the arena, where I had provided a nest tube with a fraction of a *Pheidole* colony, and within a period of 4 (test 1) and 7 days (test 2) colony B had conducted another raid. In the control colony A I noticed a worker briefly leaving the nest tube only once and then without venturing far into the arena. Although a tube containing *Pheidole* workers and brood was also provided in the arena of colony A, this colony did not conduct another raid until its supply of prey had declined considerably.

Emigration behavior

Although it is still an open question whether the Cerapachyini are nomadic, Wilson (1958, 1971) and Brown (1975) suggested that nomadism in the ant-preying cerapachyine species could well be adaptive to avoid depleting the food supply in a given neighborhood, just as it is in the army ants. This assumption of a nomadic life style is further supported by Brown's observations that the nests of many cerapachyine species appear to be impermanent, and that the "brood show a strong tendency to be synchronized, like those of army ants and nomadic Ponerinae". Brown (1975) also pointed out that the larvae of the Cerapachyini have a slender and cylindrical shape (G. C. Wheeler and J. Wheeler 1964), which makes them easy to transport longitudinally under the bodies of workers in the manner of other predatory and nomadic ants, such as *Eciton*, *Aenictus*, *Dorylus*, *Leptogenys* and *Onychomyrmex*. Although I was unable to demonstrate periodic nomadic behavior of *Cerapachys* in

the laboratory, I could easily initiate nest emigrations by removing the waterplug and thereby causing the nest tube to quickly dry out. Individual workers soon ventured into the arena and eventually discovered a new moist nest tube located approximately 20–30 cm away from the old nest. After exploring the new nest site the scout moved back to the colony. When entering the nest tube it exhibited the same behavior as when recruiting to a raid, including a repetitive lifting of the gaster. When the scout left the nest again to return to the newly discovered nest site, it was usually followed by several ants. Most of these first recruits also showed the gaster raising behavior on their return to the colony, and soon the whole colony began to leave the old nest tube and move to the new one. The larvae and pupae were carried in the manner Brown (1975) predicted, slung longitudinally under the bodies of the workers (Fig. 8). Adult transport was never observed; the ergatoid queens and even relatively freshly eclosed workers moved on their own to the nest site. The colonies did not contain males. After the workers had moved most of their own brood, they transported the prey larvae (*Pheidole*).



Figure 8. *Cerapachys* worker carrying a larva during nest emigration.

From the ants' orientation behavior it appeared that they were following chemical trails during the nest emigration. In fact, the recruitment behavior during nest emigrations and raiding appeared to be identical. The following experiments were designed to analyze further the communication mechanisms involved in both events.

Communication during emigration and raiding

Two distinct behavioral patterns were observed in *Cerapachys* ants during recruitment. (1) They seem to lay a chemical trail when returning from the target area (prey colony or new nest site) by frequently touching the abdominal tip to the ground; and (2) when close to or just entering the nest, they repeatedly raised their gaster upwards into a "calling position" and continued to do so when they moved back to the target area, usually being closely followed by a group of recruited nestmates. Since it was easier to initiate emigrations rather than raids, most of the experiments were conducted during colony emigration. Several new exocrine glandular structures have recently been discovered in ponerine ants (Hölldobler and Haskins 1977; Hölldobler and Engel 1978; Hölldobler et al. 1982; Maschwitz and Schönegege 1977; Jessen et al. 1979). The Cerapachyini were not included in these studies. We therefore conducted first a histological survey for possible exocrine glands that might be involved in the communication behavior of *Cerapachys*. Besides the known glands associated with the sting, we found a pygidial gland, which consists of a paired group of a few glandular cells under the 6th abdominal tergite. Each cell sends a duct through the intersegmental membrane between the 6th and 7th tergite (Fig. 9). The intersegmental membrane is laterally slightly invaginated, so that at each side it forms a small glandular reservoir. No particular cuticular structure on the pygidium is associated with the pygidial gland.

In a first set of pilot experiments I dissected out of freshly killed *Cerapachys* workers poison glands, Dufour's glands, hindguts, pygidial glands (6th and 7th tergites) and the last 3 sternites. For each test one organ of a kind was crushed on the tip of hardwood applicator sticks. These were then immediately inserted into the nest tube until the tip of the applicator was 2-3 cm away from the colony,

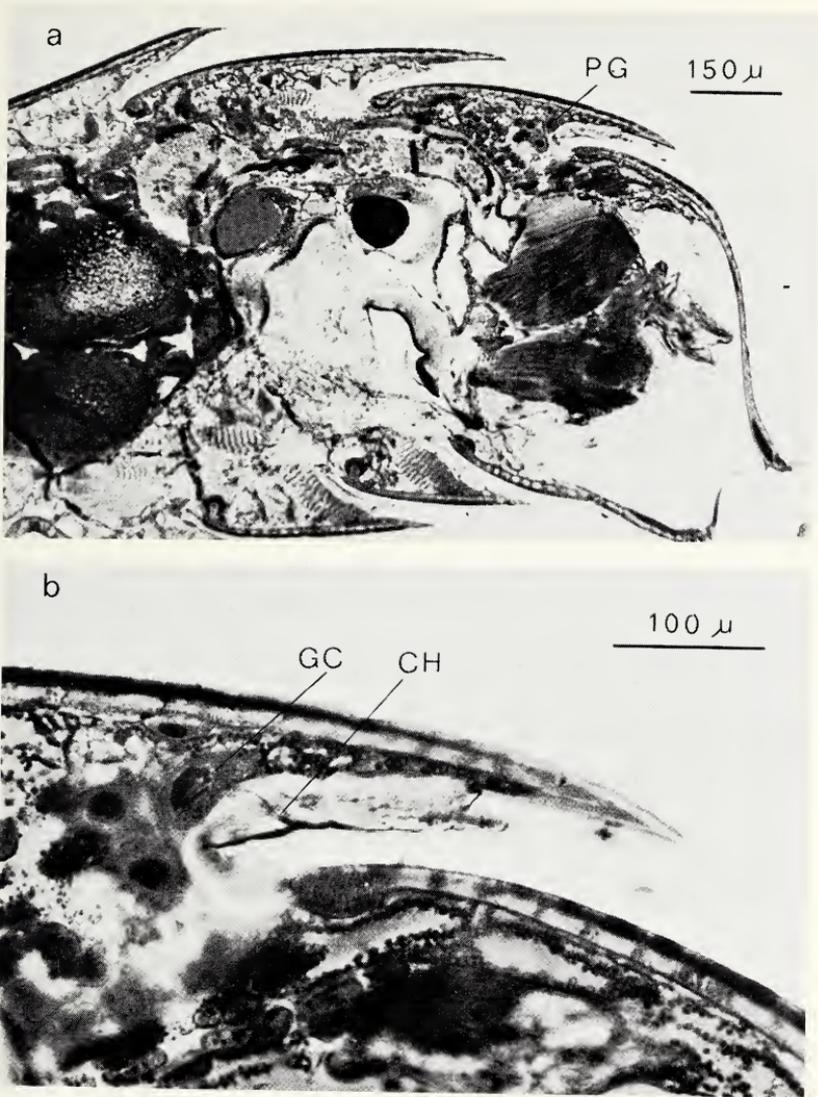


Figure 9. (a) Longitudinal section through the gaster of a *Cerapachys* worker showing the location of the pygidial gland (PG). (b) Longitudinal section through the pygidial gland; GC: glandular cells; CH: glandular channels through intersegmental membrane.

which usually had gathered near the cotton plug. In the following 30 seconds I observed the reaction of the ants, and between each test I waited at least 10 minutes before another sample was inserted into the nest tube. These pilot tests (3 repetitions with each organ) clearly indicated that only crushed poison glands and pygidial glands elicited increased locomotory activity and attraction in *Cerapachys* workers. The ants did not exhibit any particular behavioral reaction when sternites, hindgut or crushed Dufour's glands were introduced.* For the next series of experiments I first initiated colony emigrations either by following the procedure described above, or by shaking the colony out of the nest tube onto the arena floor. Before each experiment the arena was provided with a new paper floor. A new nest tube was offered 15-20cm away from the old nest tube or the displaced colony.

Once the colony emigration to the new nest tube had commenced, I covered the floor area between the colony and the new nest site with a cardboard, onto which I had drawn two artificial trails, one with a crushed glandular organ to be tested, and a second one with a drop of water (control). The trails were made to originate either from the entrance of the nest tube or from the periphery of the clustered colony. Each trail (test and control) diverged through an angle of 45° to either side from a possible natural trail (which was of course covered by a piece of cardboard). In addition the whole paper floor was rotated for 90° , in order to control for possible visual orientation (Fig. 10). During the following 2 minutes I counted the ants following the trails (10cm long) to the end. Only trails drawn with crushed poison glands elicited a precise trail following behavior in *Cerapachys* workers. There was some initial following response to trails drawn with crushed pygidial glands, but the ants followed only through the first 1-3cm, then usually turned or meandered off the trail. Only once was it possible to conduct a similar test during raiding behavior of *Cerapachys*. In this instance the ants followed only an artificial trail drawn with a crushed poison gland.

Although pygidial gland secretions did not release trail following behavior in *Cerapachys*, it clearly elicited increased locomotory

**Cerapachys* has also a very well developed sting sheath gland. It was not possible to test whether or not secretions of the gland play a role in communication.

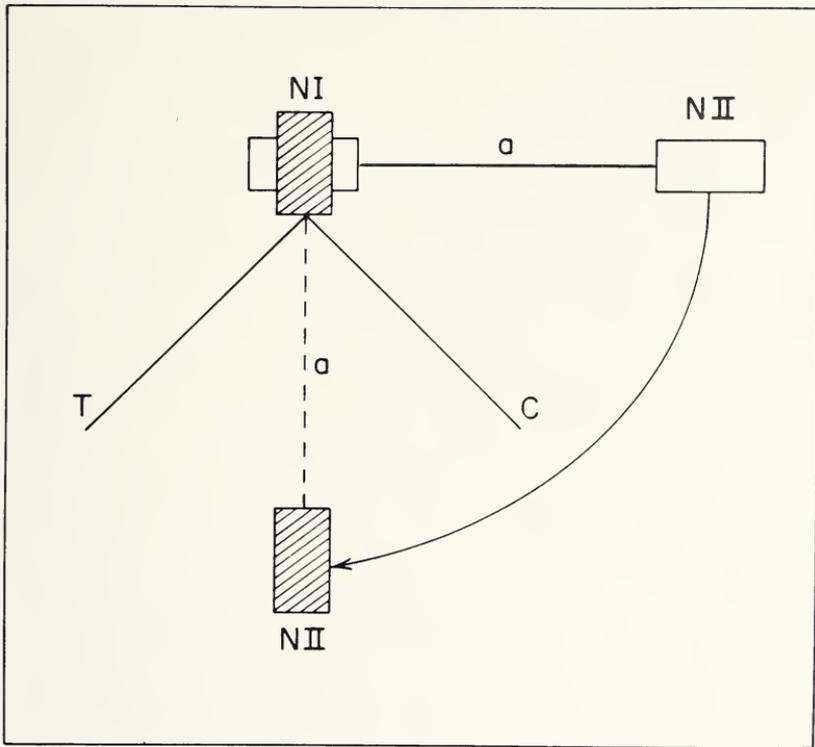


Figure 10. Schematical illustration of the experimental arrangement during trail tests. The colony was emigrating from nest NI to nest NII along a natural trail *a*. During the trail tests, the whole arrangement was turned 90° (arrow). The natural trail *a* was covered by a cardboard, on which the test trail (T) and a control trail (C) were offered, each deviating from *a* in an angle of 45° .

activity and attraction in the ants. I hypothesized therefore that the recruiting ant might discharge pygidial gland secretions when it exhibited the gaster raising behavior. The pygidial gland pheromone might function as an additional recruitment signal by which the recruiting ant keeps the raiding party stimulated when leading it to the prey colony. In order to test this hypothesis, I tried on four different occasions to close the opening of the pygidial gland by applying colophonium wax between the 6th and 7th tergites. Unfortunately these experiments failed; apparently the ants were too disturbed by the procedure. During two raiding expeditions of

Cerapachys we succeeded, however, in diverting individual ants from the raiding column over a distance of at least several centimeters by presenting two applicators in front of them, one contaminated with pygidial gland secretions and the other with water. Both applicators were slowly moved away from the columns in opposing directions. Of a total of 10 ants tested, 4 responded by following for a few centimeters behind the applicator with the pygidial gland secretions; no ant followed the control applicator. Although these results can be considered only preliminary, they do suggest that pygidial gland secretions might be involved in the recruitment process of *Cerapachys*. This suggestion was further supported by the results of a series of experiments in which I offered artificial trails drawn with crushed poison glands. I compared the trail following response of *Cerapachys* (within the first two minutes) successively either to trails drawn with poison gland secretions only or to poison gland trails offered simultaneously with pygidial gland secretions. For each kind a total of 6 experiments was carried out. Between each test at least one day had elapsed. The following response appeared to be stronger to poison gland trails when offered together with pygidial gland secretions (5.5 ± 2.9) than to those offered without pygidial gland secretions (3.0 ± 1.4) ($0.1 > p > 0.05$; Students t-test). Because of lack of material this series could not be extended, and thus the results remain only suggestive.

The two final experiments demonstrated that a trail (10cm long) drawn with one crushed poison gland, was still effective as an orientation cue several hours after it had been drawn. Using the same experimental arrangement described above (Fig. 10), I was able to show that emigrating *Cerapachys* would follow poison gland trails, 2 and 6 hours old, when they were offered after the natural trail had been covered. On the other hand, crushed poison glands introduced into the nest tube after 2 and 6 hours, or poison gland trails offered 2 and 6 hours after they had been drawn, did not elicit excitement or spontaneous trail following behavior. From these results it appears that the poison gland material might contain a short lasting stimulating component as well as a longer lasting orienting component.

DISCUSSION

Raiding expeditions in *Cerapachys turneri* are organized by individual scout ants, that return to the colony after having discovered a nest of the prey species. The scout lays a chemical trail with secretions from the poison gland, which serve as recruitment and orientation signals for the nestmates. Circumstantial evidence suggests that in addition the scout releases a stimulating chemical recruitment signal from the pygidial gland. This occurs probably when the scouts move with their gaster held slightly upwards in a calling position.

Wilson (1958) reports the field notes made by H. Potter on the cerapachyine species *Phyracaces potteri*, which contain the only available description of the early stages of a complete raid observed in the field. Before the raid started Potter noted a few workers moving rapidly about, "each with its abdomen raised upwards". These observations match closely my findings in the laboratory and lend further support to the hypothesis that in addition to the trails laid with poison gland secretions, another stimulating signal is discharged, presumably from the pygidial gland of the recruiting ants.

Wilson (1958) observed groups of *Phyracaces* moving along a raiding trail laid down by a raiding party on the previous day. In this case no individual leadership was involved and the foragers seemed to emerge from the nest randomly without a special recruitment stimulation by scout ants. Obviously these ants were following an established foraging trail, leading to a previously raided *Pheidole* nest which appeared to be vacated this time. Small exploratory parties conducted brief excursions to the side, but in most cases they turned back to the main trail. No nest suitable for raiding was found during these explorations.

These observations strongly suggest that chemical trails laid during raiding expeditions might still function as orientation cues one day later and that foraging parties can follow these established trails without the leadership of a recruiting scout ant. Indeed, my laboratory experiments with *Cerapachys* have demonstrated that artificial trails drawn with poison gland material are effective as orientation cues at least for several hours.

Although the raiding cerapachyine ants are usually enormously outnumbered by the worker force of the prey species, not one *Cerapachys* worker was lost during all the raiding experiments in the laboratory. As can be seen from Fig. 2, *Cerapachys* and *Sphinctomyrmex* are excellently protected by a heavily sclerotized cuticle. The intersegmental joints, that is, the joints between head and thorax, and between thorax, petiole and gaster, are covered by cuticular projections so that no intersegmental membrane is exposed, even if the ant is twisted and bent to an extreme degree.

In addition, *Cerapachys* and probably all the other cerapachyine ants have a most powerful sting that immobilizes the opponents within seconds. Not only the adults of the raided colony, but also the captured larvae and pupae are stung by the raiders before they are retrieved to the *Cerapachys* nest. Observations and experiments demonstrated that the prey larvae are kept in a stage of metabolic stasis and can thereby be stored for a period of more than two months. This food storage system enables *Cerapachys* to adjust the raiding activities to food requirement and supply. From the laboratory experiments we can conclude that *Cerapachys* does not conduct daily or periodic raiding expeditions. The frequency of raiding expeditions depends on the food supply stored inside the *Cerapachys* nest.

I was unable to demonstrate periodic nomadic behavior in *Cerapachys* in the laboratory. I assume that nest emigrations might occur relatively frequently in this species, but that they do not follow a periodic pattern. Instead, environmental factors such as food supply or physical conditions of the nest site are likely to play the important role in inducing a *Cerapachys* colony to emigrate.

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DESIGNATION OF A TYPE-SPECIES FOR
CYCLOGASTER MACQUART, 1834, AND THE
RESULTING SYNONYMY (DIPTERA: STRATIOMYIDAE)*

BY NORMAN E. WOODLEY
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138

The generic name *Cyclogaster* Macquart (1834) has been used in combination with specific names for taxa of Stratiomyidae from diverse regions of the world. It has remained more or less in synonymy with *Lasiopa* Brullé (1832) since the time of Brauer (1882), although Pleske (1901: 336) described *Cyclogaster caucasica* (Palaeartic) and Hutton (1901: 10) described *C. peregrinus* from New Zealand after Brauer's work appeared. Kertész (1908) also considered the two names synonymous, and placed 15 species in *Lasiopa*. These species are placed in at least five genera at the present time.

The purpose of this paper is to designate a type-species for *Cyclogaster*, which to my knowledge has never been done, in order to stabilize the generic synonymy as it is presently used by workers in the Stratiomyidae. A brief review of the history of the name *Cyclogaster* and generic names associated with it is necessary to understand the situation fully.

Macquart (1834: 256) first proposed the name *Cyclogaster* in the Diptera, and included in that taxon two species, *Nemotelus villosus* Fabricius (1794: 270; Palaeartic) and *Stratiomys atrata* Fabricius (1805: 83; Neotropical). No single type-species was designated.

The generic name *Inermyia* Bigot (1856: 82, 63) was proposed for the South African species *Stratiomys edentula* Wiedemann (1824: 29). Gerstaecker (1857: 322) and Loew (1860: 7) both considered *Stratiomys edentula* a member of *Cyclogaster* Macquart and Kertész (1908: 30) listed *Inermyia* as a synonym with a query. Lindner (1972: 32) considered the species to be congeneric with the true, Palaeartic *Lasiopa*, and it is listed as such by James (1980: 260).

Kirkaldy (1910: 8) noted that the name *Cyclogaster* was preoccupied in zoology by *Cyclogaster* Gronovius, in the fishes (this name will be discussed in more detail below). He proposed a replacement name for the name in the Diptera, *Neotropicalias*. No reference was made to any specific names, although one might infer he was think-

ing of the Neotropical species that Macquart had originally included in *Cyclogaster*.

Enderlein (1914: 579, 615), without any reference to Kirkaldy (1910), but evidently realizing that the two species originally included in *Cyclogaster* were not congeneric, proposed the name *Labocerina* for *Stratiomys atrata* Fabricius. In his paper, the new name was spelled *Labocerina* twice (pp. 579, 615), and "*Labacerino*" once (p. 615), and has subsequently been spelled "*Labocerino*" by James (1940: 124). These latter two spellings were regarded as errors by James (1973: 26.29). In the same paper, Enderlein considered *Cyclogaster* a synonym of *Lasiopa*.

The name *Cyclogaster* Gronovius (1756: 9; 1760: 265; 1763: 55) was in dispute, as were all of his generic names, because many authors felt his work was not truly binomial. His *Cyclogaster* was first published in 1756, but this is pre-Linnean. The 1760 work is clearly not binomial, although this is the date of the name usually found in zoological nomenclators, being the first post-Linnean publication of it. In 1954, the International Commission on Zoological Nomenclature formally ruled that Gronovius' 1763 work, as well as an index of it subsequently published by Meuschen, be placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature. Thus Macquart's *Cyclogaster* became the earliest valid use of the name in zoology.

Lindner (1958: 432), while discussing "*Cyclogaster*" *peregrinus* Hutton from New Zealand, recounted most of the above briefly, and noted that no type-species had been designated for *Cyclogaster* Macquart, but was apparently not aware of the I. C. Z. N. ruling. He also mentioned that *Nemotelus villosus* Fabricius was the type-species of *Lasiopa* (as had Enderlein, 1914: 613, and several other authors), which is erroneous, as the only species name associated with *Lasiopa* in Brullé's original description was *Lasiopa peleteria*, which was described concurrently and is still regarded as a valid species.

As I interpret the situation, a type-species designation is necessary for *Cyclogaster* Macquart in order to stabilize generic synonymy, and as far as I am aware, this has never been done. In order to preserve the presently accepted generic synonymies, I hereby designate *Nemotelus villosus* Fabricius, originally included in *Cyclogaster* by Macquart, as type-species for that genus. The following

synonymy for *Lasiopa*, the senior generic name, results:

Lasiopa Brullé, 1832: 307. Type-species: *L. peleteria* Brullé, 1832: 308 (by monotypy).
Cyclogaster Macquart, 1834: 256. Type-species: *Nemotelus villosus* Fabricius, 1794: 270 (by present designation).

Inermia Bigot, 1856: 82. Type-species: *Stratiomys edentula* Wiedemann, 1824: 29 (by original designation, *op. cit.*:63).

Neotropicalias Kirkaldy, 1910: 8; replacement name for *Cyclogaster* Macquart, 1834, *nec* Gronovius, 1763. Type-species: *Nemotelus villosus* Fabricius, 1794: 270 (by autotypy).

The above type-species designation thus stabilizes the long-used synonymy of *Cyclogaster* with *Lasiopa*, while retaining the name *Labocerina* Enderlein for the Neotropical *Stratiomys atrata* Fabricius. The name *Neotropicalias* Kirkaldy became an unnecessary, and therefore invalid, replacement name when *Cyclogaster* Gronovius was rejected by the I. C. Z. N. ruling.

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ORB PLUS CONE-WEBS IN ULOBORIDAE (ARANEAE),
WITH A DESCRIPTION OF A NEW GENUS
AND FOUR NEW SPECIES

BY Y. D. LUBIN,¹ B. D. OPELL,² W. G. EBERHARD,³
AND H. W. LEVI⁴

INTRODUCTION

Spiders of the genus *Uloborus* (Uloboridae) characteristically spin horizontal orb-webs with a sticky spiral of cribellar silk. We describe here the webs of *U. conus*, *U. albolineatus*, *U. bispiralis*, *U.* #2072, *U. trilineatus*, and *Conifaber parvus* which are modifications of this basic uloborid orb-web form and include cones composed of regular arrays of threads beneath the orbs' lower faces. The web building and prey capture behaviors of *U. conus* (observations of YDL) are also described, and descriptions of *Conifaber parvus* new genus, new species and the new species *U. conus*, *U. albolineatus*, and *U. bispiralis* are provided (by BDO).

STUDY SITES AND METHODS

Uloborus conus was found at three localities in Papua New Guinea: 1) in lowland wet forest, Gogol Forest Reserve near Madang, Madang Province, 2) in a *Pandanus* swamp (freshwater) and a mangrove swamp (brackish) at Buso, Morobe Province, and 3) in the understory of klinki pine (*Araucaria hunsteinii*) plantations at 1200 m elevation in McAdam Memorial Park near Wau, Morobe Province. Webs were built about 0.5 to 2.0 m above the ground in gaps formed by the uppermost, generally vertical branches of small shrubs and saplings. They were always found in humid, shaded

1. Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama and Department of Zoology, University of Florida, Gainesville, Florida, 32611.

2. Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

3. Smithsonian Tropical Research Institute and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria "Rodrigo Facio", Costa Rica.

4. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

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locations. Several individuals were kept and observed in an insectary at the Wau Ecology Institute (WEI).

Uloborus albolineatus and *U. bispiralis* were found on the Gazelle Peninsula, East New Britain (ENB), Papua New Guinea. The webs of *U. bispiralis* were observed on the Lowlands Agricultural Experimental Station (LAES) at Kerevat, ca. 100m elevation, in cocoa plantations and in secondary growth lowland forest and near Malasat (ENB) at ca. 600m elevation. One web of *U. albolineatus* was observed at LAES in secondary-growth forest along a river.

A single mature female of *Uloborus* #2072 (numbers refer to specimen numbers placed in vials) was found (by WGE) near Dandeli, Karnataka, India, in the foliage of a bush growing in a teak forest. *Uloborus trilineatus* is common in undergrowth of gallery forest in eastern Colombia where WGE worked extensively. The webs described here were found at Finca Chenevo, about 20 km SW of El Porvenir, Meta, and Finca Mozambique, about 15 km SW of Puerto Lopez, Meta. *Conifaber parvus* was also found at Finca Mozambique (by WGE) where it occurred in periodically flooded forest but not in surrounding savanna.

Webs were first dusted with cornstarch or talcum powder using either the method described by Eberhard (1977a) or Carico's (1977) modification of this method, and then measured and photographed. All specimens mentioned in this paper are deposited in the Museum of Comparative Zoology.

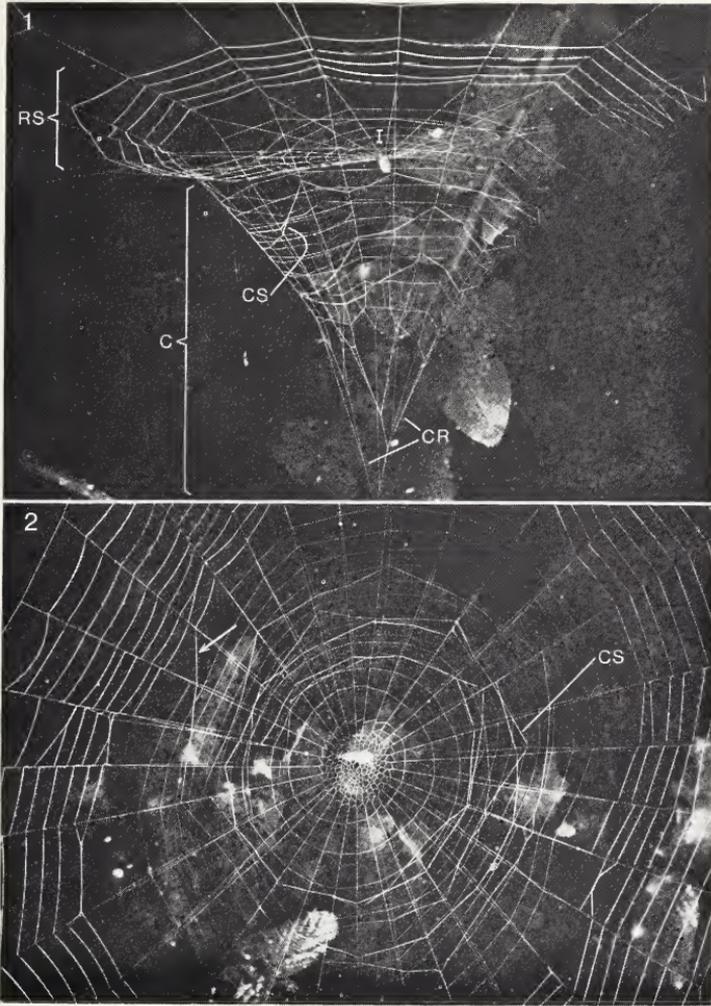
OBSERVATIONS

*Uloborus conus**

The Web

The web of *U. conus* has three parts: the inner orb, the rim, and the cone (Fig. 1). The inner orb and rim are in nearly the same plane and are more or less horizontal. The inner orb consists of a closed hub, radii and a few loops of non-sticky spiral, while the rim has several loops of sticky, cribellar spiral which end where the rim radii join those of the inner orb. Rim radii are continuous with those of the cone, and those of the inner orb are attached to them. Cone radii are attached in groups of two or three to a central guy thread which

*This is a new species described below.



Figures 1-2. Web of *Uloborus conus*. 1. Side view showing the rim sticky spiral (RS), inner orb (I), cone (C) with jagged sticky spiral (CS) on a framework of radii and non-sticky spiral, and cone radii (CR) converging toward a central guy thread. Note that 2-3 cone radii are attached together to form one thread which attaches to the cone guy thread, and that these attachments are dispersed along the guy thread so that there is no single apical point to which all cone radii attach. 2. Top view showing typical *Uloborus*-type hub and non-sticky spiral of the inner orb. The cone with its jagged sticky spiral (CS) is seen through the plane of the orb. Note the gap between the non-sticky spirals of the cone and inner orb on the one hand and the rim sticky spiral on the other. The cone sticky spiral can be seen as a continuation of the rim spiral (arrow points to beginning of cone sticky spiral).

is in turn attached distally to a leaf or branch. The cone has a non-sticky spiral and a few irregularly-spaced, jagged turns of cribellar silk. This jagged sticky spiral is a continuation of the innermost sticky spiral loop in the rim (Figs. 2, 4).

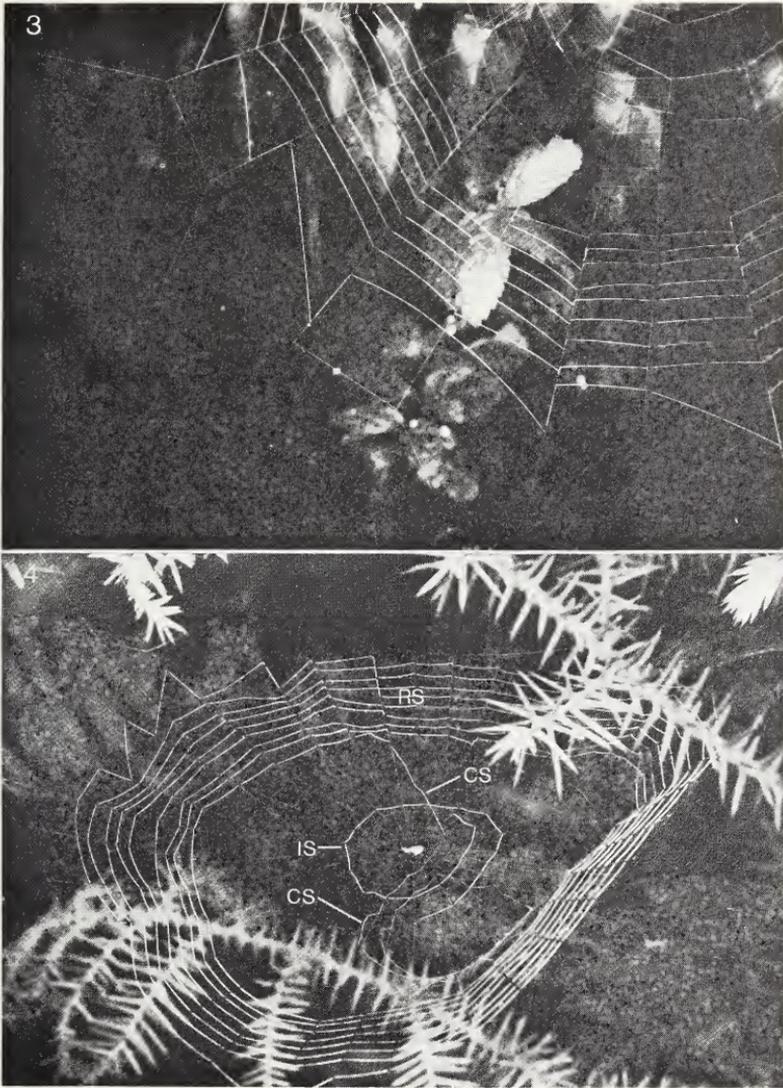
The hub of the inner orb (Fig. 2) is similar to that of other uloborid orbs, e.g. *U. diversus* (Eberhard, 1972), and its spiral continues outward to form the non-sticky spiral of the inner orb. There is always a large gap between the last turn of this spiral and the innermost loop of sticky rim spiral (Figs. 1, 2).

Sticky spiral loops in the rim are more tightly spaced than are either the non-sticky spiral loops of the inner orb and cone or the cone's sticky spiral. The outermost loop of rim spiral often follows a zigzagging path, with some segments of the sticky silk found on the radii (Figs. 2, 3). This zigzagging was more pronounced in some webs than in others and was generally most evident on the side of the orb which was larger (the orbs were rarely perfectly symmetrical).

Variations on this basic pattern were seen. Webs of immatures frequently had only a narrow rim, sometimes with only a single loop of sticky spiral. Some webs had a few loops of sticky spiral on the inner orb, with the non-sticky spiral left intact (Fig. 4). Webs of two adult females and several immatures had thin linear stabilimenta at their inner hubs. Adult males were found sitting on webs similar to those of immatures, but it was not determined if these were of their own construction. Adult males did not build webs in captivity.

Web Building Behavior

Web building by two adult females was observed from start to finish and various stages of web construction were seen on four other occasions. Durations of different stages of construction were noted for one of the adult females. Web construction began late at night or in early pre-dawn hours. The inner orb and cone of the old web were probably removed early in the night, but this behavior was not observed. One WEI female was found sitting at the center of a rudimentary web consisting of a partly collapsed rim and a few radii, and had a ball of silk in her mouthparts which shrank visibly as it was (presumably) ingested. This spider removed the rest of the rim and added the material to the ball of silk in her chelicerae before building the new web. Reusing frame threads from the previous web, the spider began construction by laying new radii.



Figures 3-4. Web of *Uloborus conus*. 3. Detail of first (outermost) loop of rim sticky spiral showing zigzag path with sticky silk laid directly on the radii. 4. Top view of web with $1\frac{1}{2}$ loops of sticky spiral (IS) in the inner orb (IS). Also visible is the cone sticky spiral (CS) continuing in from the rim spiral (RS) and the zigzag outer loop of rim sticky spiral.

Radii and non-sticky spiral were laid as in *U. diversus* (Eberhard, 1972) and their construction lasted 5 and 1.5 minutes, respectively. Radii were laid by walking out from the hub on an existing radius with a dragline, attaching the dragline to a frame thread, and then doubling it by walking back to the hub with another dragline. At the hub the dragline was attached to a succession of adjacent radii (forming the closed hub spiral) before the next radius was laid. When most of the radii were completed, the spider continued the hub spiral outward to form the non-sticky spiral, laying occasional "tertiary radii" (Le Guelte, 1966) during the process. This non-sticky spiral did not reach the frame threads.

At the start of the sticky spiral even very faint light falling on the spider caused her to cease spinning and bounce up and down on the web. Consequently, observations of sticky spiral construction were made only sporadically, using indirect lighting. The first (outermost) loop of non-sticky spiral was completed in 13 min. During sticky spiral construction the spider reversed directions five times in the larger part of the web. The sticky spiral was attached to each radius that it crossed, and the spider broke non-sticky spiral loops as she laid the sticky spiral. One immature female was observed laying a zigzag outer loop of sticky spiral. The sequence of attachments of the cribellar silk to produce the zigzag loop (Fig. 5a) was distinct from that involved in laying the normal sticky spiral loops (Fig. 5b).

After meticulous, slow sticky spiral construction, which in one case lasted 3 hrs. 6 min., the spider suddenly began spinning out cribellar silk in a rapid and seemingly reckless fashion while moving inward toward the hub at an angle of about 25° to the last turn of the regular sticky spiral (Figs. 2, 4). After completing half a loop, the spider reversed direction and continued spiralling toward the hub, laying a jagged and irregularly spaced sticky spiral. The jagged spiral was attached to only a few radii, crossing 3-7 radii and, in some cases, several non-sticky spiral loops between attachments. The non-sticky spiral was left intact. This entire phase was very rapid and in one case the four jagged loops were completed in just 6 min. This jagged spiral was to become the sticky spiral of the future cone.

After completing the cone sticky spiral, the spider moved to the hub and slowly turned in a circle, pulling on successive radii with the first legs. After 2 min. she went out to the end of a radius and

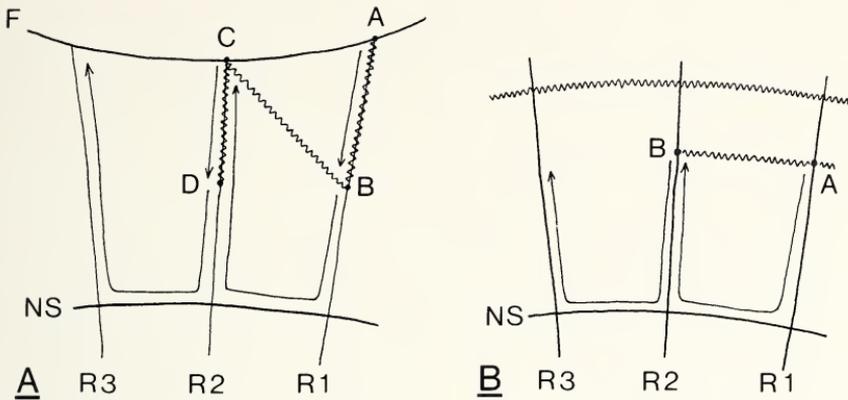


Figure 5. Construction of *U. conus* web. (a) Sequence of attachments of sticky silk to produce the outer zigzag loop of rim sticky spiral. The spider started at the junction of the radius (R1) and frame thread (F), attaching the cribellar thread at point A, walked along R1 toward the hub and attached the cribellar thread at point B, about half way between the frame thread and outer loop of non-sticky spiral (NS). The spider then continued inward along R1, combing out cribellar silk, reached the non-sticky spiral and ran rapidly across it and 2/3 of the way out on R2 without combing out additional silk. It then continued to walk out on R2, combing out cribellar silk and attached the thread at point C, the junction between R2 and the frame thread. The sequence was then repeated, walking in along R2, attaching cribellar thread at point D, etc. (b) Sequence of attachments of cribellar silk to produce the normal sticky spiral. The spider attached cribellar thread at point A on radius R1, walked in on R1, combing out cribellar silk, until it reached the temporary, non-sticky spiral loop (NS), then ran along the non-sticky spiral and out on radius R2 without combing out cribellar silk and attached the cribellar thread to R2 at point B.

dropped from it to a leaf below, attached her dragline to the leaf, and went back up the dragline and across the web to its hub on a radius, attaching the new dragline from the leaf to the hub. This formed the central guy thread of the cone. The spider then went down the guy thread, broke it, reattached it to a different point on the leaf, and then returned to the hub. By this time the hub was already drawn down under tension, and the web formed a shallow cone. The cone was then elongated by cutting radii at their attachment to the hub, lowering their tension and then attaching them to the central guy thread by the sequence of behaviors shown in Fig. 6a, b.

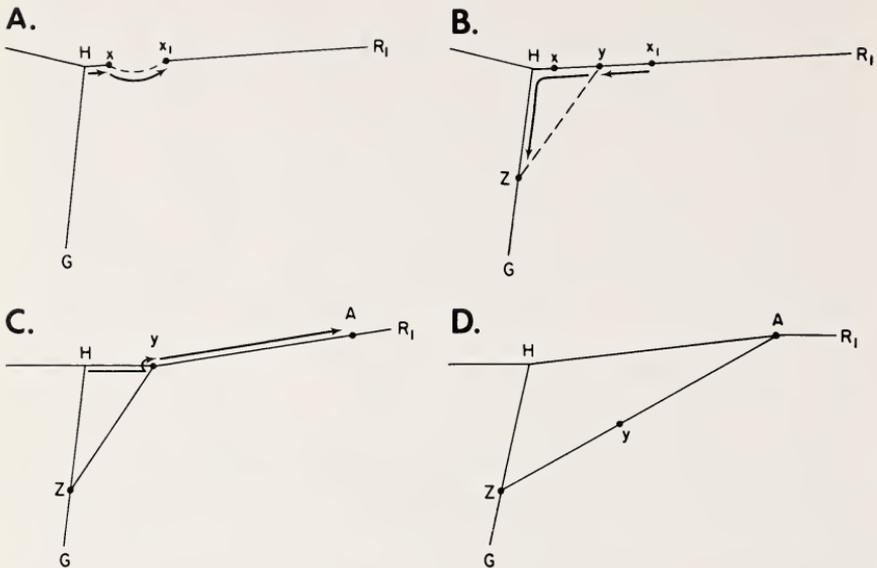


Figure 6. Construction of *U. conus* web. Sequence of thread attachments in forming the cone (web viewed from the side). Arrows indicate direction of movement of the spider. Dots are points where attachments were made or broken. (a) The spider went to point X on radius R1 at the edge of the hub, cut the radius, attached its dragline to the inner broken end and then let out additional dragline as it faced away from the hub. This was then attached to the outer broken end which had now moved to point X1. Usually adjacent radii were also broken and attached to radius R1 at point X1 (see also Fig. 1). (b) The spider then walked back toward the hub to point Y, attached a dragline, ran to the hub and down the central guy thread (G), attaching the dragline at point Z. Radius R1 was thus pulled down toward the apex of the cone to form the cone radius YZ while the thread HY formed a temporary inner orb radius. (c) To move the temporary inner orb radius up on the cone, the spider walked out on temporary radius HY and broke it at its attachment to the cone at point Y. The spider then attached a dragline to the broken end and walked out on radius R1, reattaching it at point A at the inner edge of the rim sticky spiral. (d) The completed cone radius is indicated by line AZ and the new inner orb radius by line HA. The section AY of the cone radius bears the cone sticky spiral. The upper portion of the guy thread (HZ) was absent in the completed web, but it is not known when it was removed.

After forming the cone, the spider cut most of the temporary inner orb radii, thus collapsing the hub and leaving only a bit of silk to which a few temporary radii were attached. The spider then began replacing these temporary inner orb radii and at the same time completing cone formation by incorporating into the cone the

section of the original orb containing the jagged sticky spiral (Fig. 6c, d). This stage followed initial cone formation without interruption, and it was difficult to determine when cone building ended and replacement and construction of new inner orb radii began. The spider went out to the cone along a temporary radius, broke the attachment to the cone and attached her dragline to the inner end of the temporary radius, then carried the radius upward by walking along radii and non-sticky spiral loops on the inner surface of the cone, and finally reattached it at or just inside (below) the innermost loop of the rim sticky spiral. She then walked back to the hub on the new radius, thereby doubling the thread. Upon reaching the center, she made attachments to form a new hub. The upper portion of the guy line was absent in finished webs, but it was not determined how it was removed.

Additional new inner orb radii were constructed in much the same manner as "normal" orb radii. The spider went out on an existing radius (or temporary radius) with a dragline, reached the cone non-sticky spiral, walked across it to the next cone radius, attached the dragline to the cone radius just below (inside) the rim spiral, and return to the hub on the new radius (doubling it). Consecutive radii were always laid with angles of more than 90° between them, perhaps serving to reduce differences in tension on all sides of the orb (Eberhard, 1981).

The last stages of web building, beginning with attachment of the dragline and ending with completion of the inner web, lasted 23 min.

Resting Postures

The spider normally sat under the hub with legs I and II slightly flexed and holding separate radii. When disturbed, the spider adopted a cryptic posture with legs I and II held together and flexed and legs III and IV pressed close to the body (Figs. 2, 4). This posture was adopted either at the hub or under a short "dragline" thread beneath the hub, which was attached to the hub at one end and to a radius at the other. When disturbed repeatedly, or when sunlight struck the web and made it visible, the spider dropped from the hub onto the dragline thread and bounced up and down on it. Spiders also bounced while wrapping prey and sometimes while going out to attack an insect or upon returning to the hub. This

bouncing may be an anti-predator behavior similar to the bouncing flight of craneflies and the rapid vibrating of opilionids and pholcids.

Prey Capture Behavior.

Successful captures of five fruitflies (*Drosophila*-size), one 4 mm long dolichopodid fly, one unidentified 1 mm fly, three 3–4 mm ants, and one 5 mm lepidopteran larva were observed (by YDL). Of these, seven were trapped in the rim and three in the cone. All but one sequence conformed to the description given below. Like other uloborids (Marples, 1962; Eberhard, 1969; Lubin et al., 1978) *U. conus* and *U. bispiralis* immobilize all insects by wrapping in silk. Spiders ran out to the cone on an inner orb radius to reach insects trapped in the rim sticky spiral, squeezed through the cone (often turning sideways to do so) and continued out onto the undersurface of the rim. If an insect was trapped on the cone sticky spiral, the spider went through the cone and ran down the outer surface of the cone. Upon reaching the insect, the spider often tapped it with legs I, turned 180° so that it faced the hub (or upward on the cone) and began to wrap. Initially the prey was wrapped from a distance by throwing sheets of silk backwards with legs IV. Later the spider moved into contact with the prey and held it with legs II and III while wrapping. The spider interrupted wrapping to cut sticky spiral attachments, then cut the inner radius attachment (toward the hub) and continued to wrap while holding the end of the radius with one leg I. Finally, the outer (distal) end of the radius was cut and the prey was held free of the web in legs II and III while the spider hung from the broken radius by legs I, bridging the gap with its body, and wrapped the prey with legs IV while rotating it occasionally with the palps or legs.

All prey were carried to the hub in the palps (with the aid of the chelicerae), held "overhead" in characteristic uloborid fashion. After transferring the prey package from the legs to the palps, the spider attached a dragline to the distal end of the broken radius and then to the proximal end, thus closing the gap. At the hub the spider again transferred the prey from the palps to legs II and III and wrapped it while hanging from the dragline thread beneath the hub. In most instances the dragline thread appeared to be broken and the spider spanned the gap with its body.

Prey Capture Sequences With Different Prey Types.

The only case not conforming to this description was that of a fruitfly caught on the inner orb; the spider wrapped it, secured it by reattaching it to the radius and fed on the prey *in situ*.

U. conus rejected or ignored a number of insects offered as prey. Five small orthopteran nymphs 3–4 mm long (probably newly emerged) were given to adult females and all were rejected. On two occasions, the spiders approached and tapped the insects with legs I and then returned to the hub. In other instances the spider pulled the radii in the direction of the orthopteran, shook the web and then ignored it. The same individuals readily attacked fruitflies offered as prey after the orthopterans. Fruitflies were not attacked on three occasions when they were offered while the spider was already wrapping a prey or feeding at the hub. Two ants (*Anopolepis longipes*, 4mm long) were rejected under the same circumstances.

Sequences With Multiple Prey.

On six occasions spiders feeding at the hub attacked second or third prey thrown into their webs. These included two ants, two fruitflies, a dolichopodid fly and an unidentified small fly. On all but one occasion the spider carried the first prey in its palps as it ran out to attack the second. In one instance a spider that had been wrapping the first prey at the hub attached this insect to a dragline thread below the hub before going out to attack the second insect.

The second prey was immobilized in the same manner as the first, but rather than cut this insect out and carry it to the hub, the spider secured the second prey at the capture site and returned to the hub to resume feeding on the first prey. While performing immobilization wrapping, the spider usually broke the radius attached to the prey on the inner side (toward the hub), but not on the outer side. Before leaving it at the capture site, the spider reattached the prey to the broken end of the radius, thus securing it at both ends.

Eggsac and Eggsac Web.

The eggsac of *U. conus* is about 8mm long by 3mm wide, with angular projections along the edges (Fig. 7). It is suspended in an eggsac web on a strengthened radius of a former web, where the hub of the inner orb had been. The web is similar to those of *U. diversus* (Eberhard, 1969) and *Miagrammopes* sp. near *unipus* (Lubin et al. 1978) and consists of frame threads, a few radii and one or more

zigzag loops of sticky silk, with some sticky silk laid directly on the radii. The radii are attached to the main eggsac radius or to the eggsac itself. One female had a three-dimensional eggsac web consisting of a rudimentary cone and inner orb radii (Fig. 7) with sticky silk in both the plane of the orb and the cone. Unlike the eggsac webs of *Miagrammopes*, these webs were retained both day and night. Insects that became entangled in the sticky threads were attacked in the usual manner.

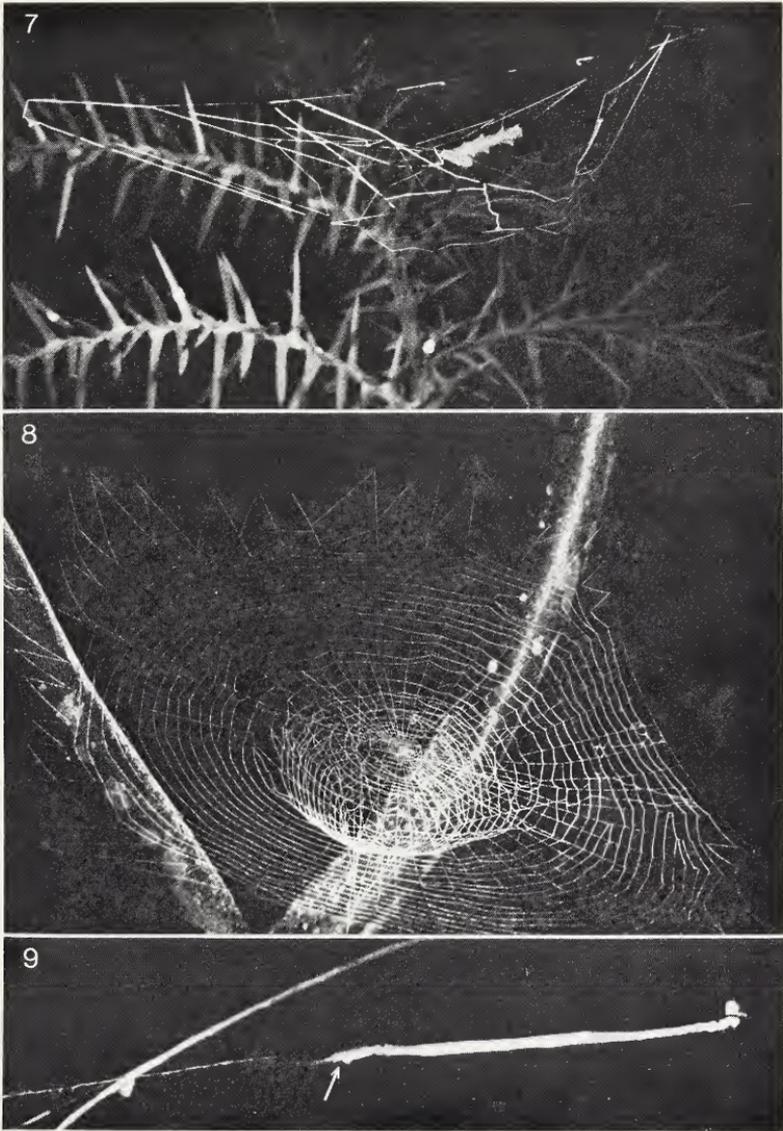
Females guarded their eggsacs (one per female) until the young emerged (13 days for one eggsac). Newly emerged spiderlings remained on the eggsac web for one or two days, then moved away and constructed typical *Uloborus*-type "baby webs", consisting of radial threads connected by a thin sheet of very fine, non-sticky silk (Szlep, 1961; Eberhard, 1977b) without any cone. One immature, however, had an orb plus cone-web with a filmy "baby web" sheet where the rim sticky spiral would normally be found and also some "baby web" sheet on the cone. Structural spirals were present in the rim and inner orb; there was no sticky spiral.

*Uloborus bispiralis**

The cone web of *U. bispiralis* (Fig. 8) is similar to that of *U. conus* in that the cone sticky spiral is continuous with that of the rim, and the outer loop(s) of rim spiral follow a zigzag path, with some sticky silk laid on the radii. Unlike webs of *U. conus*, the inner orb non-sticky spiral extends right up to the innermost (last) loop of rim sticky spiral and all webs had a few loops of sticky spiral in the inner orb. Most webs also had a thin, linear stabilimentum of white silk across the inner orb, with a spider-size gap at the hub.

Webs of juvenile females were similar in all respects to those of adults. None of the webs observed showed signs of repairs. Like those of *U. conus*, they are probably renewed daily. On one occasion only, a juvenile female was seen hanging inside the cone while an adult male fed on prey at the hub. Another adult male was observed sitting at the edge of an adult female's web and a third male was found sitting in a small cone-web (no sticky spiral was observed).

*This is a new species, described below.



Figures 7-9. *Uloborus*. 7. Eggsac and three-dimensional eggsac web of *Uloborus conus*. The female spider can be seen sitting in a cryptic posture to the left of the eggsac. Sticky threads (heavy white lines) occur in the plane of the former orb and on the rudimentary cone. 8. Web of *Uloborus bispiralis*. 9. Tubular eggsac of *Uloborus bispiralis* with female sitting in cryptic posture at one end of the eggsac (arrow).

The long, tubular eggsacs of *U. bispiralis* (34–40 mm long and 1.5 mm wide) have no angular projections (Fig. 9) and resemble those of *Miagrammopes* (Lubin et al. 1978). They are suspended along the radius of a former web of which only a few radii and frame threads remained intact. There was no evidence of sticky silk in the four eggsac webs examined. Spiders sat in line with the eggsacs, with legs I and II extended forward and legs IV grasping the eggsac, and were reluctant to move even when prodded.

*Uloborus albolineatus**

One individual of *U. albolineatus* was observed on a cone web similar to that of *U. bispiralis*. The rim spiral had one or two zigzag outer loops, and both the cone and inner orb had jagged loops of sticky spiral. The inner orb non-sticky spiral extended almost to the rim spiral. The female sat at the hub with legs I and II extended forward and held together and legs IV extended backward.

Uloborus sp. (2072)

Only a single web was seen. It consisted of a somewhat inclined orb (43° with horizontal) with a cone underneath it which contained loops of sticky spiral (Fig. 10a, b). This web differed from those of *U. Conus* in having sticky spiral threads near the center of the horizontal orb (Fig. 10c) as well as near its edge, as well as having some of the "radial lines" of the cone attached directly to the frame of the orb while others ended on radii as in *U. conus* webs.

At the hub the spider sat in a "crouched" position (Fig. 10a) similar to that of *Philoponella* (Opell and Eberhard in prep.), and was reluctant to move away when disturbed.

Uloborus trilineatus Keyserling

Most of the many webs of mature and immature *U. trilineatus* individuals observed were typical, more or less horizontal orbs like those spun by other *Uloborus* species (e.g., Szlep, 1961; Wiehle, 1927; Eberhard, 1972). Webs of mature males were similar to those of newly emerged uloborid spiderlings (Szlep, 1961; Eberhard,

*This is a new species, described below.



Figure 10. Web of *Uloborus* sp. (#2072). A. Side view with spider (arrow) at hub. B. Top view. C. Enlargement of the hub. Both cone and orb spirals are sticky. Most cone radii are attached to orb radii, but some end on frame lines. The cone sticky spiral seems not to be continuous with the orb spiral.

1977b). However, at both Finca Chenevo and Finca Mozambique one immature was found at the hub of a web like that shown in Figs. 11a, b. Each web consisted of a small, more or less horizontal orb which had only a non-sticky spiral. Below this was a cone which also had a non-sticky spiral. Only one of these spiders was collected, the other was left on its web, and the next day the web was deserted and an exuvium was found clinging to its hub. Identity of the collected immature specimen is not certain, but abundance of *U. trilineatus* at these sites plus the failure of extensive collecting of orb weavers to reveal similar species in these habitats indicates that these immatures were *U. trilineatus*.

*Conifaber parvus**

This species was fairly common in a periodically flooded forest on Finca Mozambique. Only mature females were found with webs. The webs all had an "orb" similar or identical to those spun by most newly emerged uloborid spiderlings (Szlep, 1961; Eberhard, 1977b), having radii, hub, frames, and a non-sticky spiral as in typical orbs but lacking a sticky spiral and having instead a dense mat of very fine threads (so fine that in Figs. 12a, b they do not show up as individual threads, and one only sees the grains of cornstarch). Below this orb was a conical web consisting of radii which converged below to a single downward-directed line, and a more or less regularly spaced spiral, also of non-sticky silk. The hubs were often decorated with linear stabilimenta.

The spider crouched at the hub with its legs I folded ventrally in the typical *Philoponella* posture (Opell and Eberhard in prep.). Sometimes when a spider was disturbed she let herself fall from the hub and hung suspended inside the cone on her dragline and bounced actively there. On other occasions spiders bounced on their orbs.

Attack behavior was observed twice and seemed to be typical for uloborids. The spider turned to face away from the prey and threw silk over it with her legs IV, gradually cut it loose as she wrapped it, then held it with the palps and/or chelicerae as she reattached the ends of the broken radii, took it to the hub, and then resumed

*These are a new genus and species, described below.

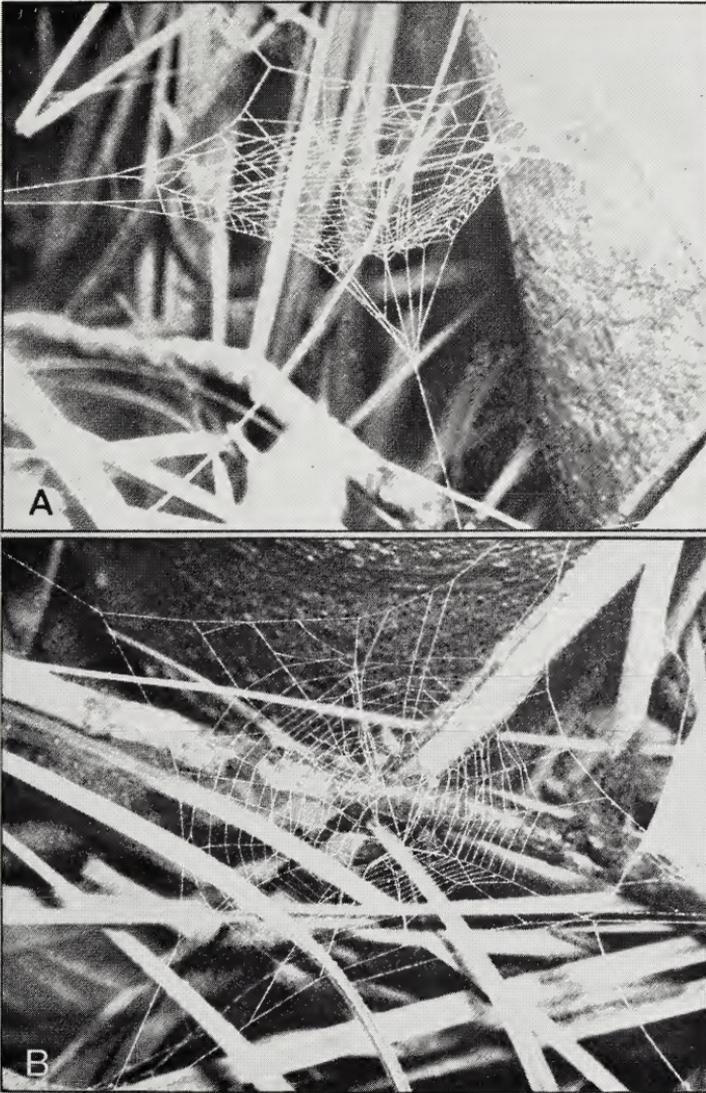


Figure 11. Web of penultimate female of *Uloborus trilineatus* Keyserling. A. Side view. B. Top view. Most (or all?) of the cone radii are attached to frame lines. The central area of the cone has fewer radii than the upper portion, and gives the impression of having been partially dismantled, perhaps during the process of being connected to the central thread as in *U. consu*.

wrapping while hanging there by her spread legs I.

The eggsacs were different from those described for any other uloborid. They were pure white, 2–3 mm diameter spheres with projecting spikes, and resembled the heads of maces; they were suspended in the plane of the orb portion of the web on a radial line (Figs. 13a, b).

DISCUSSION

While the webs of all five species are similar in having more or less horizontal orbs with cones below, the details are strikingly different. The cones of *U. conus*, *U. albolineatus*, *U. bispiralis*, and *U.* #2702 have a sticky spiral while those of *U. trilineatus* and *C. parvus* do not. In *U. albolineatus*, *U. bispiralis*, and *U.* sp. #2702 both the outer (rim) and inner portions of the orb have sticky spirals, while in *U. conus* the main capture surface is the rim sticky spiral and only occasionally is a sticky spiral present in the inner orb. The “orbs” of *Conifaber parvus* have no sticky spiral, but the dense mat serves as a trapping surface, as in uloborid “baby webs”. Orb-plus-cone webs of *U. trilineatus* have no sticky silk at all.

The function of the cone in webs of all four species is probably primarily defense of the spider at the hub against predators and parasites. The cone forms a “cage” of threads around the spider, and a defense function is suggested both by the fact that *U. conus* and *Conifaber parvus* drop from the orb and hang inside this cone when disturbed or when the web becomes visible in sunlight, and by the fact that construction of conewebs by *U. trilineatus* occurs only when the spiders are about to enter the particularly vulnerable moulting period. The sticky threads in the cones of *U. conus* and *U. albolineatus* and *U.* #2702 sometimes trap prey (some *U. conus* webs have almost no other sticky lines), but the fact that the cones of *U. conus*, *U. albolineatus*, and *U. bispiralis* have only a few, irregularly spaced sticky spiral loops while those of *U. trilineatus* and *C. parvus* lack sticky threads suggests that prey capture is a secondary consequence rather than a primary function of at least some of the cones. Placement of sticky threads in cones could have evolved as an additional defense of the spider against predation or parasitism.

The uloborid cones resemble the barrier meshes made by the araneid *Nephila maculata* (Robinson and Robinson, 1973) at one or both sides of their more-or-less vertical orbs; in young *N. maculata*

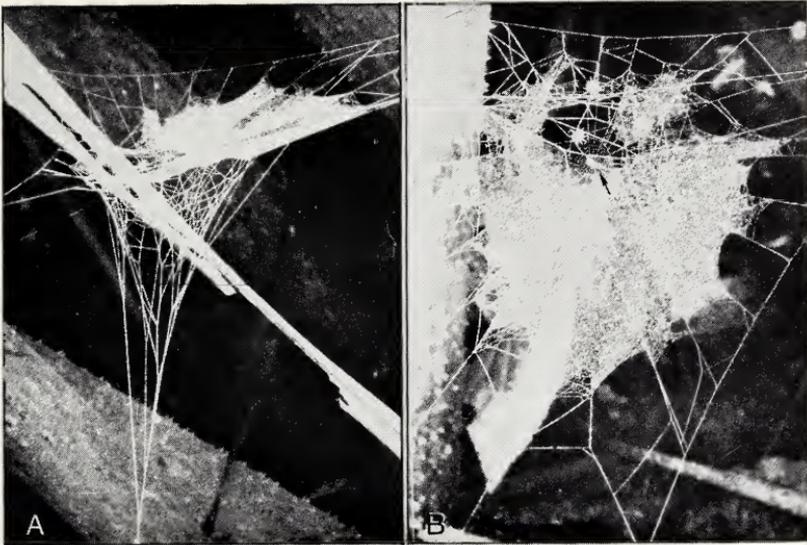


Figure 12. *Conifabar parvus* web. A. Side view showing framework threads, radii, mat of non-sticky spirals, and cone radii. B. Top view showing non-sticky spiral mat, two stellate eggsacs, and the female (arrow) resting at the web's hub.

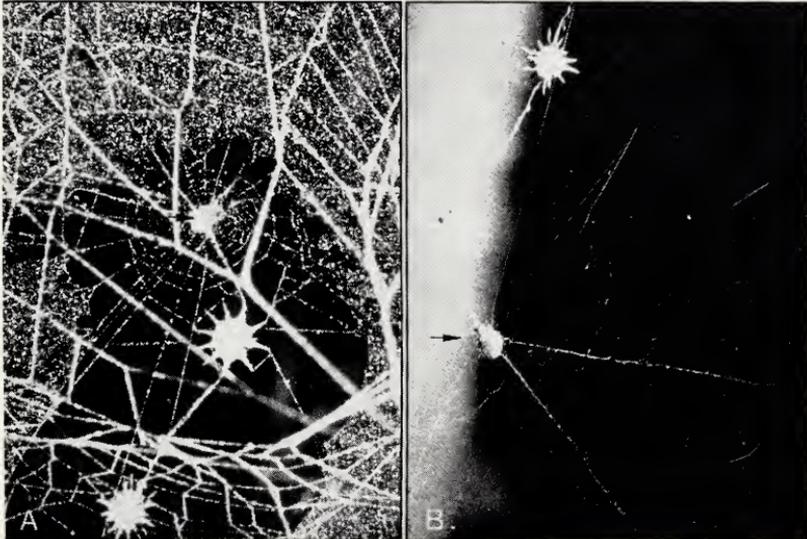


Figure 13. *Conifaber parvus* web hub and eggsacs. A. Female (arrow) resting at hub. Two stellate eggsacs and some of the horizontal web's fine, non-sticky threads are visible. B. Female (arrow) resting in crouched posture at the hub of a web decorated with linear stabilimenta.

the mesh is a cone-shaped, rudimentary orb with no sticky spiral. The Robinsons attributed a defensive function to these structures, and indeed the arguments developed here suggest that barrier meshes made by a number of other araneids (*Metepeira*, *Leucauge*, *Argiope*, *Arachnura*, *Gasteracantha*, and *Phonognatha*) may also function defensively.

The evolutionary origin of the orb-plus-cone web designs in uloborids is not clear. At least two other uloborid orb-plus-cone webs are known. Workman (1896) described the orb-plus-cone web of *Uloborus quadrituberculatus* (Thorell). His apparently schematic drawing shows a horizontal orb lacking spiral lines and a cone with a 14 loop spiral (he did not note whether or not the spiral was sticky). The cone is attached on all sides to surrounding vegetation by short lines. In Sembrong Jungle near Layang-Layang, Johore, Malaya, Frances Murphy photographed the orb-plus-cone web of a specimen matching Workman's (1896) description of *U. quadrituberculatus*. This web was constructed about 1.5 m above the ground and had a zigzag outer loop and an irregular cone spiral. An unidentified species of *Tangaroa* collected in mesophyll rainforest in the Iron Range, northeastern Queensland, Australia had an orb-plus cone web with a zigzag outer loop of rim sticky spiral (V. Todd Davies, personal communication). It is not known if the cone spiral was sticky. However, a small, unidentified *Tangaroa* species from Yap, Caroline Islands constructed a horizontal orb-web in both the field and lab (Joseph Beatty and James Berry, personal communication and BDO unpublished observations, respectively), indicating that the cone-web is not characteristic of all members of this most primitive uloborid genus (Opell, 1979) and, therefore, does not represent the "original" uloborid web design.

We do not know if the cones of the five species studied here are constructed in the same manner. Certain behaviors associated with cone construction in *U. conus* (and probably *U. albolineatus* and *U. bispiralis*) including the laying of a jagged sticky spiral with few attachments to the radii, formation of a cone by cutting and reattaching radii to a central line, replacement and reposition of radii, and pulling the orb into a cone, have not been seen in other uloborids. When one takes into account the webs of other uloborids such as *Philoponella vicina* (Peters 1953, 1955), *P. semiplumosa* (Lahmann and Eberhard 1979), *P. oweni* (Eberhard 1969), *P. divisa* (Opell 1979), and *P. para* (Eberhard, unpub.) which are more or less

reduced and modified planar or domed orbs in the midst of meshes which include sticky as well as non-sticky threads (*P. oweni* also spins orbs without meshes—Eberhard, 1969), the “orb” of *Polenecia* (= *Sybota*) which lacks sticky spirals and has instead sticky radii (Wiehle 1931), the orbs *cum* sheet webs spun by young spiderlings and mature males of several species (Szlep, 1961; Eberhard, 1977b), and the various simplified webs of *Hyptiotes* (Wiehle 1927, Marples and Marples 1937) and *Miagrammopes* (Akermann 1932, Lubin et al. 1978), it becomes clear that there is an extraordinary diversity of web forms in the relatively small family Uloboridae. It is likely that, in conjunction with morphological studies, a fuller understanding of the webs and behavior of uloborids will shed more light on relationships within the family.

SYSTEMATIC SECTION

Conifaber new genus*

Figures 14–15, 20–29

Type. The type species of *Conifaber* is *Conifaber parvus*, new species. The genus name is a masculine noun derived from the Latin nouns *conus* and *faber* and means “cone craftsman”.

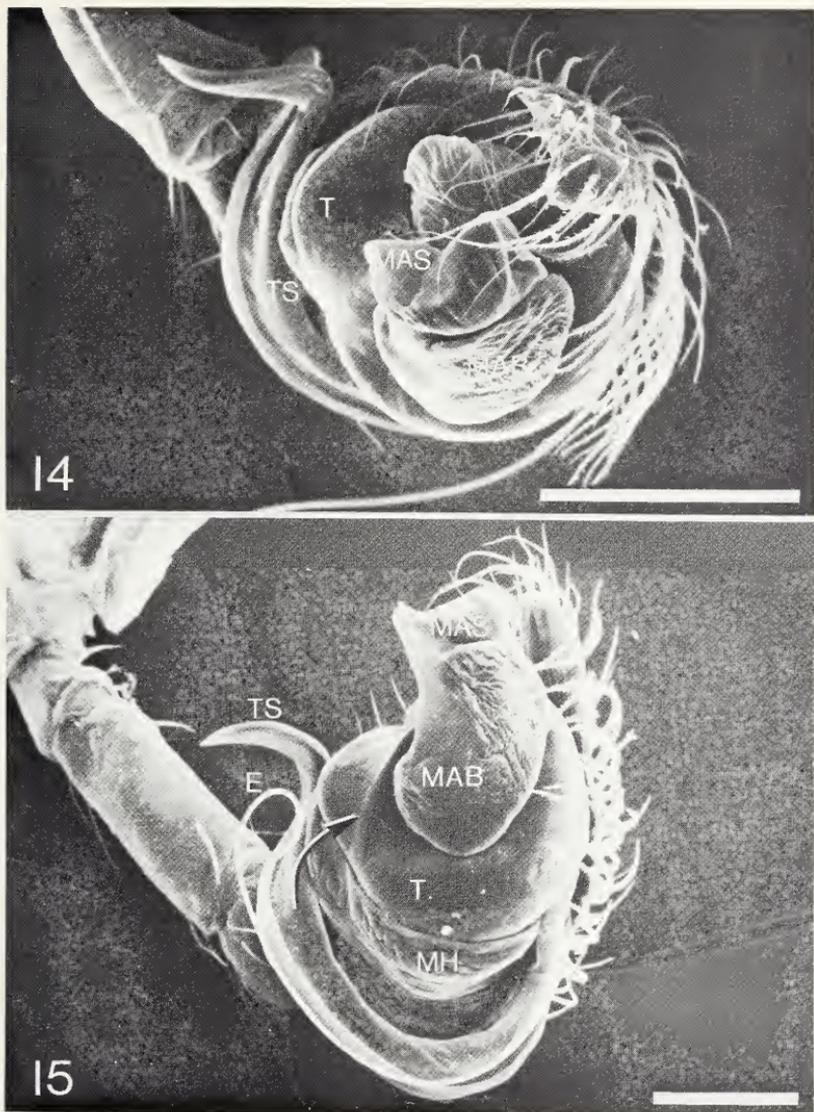
Diagnosis. *Conifaber* contains the smallest known uloborids, females being 2.0 mm and males 1.5 mm long. Because of their small size members of this genus are more likely to be confused with those of *Ariston* and *Siratoba* than with *Zosis*, *Octonoba*, and *Purumitra*, to which they are more closely related. *Conifaber* males and females are distinguished from those of *Ariston* and *Siratoba* (Opell, 1979; figs. 41, 72) by having a strongly recurved anterior eye row whose median eyes are located on a slight anterior carapace extension and have a diameter twice that of the other eyes (Figs. 20–23). Unlike *Ariston* and *Siratoba* females whose first femora are 1.5 and 2.0 times the carapace length, respectively, and whose thoracic grooves are in the carapace’s posterior two-fifths, *Conifaber* females have first femora equal in length to the carapace and have a centrally located thoracic groove. Like *Ariston*, but unlike *Siratoba*, *Coni-*

*For nomenclatural purposes B. D. Opell is the author of the genus *Conifaber* and the species *C. parvus*.

faber females lack dorsal abdominal tubercles. Like *Siratoba* but unlike *Ariston*, their clypeus height in anterior view is equal to the AME diameter. *Conifaber* males lack first femoral macrosetae present in *Ariston* and *Siratoba* males (Opell, 1979, figs. 39, 70) and, like *Ariston*, lack abdominal tubercles.

Using Opell's (1979) keys to uloborid genera, *Conifaber* males key to couplet 10, which separates *Octonoba* and *Purumitra*, and females key to couplet 10, which separates *Octonoba* and *Uloborus*. *Conifaber* males are distinguished from those of *Octonoba* and *Purumitra* by having first femora whose lengths are equal to rather than 1.5 to 2.0 times as long as the carapace, by lacking femoral macrosetae present in these genera (Opell, 1979; figs. 181, 183), and by having a longer, more conspicuous tegular spur than these genera (Fig. 14; Opell, 1979; plate 6-c, fig. 157). *Conifaber* females lack dorsal abdominal tubercles present in *Octonoba* and *Uloborus* (Opell, 1979; figs. 132, 140) and have inconspicuous, anteriorly directed epigynal lobes (Figs. 24-26) instead of conspicuous posteriorly directed lateral epigynal lobes (Opell, 1979; figs. 137, 145, 178, 184).

Description. Maximum carapace width 0.84 carapace length, attained in posterior half of female carapace and in posterior third of male carapace (Figs. 21-22). Female carapace slopes up to a point just behind PLE and then down to AME (Fig. 20). Male carapace slopes more steeply up to a point slightly forward of its center and then down to PME (Fig. 23). Shallow, transverse female thoracic groove at carapace center; deep, U-shaped male thoracic groove in posterior quarter of carapace. In both sexes anterior eye row strongly recurved so that a line across AME's posterior margins passes in front of ALE's by a distance equal to one ALE diameter. Posterior eye row slightly recurved so that a line across PME's posterior margins passes along PLE's anterior margins. Median ocular area's length and posterior width 0.8 its anterior width. Female AME diameter 0.75 that of male AME, remaining eyes equal to 0.66 female AME and 0.50 male AME. AME's 1.3 as far from one another as from ALE's, PME's 1.7 as far from one another as from PLE's. Sternum 0.80 as wide as long, widest between first and second coxae. Female endite 0.80 and male endite 1.00 as wide as long. Labium 1.40 as wide as long. First femur equal in length to carapace. Male first tibia with six or seven short and one long



Figures 14 and 15. Apical (14) and retrolateral (15) views of *Conifaber parvus* n. sp. holotype male left palpus. The arrow in 15 shows the normal position of the tegular spur (TS) embolus (E) guide as it rests in the grooved tegulum (T). MAB = median apophysis bulb, MAS = median apophysis spur, MH = middle hematocha. Scale lines are 100 μ m long.

dorsoprolateral macrosetae, two or three long proximodorsal macrosetae, and two or three distoretrolateral macrosetae (Fig. 28). Abdomen without tubercles or abrupt peak (Figs. 20–23). Female abdomen 0.98 as wide and 1.38 as high as long, male abdomen 0.70 as wide and 0.93 as high as long. Distance between cribellum and epigastric furrow 0.44 abdomen length. Abdomen and cephalothorax were separated when the epigynum was removed. Examination of the severed petiole revealed no large tracheal trunks, indicating that, as in *Philoponella* and *Daramuliana* (Opell, 1979 fig. 1), no tracheae extend into the cephalothorax or, as in *Zosis*, *Purumitra*, and *Octonoba* (Opell, 1979; fig. 2), only fine tracheoles extend into the cephalothorax.

Male Palpus. Femur without ventral tubercles. Like *Zosis*, *Purumitra* and *Octonoba* (Opell, 1979; plates 6-c,d, 7-c,d, fig. 157), *Conifaber* male palpi have a tegular spur which acts as an embolus guide (Figs. 14–15). This tegular spur is proportionately larger than those of other genera and rests in a tegular groove unique to *Conifaber*. Members of *Zosis* also have a large, grooved tegular spur, but the median apophysis bulb of *Conifaber* is a plate rather than a hemisphere, and its median apophysis spur a grooved plate rather than a hook. The tegular spur's tip may rest in the median apophysis spur's distal groove.

Epigynum. Two posterior lateral epigynal lobes extend anteriorly a short distance, concealing a pair of weakly sclerotized, anteriorly directed oval areas (Figs. 24–25). In posterior view the epigynum's posterior plate is 0.6 as high as broad and has slightly curved and rounded ventral rim about one third the height of the posterior plate (Fig. 26). A highly coiled duct leads from each weakly sclerotized oval to a spherical spermatheca whose short fertilization duct appears to connect to the vagina's ventrolateral margin (Fig. 27).

Distribution. This genus is known only from the type localities in eastern central Colombia.

***Conifaber parvus* new species**

Figures 14–15, 20–29

Types. Male holotype, male paratype, and female paratype from Finca Mozambique, 15 km S.W. of Puerto Lopez in the

Colombian department of Meta; collected 1978 by W. G. Eberhard, in the Museum of Comparative Zoology. The specific epithet is a Latin noun in apposition, referring to the small size of members of this species.

Description. As most features of this species are presented in the genus description, only those of color and size are given here. Total length of female 1.92 mm, of males 1.50 mm. Female carapace 0.72 mm long, male carapace 0.66 mm long. Female sternum 0.44 mm long, male sternum 0.38 mm long. Female AME diameter 60 μm , male AME diameter 80 μm , remaining eyes of both sexes 40 μm in diameter. Female leg length (I–IV): 2.86, 1.78, 1.52, 2.42 mm. Male leg length: 2.70, 1.56, 1.33, 1.94 mm. Female calamistrum composed of 10 setae and 0.22 mm long, extending 0.52 the metatarsus length. Female cribellum 180 μm wide, 60 μm long. Female anterior spinnerets 0.30 mm long, male 0.16 mm long. Female posterior spinnerets 0.27 long, male 0.18 mm long. Female anal tubercle 0.14 mm long, male 0.10 mm long.

Except for dark circles around the eyes (Figs. 21–22) members of neither sex have conspicuous color markings. The thoracic groove is slightly darker than the rest of the carapace, and white guanine deposits under the abdomen's integument are interrupted by the cardiac area which creates a tan median stripe (Figs. 21–22). Lacking these deposits, the anterior third of the female's abdomen is also tan rather than white.

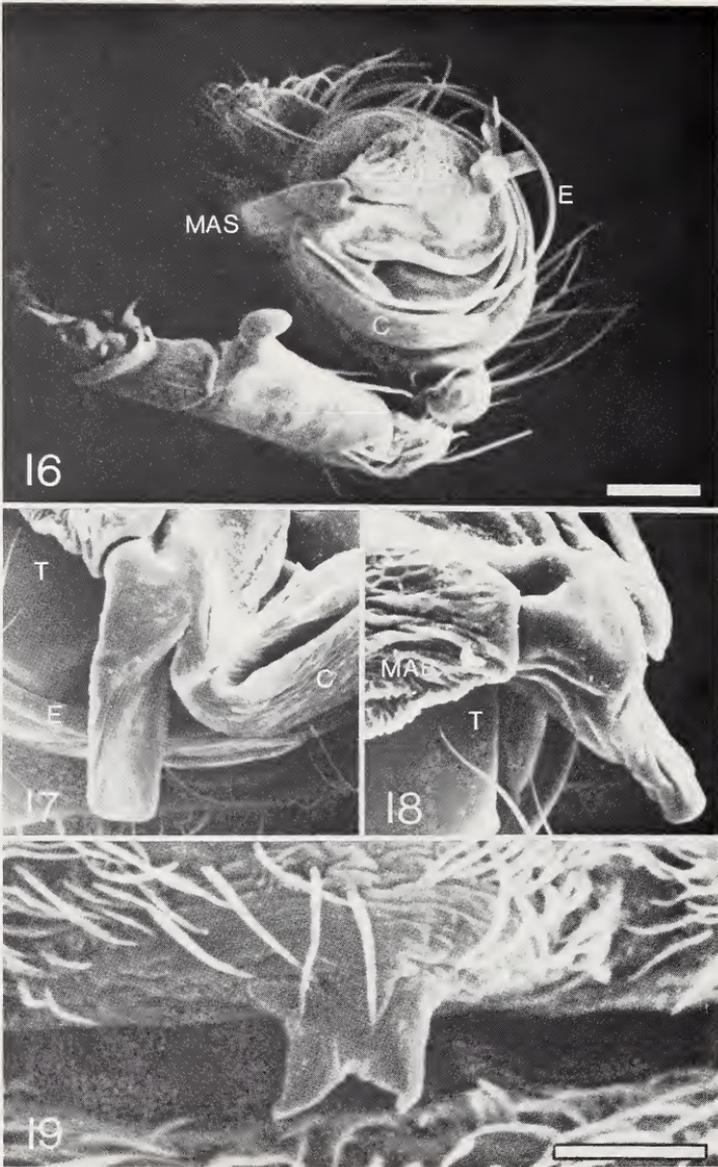
Distribution. Known only from the type locality in eastern central Colombia.

Uloborus conus new species*

Figures 16–19, 30–35

Types: All types from Papua New Guinea. Female holotype and paratype from Madang Prov., 40 km south of Madang, collected 21 March 1979 by H. W. Levi and Y. D. Lubin. Two male and three female paratypes from Morobe Prov., Buso Forest Reserve, collected 25 Oct. 1979 by Y. D. Lubin. Four female paratypes from

*For nomenclatural purposes B. D. Opell is the author of this species.



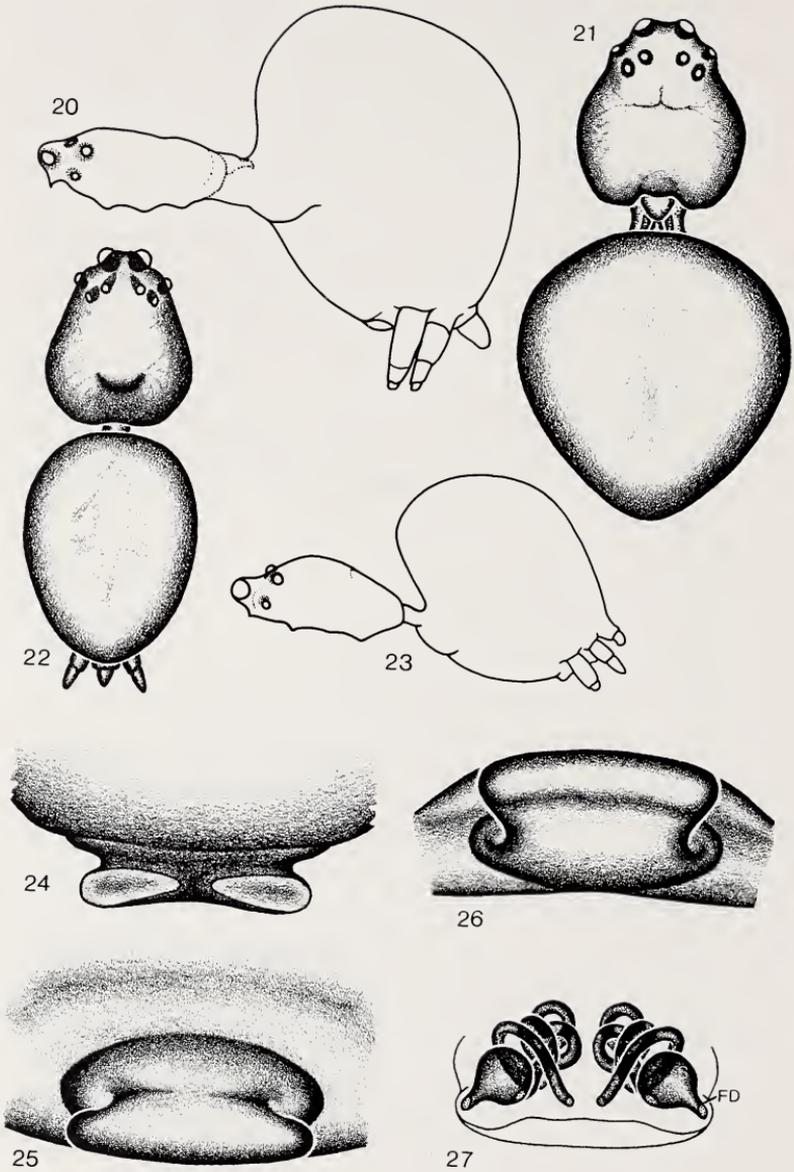
Figures 16-19. *Uloborus conus* n. sp. 16. Retrolateral view of holotype male left palpus (a trilobed piece of debris is lodged at the upper right). 17. Retrolateral view of MAS. 18. Apical view of MAS. 19. Ventral view of female paratype epigynum. C = conductor; other abbreviations as in Figures 14 and 15. Scale lines are 100 μm long.

Central Prov., along Brown River, near Port Moresby, collected 29 April 1980 by Y. D. Lubin. One male and one female paratype deposited in the American Museum of Natural History, the remaining types are deposited in the Museum of Comparative Zoology. The specific epithet is a Latin noun in apposition, referring to the conical web produced by members of this species.

Diagnosis. Males and females are distinguished by a carapace length of less than 1.00 and 1.30 mm, respectively. Males have a long, lobed palpal femoral tubercle, a reduced, flattened median apophysis, a long, broad conductor, and a blunt median apophysis spur (Figs. 16–18). Length of female femur I less than 1.2 carapace length rather than 1.4–1.5 carapace length as in other uloborids. Central region of epigynum from which lobes arise about one third rather than half as wide as the posterior plate (Figs. 19, 34).

Description. Female. Total length 2.80–3.40 mm ($X = 3.20$), carapace length 1.00–1.30 mm ($X = 1.09$), maximum carapace width 0.90–1.00 ($X = 0.96$), carapace width at PLE's 0.58–0.64 mm ($X = 0.60$), area. All eyes except AME's surrounded by small black circles (Fig. 30). PLE nearer midline than in other *Uloborus* species. Sternum tan. Leg I of most specimens as shown in Fig. 33, but nearly black in two dark specimens. Dorsum of femur I of all specimens black. Abdomen of most specimens light tan or white. Abdomen of two dark specimens with white dorsum, black venter and two broad, white lateral stripes extending from anterior apex to posterior tips. Epigynum consists of two small, weakly sclerotized posterior lobes (Fig. 19) whose combined basal width is one-third that of the posterior plate (Fig. 34). An epigynal opening found dorsal to each lobe leads to a large, irregular spermatheca from whose posterior lateral margin a short fertilization duct extends (Fig. 35).

Male. Total length 2.00–2.20 mm, carapace length 1.00 mm, maximum carapace length 0.85 mm, carapace width at PLE's 0.66 mm, sternum length 0.56 mm. Carapace and sternum coloration similar to that of female except that broad gray streaks extend anteriorly from the posterior eyes (Fig. 31). Legs light tan, tibiae II–IV with light gray dorsal tip. Femur I with three prolateral, one dorsal, central; and one distal, retrolateral macrosetae (Fig. 32).



Figures 20–27. *Conifaber parvus* n. sp. 20. Lateral view of female. 21. Dorsal view of female. 22. Dorsal view of male. 23. Lateral view of male. 24. Anterior view of epigynum. 25. Ventral view of epigynum. 26. Posterior view of epigynum. C = conductor, D = other abbreviations as in Figures 14 and 15. Scale lines are 100 μ m long.

Tibia I with eight prolateral, seven dorsal, and three retrolateral macrosetae. Sternum and abdominal venter with orange setae. Abdomen gray with a pair of thin, white, lateral longitudinal stripes running nearly its full length. Palpal femur with a large, lobed retrolateral tubercle and a very small prolateral tubercle (Fig. 16). Median apophysis bulb small and flattened (Fig. 16); median apophysis rectangular with a blunt apex (Figs. 17–18). Conductor long and broad, extending from median apophysis spur to area of palp adjacent to patella.

Distribution. Known only from the type localities in Papua New Guinea.

Uloborus albolineatus* new species

Figures 36–39.

Type. Female holotype from Lowlands Agricultural Experimental Station, Kerevat, East New Britain, Papua New Guinea, collected 6 July 1980 by Y. D. Lubin, deposited in the Museum of Comparative Zoology. The specific epithet is a noun in apposition, referring to the species' white median abdominal stripe.

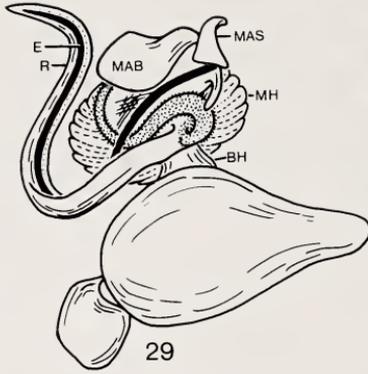
Diagnosis. Males are unknown. The female is distinguished by having reddish brown median eyes, a very convex sternum (Fig. 37), white guanine deposits in the cardiac region (Fig. 36), and weakly sclerotized epigynal lobes rising from the center rather than posterior of a transparent epigynum (Fig. 38). Unlike many *Uloborus* species, the carapace lacks a conspicuous median light stripe.

Description. Female. Total length 2.40 mm, carapace length 0.92 mm, maximum carapace width 0.74 mm, carapace width at PLE's 0.50 mm. Carapace tan with gray, reticulate lateral markings (Fig. 36). Median eyes reddish brown. AME's on a more conspicuous tubercle than most *Uloborus* species. Sternum tan, widest at coxae I rather than between coxae I and II as in other *Uloborus* species. Legs light tan with faint gray distal rings on most segments. Tibia I with very sparse distal setal brush. Abdomen height and width 0.9 its length, dorsum with a pair of centrolateral tubercles, posterior

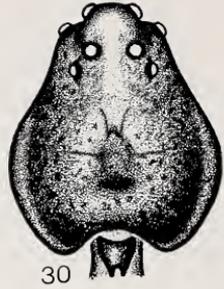
*For nomenclatural purposes, B. D. Opell is author of this species.



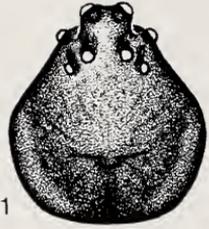
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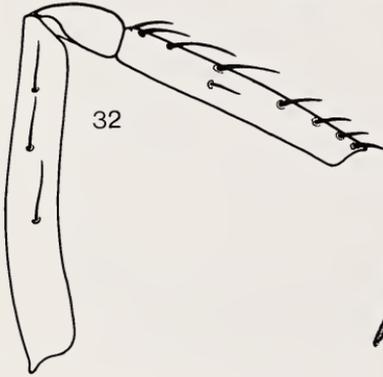
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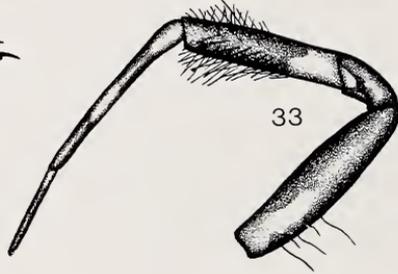
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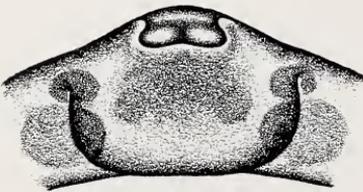
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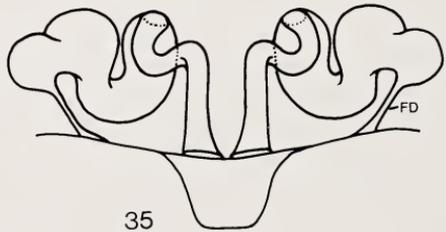
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tip projecting slightly posterior to anal tubercle's base and separated from anal tubercle by a distance one third the abdomen's height. White guanine deposits extend both in a narrow transverse band across the abdomen's anterior ventral surface and along the cardiac area. A broader, more diffuse median guanine deposit extends from the abdomen's humps to its posterior tip. A pair of large guanine spots is found anteriolaterally to the spinnerets. Epigynum convex with broad posterior extension, a pair of low, weakly sclerotized median lobes, and a transparent integument through which a single pair of spherical spermathecae is clearly visible (Figs. 38, 39).

Distribution. Known only from the type locality in Papua New Guinea.

Uloborus bispiralis* new species

Figures 40-48.

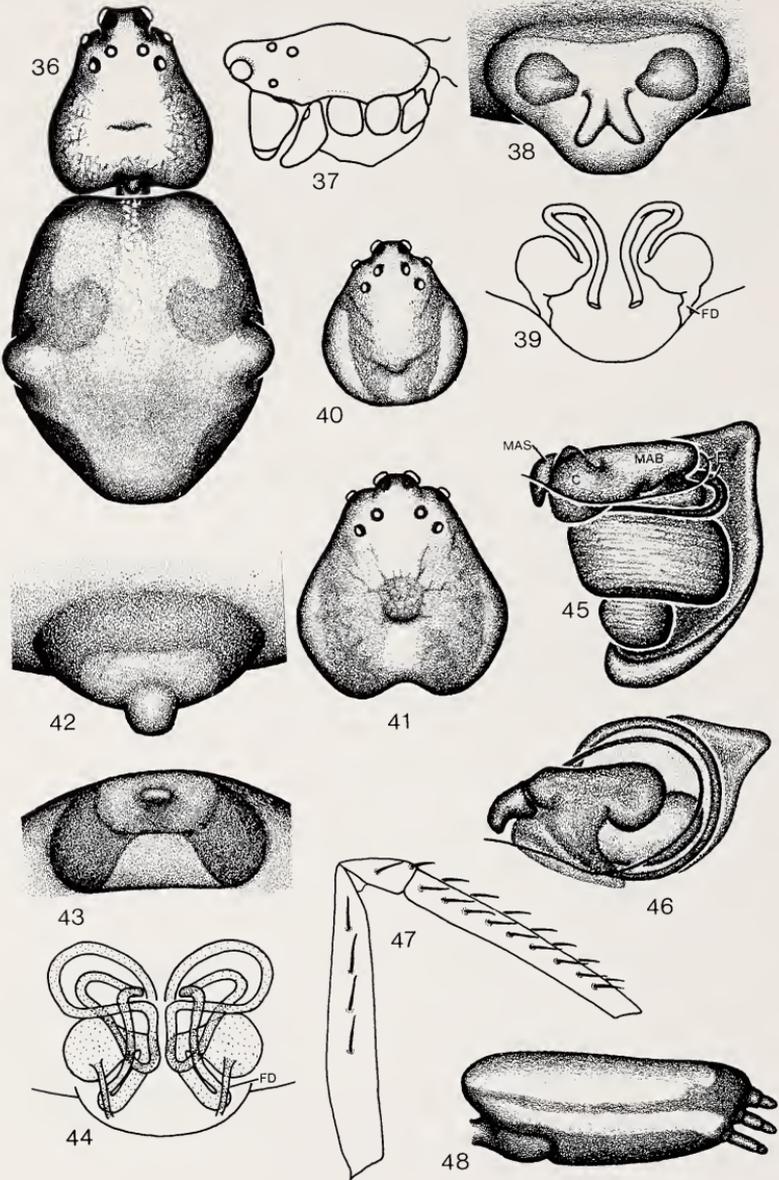
Types: Female holotype, three male and seven female paratypes from Lowlands Agricultural Experimental Station at Kerevat, East New Britian Prov., collected 2, 4, and 6 July 1980 by Y. D. Lubin. Male and two female paratypes deposited in the American Museum of Natural History, remaining types in the Museum of Comparative Zoology. The specific epithet is a latin noun in apposition, referring to the male's doubly coiled embolus.

Diagnosis. Females are distinguished by having a single, narrow median, posterior epigynal lobe (Figs. 42, 43) rather than a pair of posterior epigynal lobes, and by each epigynal duct making five rather than the usual single loop (Fig. 44). Males are distinguished by an embolus which loops twice rather than once around the

*For nomenclatural purposes B. D. Opell is the author of this species.

Figures 28 and 29. *Conifaber parvus* n. sp. 28. Dorsal view of male left first tibia. 29. Retrolateral view of expanded male left palpus (R = radix, BH = basal hematodocha, other abbreviations as in Figs. 14 and 15).

Figures 30-35. *Uloborus conus* n. sp. 30. Dorsal view of female carapace. 31. Dorsal view of male carapace. 32. Prolateral view of male first femur, patella, and tibia. 33. Retrolateral view of female leg I. 34. Posterior view of epigynum. 35. Dorsal view of cleared epigynum.



median apophysis and by a flattened, elongate median apophysis bulb which bears a broad conductor (Figs. 45, 46). Both males and females have a gray lateral abdominal stripe (Fig. 48).

Description. Female. Total length 3.28–3.68 mm ($X = 3.47$, S , 0.14, $N = 8$), carapace length 1.10–1.20 mm ($X = 1.15$, $SD = 0.04$), maximum carapace width 0.94–1.04 ($X = 0.98$, $SD 0.04$), carapace width at PME's 0.54–0.58 mm ($X = 0.56$, $SD 0.01$). All eyes except AME's surrounded by small black circles (Fig. 41). Carapace with light lateral margins, light posterior median stripe, and central gray patch. Sternum tan. First and second legs light gray with tan proximal ring on tibia, metatarsus, and tarsus. Tibia I without a conspicuous setal brush. Third and fourth legs tan with gray distal rings on tibia, metatarsus, and tarsus. Abdomen without humps, dorsal and lateral surfaces densely covered by white guanine spots except in cardiac region and along a faint lateral stripe similar to but not as sharply defined as that shown in Fig. 48. Venter tan with only sparse guanine spots. Epigynum a raised mound with single median lobe (Figs. 42, 43), probably representing a pair of fused lateral lobes. Under normal light microscopy a clove oil-cleared epigynum showed only a pair of oval spermathecae with a fertilization duct leading from the posterior lateral margin of each and a short, broad duct extending from the median surface of each to epigynum's posterior margin. Examination with Nomarski optics revealed the more extensive system of thin-walled ducts shown in Figure 44. It was not possible to determine precisely where the ducts opened externally, but this appears to be between the spermathecae and near the base of the epigynal lobe.

Male. Total length 2.32–2.40 mm, carapace length 0.98–1.00 mm, maximum carapace width 0.78–0.80 mm, carapace width at PLE's 0.50–0.52 mm. Carapace and sternum coloration similar to that of

Figures 36–39. *Uloborus albolineatus* n. sp. 36. Dorsal view of female holotype. 37. Lateral view of female carapace. 38. Ventral view of epigynum. 39. Dorsal view of cleared epigynum.

Figures 40–48. *Uloborus bispiralis* n. sp. 40. Male carapace. 41. Female holotype carapace. 42. Ventral view of holotype epigynum. 43. Posterior view of epigynum. 44. Dorsal view of cleared epigynum. 45. Retrolateral view of male palpus. 46. Apical view of male palpus. 47. Prolateral view of male first femur, patella, and tibia. 48. Lateral view of male abdomen.

females except for absence of central gray carapace spot (Fig. 40). Legs reddish brown. Femur I with three or four prolateral macrosetae, tibia I with nine prolateral, six or seven dorsal, and three retrolateral macrosetae (Fig. 47). Abdomen with fewer guanine spots than female, dorsum and lateral surface tan; gray lateral stripe, gray venter and gray posterior tip (Fig. 48). Palpal femur with a large proximal retrolateral tubercle and small prolateral tubercle. Median apophysis bulb flat and elongate (0.16 mm long), terminating in a bent median apophysis spur (Figs. 46, 47). Unlike other members of the genus, the embolus loops twice around the median apophysis bulb before passing into a broad, weakly sclerotized conductor.

Distribution. Known only from the type locality in Papua New Guinea.

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POPULATION STRUCTURE AND SOCIAL ORGANIZATION
IN THE PRIMITIVE ANT *AMBLYOPONE PALLIPES*
(HYMENOPTERA: FORMICIDAE)

BY JAMES F. A. TRANIELLO¹
Harvard University,
Museum of Comparative Zoology Laboratories
Cambridge, Massachusetts 02138, U.S.A.

INTRODUCTION

The genus *Amblyopone* contains the most morphologically and behaviorally primitive species in the poneroid complex of ants, and a detailed examination of their social structure could significantly contribute to the reconstruction of social evolution in the Formicidae. But because of their cryptic habits and distribution, the biology of the majority of species of *Amblyopone* and the related genera *Mystrium*, *Myopopone*, *Prionopelta*, and *Onychomyrmex* remains almost entirely unknown. Previous investigations have provided information on colony foundation (Haskins, 1928; Haskins and Enzmann, 1938; Haskins and Haskins, 1951), ecology, behavior, and taxonomy (Wheeler, 1900; Brown, 1960; Gotwald and Levieux, 1972; Baroni Urbani, 1978), and physiology (Whelden, 1958). Still, many of the details of social organization in *Amblyopone* are lacking. I present in this paper the results of a two-year study on the behavior and ecology of *Amblyopone pallipes*.

MATERIAL AND METHODS

Study areas and nest collection

Thirty-one colonies of *A. pallipes* were collected under stones in a damp, white pine woodland in Westford, Massachusetts. A single colony was taken under the bark of a rotting log. Nests generally consisted of one or two shallow (6-10 mm) depressions in the soil immediately beneath the stone, from which a single gallery opened to subterranean chambers. Gentle excavation usually revealed one or two additional loosely structured chambers. Workers, queens,

¹Present address: Department of Biology, Boston University, Boston, Massachusetts 02215

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sexualls, and brood were found at all levels of the nest and were quickly aspirated.

Distribution and natural history

A. pallipes has been found in the eastern United States and in the St. Lawrence Valley in Canada in cool, moist, forested areas (Brown, 1960). General references on the natural history of this species are given by Wheeler (1900) and Haskins (1928).

Laboratory arrangements

Colonies were housed in artificial nests composed of a thick, moist filter paper bottom with cotton sides approximately 6mm high covered with a glass plate. The nests were placed in 15 × 22 cm plastic boxes in which the humidity was kept high. The total nest area was roughly 10cm². A second chamber, similar in structure but somewhat larger, was connected to the nest as a foraging arena, where live prey were offered. Colonies were fed on whole, live geophilomorph and lithobiid centipedes; in addition, elatryid, buprestid, and tenebrionid beetle larvae were acceptable to the ants. This method of culture proved successful and greatly facilitated studies of social interaction since the activity of an entire colony could be monitored on the stage of a dissecting microscope. Ethogram data were compiled in this manner, and were analyzed using the methods of Fagen and Goldman (1977).

RESULTS AND DISCUSSION

1. Life cycle and population structure.

Nest distribution and colony size. The spatial distribution of colonies at the principal study site in Westford is presented in Fig. 1. An interesting feature of this population, in addition to its clumped distribution pattern is that three colonies were collected under stones in 1978 precisely where colonies were found the year before. This suggests that the colonies that were collected represented subunits of a large, subterranean population. Each unit is small (modal size class = 9–16 workers). Complete collection data are presented in Fig. 2. Although distributional data are not given, a population of seemingly comparable density was discovered by Wheeler (1900), who uncovered 30 nests in a three hour period. Also, the colony size data correspond closely to the data of Francoeur (1965, 1979, and personal communication).

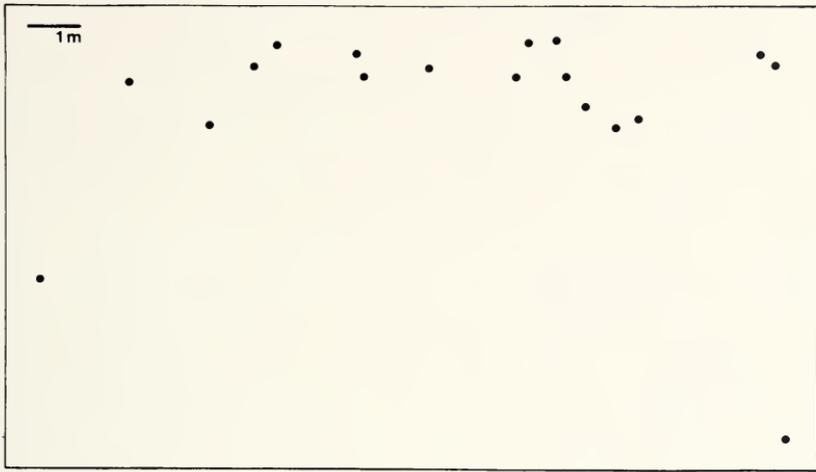


Fig. 1. — The spatial distribution of nests at the principal study site.

Queen number. The frequency distribution of the number of queens in a colony is given in Fig. 3. Of 19 queenright colonies, 10 (52%) contained more than one dealate female. Observations of multiple queened colonies in the laboratory revealed that in at least some of these colonies each queen was functionally reproductive. However, many queens in apparently polygynous colonies did not lay eggs, and engaged primarily in worker tasks.

Life cycle, colony reproduction, and population structure. Because colonies were collected and censused throughout the spring and summer of 1977 and 1978, it is possible to outline the life cycle of *A. pallipes* (Fig. 4). Eggs are laid in late April or early May and larvae hatch and develop throughout June and July. Mature larvae pupate in mid-July and early August, and adults eclose approximately two to three weeks later. Although small numbers of eggs and larvae are present in most colonies throughout the spring and summer, it appears that only one brood matures per year. The large number of eggs found in colonies collected in August hatch before September and overwinter as larvae (Talbot, 1957). It is possible that the winter chilling results in the determination of these larvae as sexuals. In late August and early September workers and sexuals simultaneously eclose unassisted from their pupal cases. The adults which eclose at this time are predominantly workers. In four colo-



Fig. 2. — Frequency distribution of colony sizes for 35 nests.

nies collected in late August which reared brood in the laboratory, the ratio of ♂:♀:♂♂ was as follows: 2:1:36; 0:5:13; 3:0:7; and 0:4:19. In all cases the worker population of a colony was at a maximum at this time. If this is considered in conjunction with the available information on nuptial flights in *A. pallipes*, then it is possible to speculate on colony reproduction and population structure.

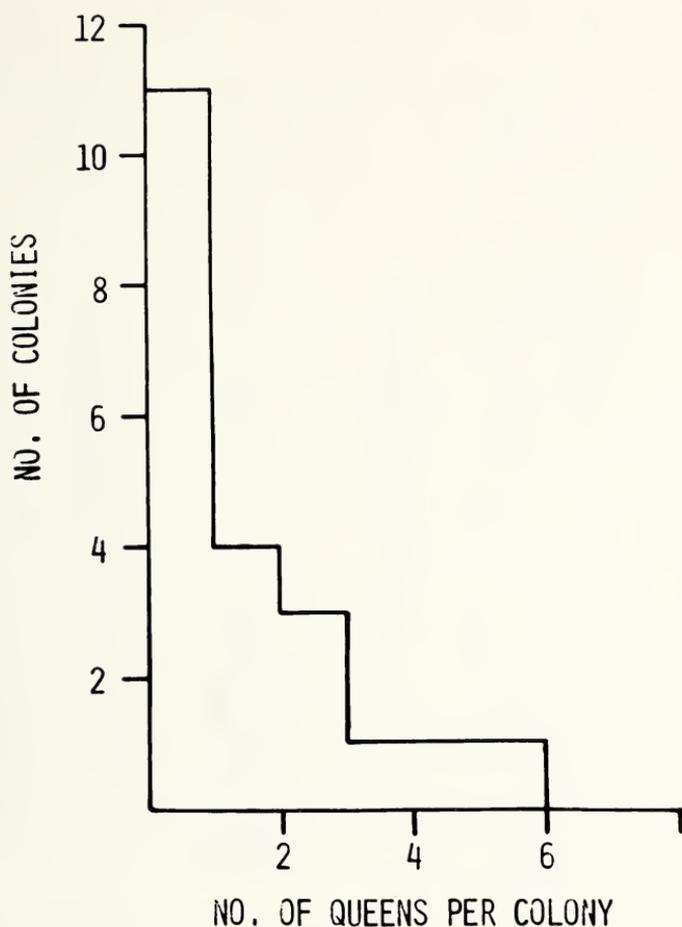


Fig. 3. — Frequency distribution of the number of dealate females in 19 queenright colonies.

Although the complete sequence of colony reproduction has not been observed, the studies of Haskins (1928, 1979) and Haskins and Enzmann (1938) provide some evidence of its organization. Early in September, winged females leave the nest and disperse over short distances, finally alighting on the ground or low vegetation. Then, with gaster arched and sting partially extruded, they “call” males with a chemical sexual attractant. Males quickly locate females, copulation ensues, and soon after insemination females shed their wings and re-enter the soil; perhaps they return to the parent nest.

At this point in the life cycle, the worker/queen ratio is highest, as described above, yet colonies collected in the late spring are much smaller in size (approximately 50%). Therefore, colony reproduction by budding may occur if one or more fecundated queens depart with a portion of the worker force. This hypothesis has previously been considered by Wheeler (1900) and Brown (1960), and is supported by my data on colony growth, nest distribution, and nest structure. An additional feature of the nest distribution pattern supports the hypothesis of limited dispersal. The most dense population of colonies occurred on the south side of an early stone wall (<1 m high), although nest sites were abundant on both the north and south sides, and soil, vegetational, and exposure parameters appeared to be identical. Also, laboratory observations indicate that alate females may shed their wings before mating occurs. On several occasions newly eclosed females left the nest, shed their wings, and returned to the nest. Because mating occurs on the ground, such behavior does not exclude the possibility that these individuals could eventually become inseminated. These females may then return to the parent nest or may be adopted by a nearby colony. In several laboratory experiments queens were introduced into other queenright nests or orphaned colonies. In all cases they were accepted by both workers and queens. Similarly, workers could be transferred from one colony to another without aggression. Therefore, populations of *A. pallipes* appear to be unicolonial and secondarily polygynous. Ecologically, the patchy distribution of this ant correlates with this type of population structure.

2. Social organization

The social ethogram. Social ethogram data were gathered from five colonies which were observed for a total of 73 hours, during which 6,500 individual acts were recorded. The behavioral catalog of a single colony of *A. pallipes* (2 queens, 18 workers, brood) that was studied for 25.7 hours is given in Table I. The total number of acts observed was 42 (95% confidence interval for catalog size [27, 47]), and the sample coverage was 0.9992. Behaviors listed in the ethogram having a frequency of 0 were observed in other colonies and are included as part of the species repertory. The majority of activities are common to many ant species; those that are unusual will be discussed briefly. Antennal tipping is a behavior previously described in *Zacryptocerus varians* (Wilson, 1975) which occurred

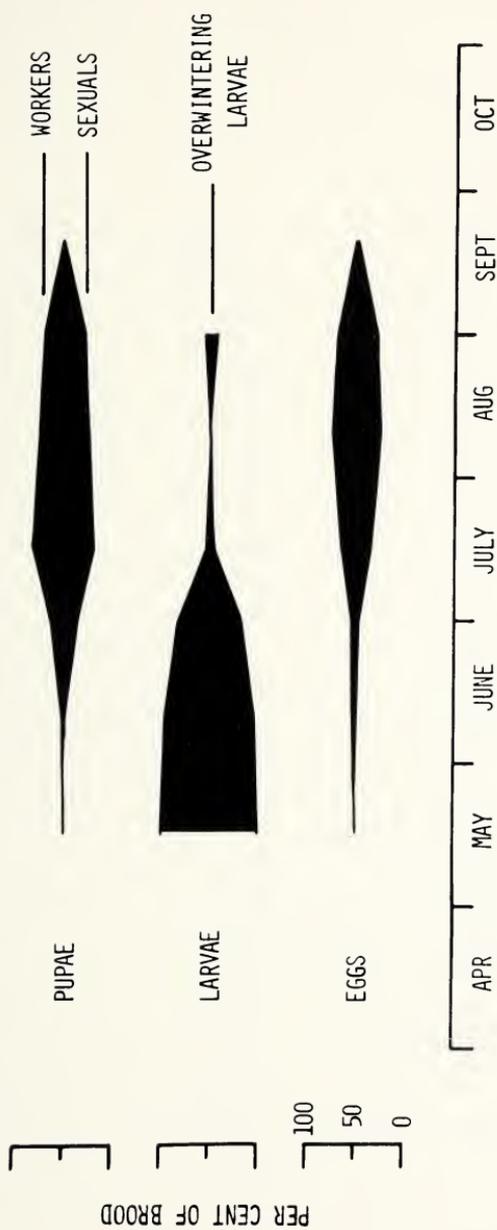


Fig. 4. — Brood development during the annual cycle of an *A. pallipes* colony.

Table I. — The social ethogram. N = number of acts observed in each caste.

Behavioral Act	Workers (16) N=2525	Queens (2) N=158
1. Self-groom	0.3303	0.4114
2. Allogroom queen	0.0044	0
3. Allogroom worker	0.0384	0
Brood care:		
4. Lay egg	0	0.0127
5. Carry egg or egg pile	0.0123	0.0696
6. Lick egg	0.0305	0.1013
7. Lick larva	0.0950	0.1139
8. Carry, drag, or role larva	0.0337	0.0633
9. Bank mature larva with soil	0.0048	0
10. Carry pupa	0.1200	0
11. Lick pupa	0.0824	0.0127
12. Place larvae on prey	0.0032	0
13. Assist removal of meconium	0.0004	0
14. Assist larval molt	0.0012	0
15. Lick ecdysial skin	0.0063	0.0380
Aggressive display:		
16. Undirected	0.0250	0
17. To worker	0.0051	0.0127
18. To queen	0.0004	0
Predatory behavior:		
19. Forage	0.0158	0
20. Sting prey	0.0040	0
21. Drag prey to nest	0.0019	0
22. Drag prey within nest	0.0048	0
23. Lick prey	0.0578	0
24. Handle prey within nest	0.0051	0
Nest maintenance and defense:		
25. Guard	0.0083	0
26. Handle nest material	0.0190	0
27. Repair nest wall	0.0277	0
28. Lick nest material	0.0012	0
29. Excavate nest	0.0111	0
30. Bury noxious object	0.0004	0
31. Carry or drag dead worker	0	0
32. Carry or drag live worker	0.0004	0
33. Extrude sting	0.008	0.0190
34. Remove empty pupal case	0.0008	0
35. Jitter	0.0055	0.0190
36. Jolt body	0.0135	0.0633
37. Lick meconium	0.0008	0
38. Tip antennae	0.0008	0
39. Flick antennae	0.0099	0.0127

Behavioral Act	Workers (16) N=2525	Queens (2) N=158
40. Pinch larvae	0	0.0063
41. Cannibalize larva	0.0170	0.0380
42. Discharge subpharyngeal pellet	0	0.0063
Totals:	1.0	1.0

infrequently in *A. pallipes*. During this behavior the body is raised, the gaster is curved forward, and with the mandibles agape the antennae are held forward with their terminal funicular segments slightly inclined toward each other. The significance of antennal tipping is unknown, but it appeared to be part of a grooming sequence. Vibrational displays were given by workers if the nest wall was breached or if an individual was mechanically disturbed. If the stimulus was intense enough, other workers would show the same vigorous jittering behavior, consisting of rapid vertical movements of the head and thorax. This behavior had the effect of producing a general arousal within the colony and resulted in an increase in the number of workers appearing at the source of stimulation. In the case of nest damage, building behavior eventually occurred but did not immediately follow. This signal appears to be a primitive form of mechanical communication, in which alarm is propagated directly through body contact. A similar vibratory display has been documented in *A. australis* (Hölldobler, 1977).

Workers and queens of *A. pallipes* have retained a number of behaviors that appear to reflect their wasp ancestry. Queens were seen grasping larvae and squeezing them in the neck region with their mandibles, thus causing them to regurgitate a droplet of clear liquid which they then consumed. Workers were never observed to regurgitate with other workers, queens, or larvae, and all individuals fed directly on prey. Aggression was observed between workers and queens. An aggressive display typically consisted of opening the mandibles and rising up on the extended legs. This behavior was usually exhibited by queens in the area of the egg pile and seemed to produce avoidance in contacted workers. These observations raise the question of whether queens maintain their reproductive status through behavioral dominance or inhibitory pheromones.

Polyethism. Studies on the division of labor within the worker caste have revealed that temporal castes are absent in the species. A

complete account of polyethism in relation to the life history of *A. pallipes* is given by Traniello (1978).

Predatory behavior. Prey were found in only three of the colonies collected. In two colonies larvae were found clustered around lithobiid centipedes (length = 1.5–2.0 cm), and in the third colony a carabid beetle larva was taken. In the laboratory, colonies were offered a variety of live arthropods that workers might encounter in leaf litter, soil, or rotting wood. Wood lice (*Oniscus*), house centipedes (*Scutigera*), and various millipedes were consistently rejected while small elatyrinid, tenebrionid, and buprestid beetle larvae were carried to the nest and fed upon. The diet of *A. pallipes* appears to be restricted to live, linear-shaped arthropods that can be captured by workers. A related species, *A. pluto*, is entirely specialized on geophilomorph centipedes (Gotwald and Lévieux, 1972). When large, robust-bodied centipedes (*Lithobius* sp.) were offered to colonies of *A. pallipes*, workers were unable to grasp the prey due to its escape movements and body diameter. It is difficult to imagine a condition under which large prey could be captured, even if they were "cornered" in a narrow gallery. When *Lithobius* of similar size were held with forceps, workers were still unable to subdue the centipede. Freshly killed centipedes were not accepted. It is therefore difficult to support the hypothesis of a nomadic life style for *A. pallipes*. Although this species of Amblyoponini does not appear to move its colonies to the location of large, previously captured prey, other species, such as *Onychomyrmex* do provide evidence linking group predation and nomadism in this primitive group of ants (Wilson, 1958).

Prey capture and retrieval is very stereotyped, and solitary huntresses stalk prey in a highly methodical manner. As prey are approached, workers advance cautiously, apparently orienting to odors or air microcurrents produced by the prey. When within striking range (2–3 mm) the mandibles are opened and the head is oriented orthogonal to the long axis of the prey. Then in a single motion the mandibles close around the prey, the legs elevate the body, and the gaster is swung forward. The prey is then repeatedly stung and the venom soon shows its paralytic effects. Initially, only the area adjacent to the cuticle penetrated by the sting is immobilized, and stinging continues until escape movements stop. Subsequently, the retrieval of the prey begins after a brief period of self-

grooming. The retrieval process varies in duration depending upon prey size, but even long (4.0–5.0 cm, 2.0–2.5 mm in diameter) geophilomorph centipedes are easily dragged to the nest. A number of orientation trips made between the prey and the nest generally preceded retrieval. During these orientation runs, which were made throughout the retrieval process, workers continually checked their position relative to the nest. The prey was then dragged several centimeters; the worker then stopped, released the prey, and continued homeward until she contacted the nest entrance. She then returned to the prey and repeated this sequence, alternating prey movement with orientation trips. Once the prey was in the nest, other workers approached and began vigorously licking the areas of the prey's body opened during capture. Larvae were either carried to the prey or, if close enough, moved toward it and adjusted their position on its body on their own accord. At times workers assisted in positioning larvae. Additional details of feeding behavior are nearly identical to those described by Gotwald and Lévieux (1972).

Communication during foraging. At times, two or three ants attempted to jointly carry prey, but cooperative efforts were haphazard and inefficient. But cooperative retrieval seems unnecessary due to the physical capabilities of individual ants. The critical element in prey capture is probably not retrieving, but subduing relatively large arthropods. Often after a worker began stinging a prey item, a second or third worker approached and assisted in paralyzing the prey. The fact that workers were attracted to the point of prey capture suggested that additional ants may be recruited over short distances by orienting to prey odor, air currents, or some signal produced by the forager. To test the hypothesis that pheromones are involved in this process I stimulated foragers to grasp and attempt to sting the tip of a pair of forceps and then lowered the worker, still attacking the forceps tip, in front of the nest entrance. The response of workers in the nest was dramatic. In five replicates, 5.8 ± 2.3 workers/0.5 min approached the nest entrance under the experimental conditions. Only 0.2 ± 0.1 workers/0.5 min were attracted to the nest entrance in controls (agitated forceps alone). This difference is statistically significant ($.001 < p < .01$; $t = 6.1$, Student's t-test). Although the possibility that stridulatory signals might be involved could not be ruled out, the results of these experiments suggest that chemical cues are involved in the attraction

response. Subsequently, crushes of the head, thorax, and gaster were offered on applicator stick tips at the nest entrance. Also, crushes of dissected poison and pygidial glands (Hölldobler and Engel, 1979) were offered. Only head crushes produced attraction. Whelden's (1958) studies, in addition to our own histological investigations, revealed a group of large glandular cells at the base of the mandible. The indirect evidence described above suggests that during prey capture the contents of these cells are released, attracting workers in the vicinity to assist in subduing prey.

3. Ecology and social evolution

The results of this study and previous investigations suggest that populations of *A. pallipes* are unicolonial. Workers from different subnests within a population show no aggression toward each other. Such worker compatibility has been demonstrated in *Rhytidoponera metallica* (Haskins and Haskins, 1979), whose populations appear to be structurally similar to those of *A. pallipes*, but occupy larger area geographically. Workers taken from nests three miles apart were not mutually hostile. The lack of aggression was consistent within, but not between populations. *Ambylopone pallipes* colonies appear to be similarly viscous, but do not occupy as extensive an area.

Observations in the laboratory are in accord with Brown's (1960) position which states that after mating, females "always or usually return to the parent nest". Secondary polygyny in this species, in addition to its patchy distribution, indicates that this species is in the terminology of Hölldobler and Wilson (1977) a habitat specialist. The characteristic *A. pallipes* habitat is cool, damp, heavily shaded woodland. Nest site and prey abundance are also important features. Populations apparently grow slowly, and through reproduction by budding, eventually saturate the habitat. Such a scheme does not rule out the occurrence of dispersal flights, which have been witnessed on occasion (Haskins, 1928). As colonies become more populous within a habitat, dispersal flights should occur more frequently in order to colonize additional areas. Once a founding queen locates a preferred habitat, colony reproduction again is accomplished through budding. The strategy may be similar to that of the mound building species *Formica exsectoides*. However, it must be noted that in laboratory situations, *A. pallipes* queens have never been observed to successfully found colonies (Haskins, per-

sonal communication). But it is difficult to determine whether this is an abnormality which occurs only in the laboratory or represents an inability of *A. pallipes* queens to found a colony alone. Newly inseminated queens of *A. australis* found colonies in the partially claustral mode (Haskins and Haskins, 1951). However, *A. australis* is monogynous.

Within a habitat, *A. pallipes* escapes competition with the more advanced groups of ants by additional specializations on microhabitat and diet. This is in contrast to other unicolonial species which are broad generalists.

Behaviorally, *A. pallipes* exhibits both primitive and advanced social traits, and many of the primitive characters are more conservative than those of *Myrmecia*. Age polyethism is lacking, and communication between individuals is primarily mechanical, although a rudimentary short-range recruitment system that is mediated by pheromones exists. Among the primitive trophic characteristics is the use of the sting to paralyze prey, which are subsequently fed directly to the larvae without prior dismemberment. Employing the sting to paralyze prey appears to be widespread in the Ponerinae, and recently Maschwitz et al. (1979) have demonstrated that the venom of the oriental ponerine species *Harpegnathus saltatus* and *Leptogenys chinensis* indeed has paralytic, and not toxic, effects. Prey paralyzation also occurs in *Daceton armigerum* and *Paltothyreus tarsatus* (Wilson, 1962; Hölldobler, pers. comm.). This is contrasted to myrmicine species which use the sting as a defensive weapon. The importance of paralyzing but not killing arthropod prey in *Amblyopone pallipes* is obviously related to the direct provisioning of larvae; prey must be kept from decomposing until they are consumed. Also, immobilization is necessary for successful retrieval, and energetically it is more efficient for solitary foragers to carry paralyzed prey. The absence of regurgitation which is characteristic of the Ponerinae, also is a primitive trait. Although one of the more distinctive features of *A. pallipes* and other Amblyoponini, prey specialization, appears to be a conservative formicid trait, it is also possible that specialization was a response to competition.

Finally, based on the theories of Malyshev (1968), Wilson (1971) has speculated that the Amblyoponini may have approached eusociality in a way very different from the partially claustral colony founding route assumed by Haskins and Haskins (1951). Because

these ants appear to be specialized on large arthropods, they may have passed through a phase of subsociality similar to that of the bethylid wasp *Scleroderma*. Although the evolution of ants from *Scleroderma*-like ancestors has been ruled out on morphological grounds, the possibility remains that the Amblyoponini represent an independent venture into eusociality. The present study, which suggests that *A. pallipes* is not dependent upon large arthropod prey, and the studies of Haskins (1928) and Haskins and Haskins (1951) on colony foundation, do not support or refute this theory. Additional studies must be carried out on the behavior of newly inseminated females, their prey preferences during colony foundation and their reproductive physiology to test this hypothesis.

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SUMMARY

1. The behavior of ecology of the primitive ponerine ant *Amblyopone pallipes* was studied in the laboratory and the field. Thirty-three colonies were collected over a two-year period, 94% of which were excavated from one locality where 68% of the colonies were strongly clumped in their spatial distribution. Workers and queens could be transferred between these nests without hostility.

2. The inability of workers to recognize members of other colonies within a population, the colony life cycle, limited dispersal, the presence of multiple queens in nests, and circumstantial evidence on the adoption of newly inseminated females by their parent nest suggest that *A. pallipes* is secondarily polygynous and unicolonial. Although dispersal flights do occur, colony reproduction seems to be accomplished through budding.

3. Studies on the ethology of *A. pallipes* show that this species has retained many conservative behavioral traits. Among these are the absence of age polyethism and the provisioning of larvae with whole prey (chiefly chilopods and beetle larvae). Observations of predatory behavior do not support the hypothesis that colonies are nomadic. Prey are paralyzed by stinging and are then retrieved. Larvae feed directly on the body of the prey.

4. A primitive form of alarm communication, presumably transmitted through body contact, is mediated by a vibratory display. Workers show attraction to head crushes, and mandibular gland pheromones appear to be involved in a weak form of recruitment.

5. Because of the lack of precise information on the behavior of colony founding queens, the question of whether sociality in the Amblyoponini arose in a manner different from the partially clausal colony founding mode of *Myrmecia* remains an enigma.

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THE BIOLOGY OF NINE TERMITE SPECIES
(ISOPTERA: TERMITIDAE)
FROM THE CERRADO OF CENTRAL BRAZIL

BY HELEN R. COLES DE NEGRET¹ AND KENT H. REDFORD²

INTRODUCTION

The Neotropical region is second to the Ethiopian in numbers of described termite species (Araujo 1970). However, little is known of their biology. The literature on Brazilian termites is largely restricted to isolated taxonomic descriptions of species from the Amazon Basin and southern states of Brazil (Araujo 1961, 1969, 1977 and Fontes 1979). Exceptions to this include information relating termite species and their distribution to vegetation types in Mato Grosso State (Mathews 1977), the effect of deforestation on termites in the Amazon (Bandeira 1979) and data on the ecology and defense of termites in the cerrado vegetation of the Distrito Federal (Coles 1980).

The present study was done in conjunction with a study on mammalian termite predators, in particular the giant anteater, *Myrmecophaga tridactyla* (Coles 1980 and Redford in prep.). Six aspects of termite biology of importance in defense by termites against mammalian predators were studied for nine of the most common mound-building termite species in the Distrito Federal, Brazil. Reported here are individual weights, morphology of soldier castes, worker-soldier ratios, mound sizes and forms, mound hardnesses and nest materials, distributions and abundances of nests and feeding habits for these nine species.

All species studied were from the family Termitidae (see Fig. 1 for comparison of soldier heads), subfamily Apicotermitinae, *Grigiotermes metoecus* (Mathews); subfamily Nasutitermitinae, *Armitermes*

¹Laboratoria de Zoologia e Ecologia Animal, Universidade de Brasilia, Brasilia D. F. 80910, Brazil.

²Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138; and Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.

euamignathus (Silvestri), *Cornitermes cumulans* (Kollar), *Cortaritermes silvestri* (Holmgren), *Nasutitermes* sp., *Procornitermes araujoi* (Emerson), *Syntermes dirus* (Burmeister), *Velocitermes paucipilis* (Mathews); subfamily Termitinae, *Orthognathotermes gibberorum* (Mathews).

METHODS AND RESULTS

This study was conducted primarily in the Distrito Federal, Brazil (15 47'S 47 56'W) with supporting work done in Emas National Park, Goias State (18 19'S 52 45'W). Both areas are located within the cerrado *sensu lato* vegetation type. Cerrado (*sensu lato*) is a semi-deciduous xeromorphic savanna vegetation found in the intermediate rainfall (750-2000 mm/yr) area of Brazil. It is characterized by woody plants with thick bark and coreaceous leaves and a seasonal ground layer of grasses and herbs. Although geographically and floristically the cerrado vegetation zone is very uniform, physionomically it shows considerable variation (Eiten 1972). The types of cerrado *sensu lato* which were examined in this study are *campo limpo* (grassland), *campo sujo* (grassland with shrubs), *cerrado sensu strictu* (woodland) and *cerradão* (dense, tall cerrado). Within the cerrado zone, gallery forest vegetation is found on the wet, more fertile soils along river courses; however this was excluded from the present study as it supports a termite fauna which differs greatly from that of the other vegetation types (Coles 1980).

I. THE TERMITES

A. Comparative Morphology

Figure 1 depicts soldiers of the eight species of termites examined in this study, with a worker head of the soldierless species *Grigiotermes* provided for comparison, while Tables 1 and 2 provide information on the fresh weights and total body lengths. Table 2 also provides measurements of mandible length, nasus length, head length, head width and head depth for the soldiers (position of measurements depicted in Figure 2).

As can be seen from these data, the termite species in this study can be placed along a spectrum based on soldier and head shape. The two ends of this spectrum are 'well-developed nasus/vestigial mandibles' (such as *Nasutitermes*) and 'no nasus/very well-devel-

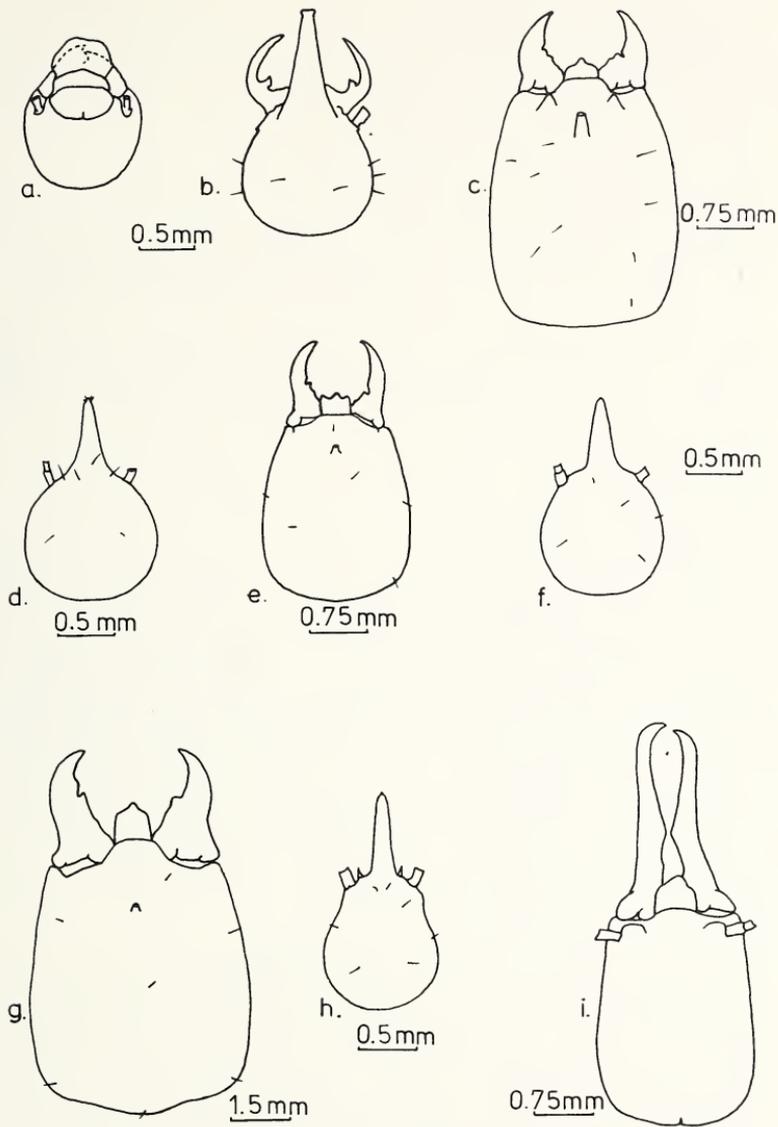


Figure 1. Soldier heads of eight of the species of termites studied; *Grigioterms metoecus* worker included for comparison: a, *Grigioterms metoecus*; b, *Armitermes euamignathus*; c, *Cornitermes cumulans*; d, *Cortaritermes silvestri*; e, *Procornitermes araujoi*; f, *Nasutitermes* sp.; g, *Syntermes dirus*; h, *Velocitermes paucipilis*; i, *Orthognathotermes gibberorum*.

loped mandibles' (*Orthognathotermes*). Intermediate positions are occupied by forms with 'slight nasus development/well-developed mandibles' (such as *Cornitermes*) and 'well-developed nasus/well-developed mandibles' (*Armitermes*). *Grigiotermes*, with no soldier caste, cannot be placed on this spectrum.

These data also show that soldiers with very well- to well-developed mandibles and poorly developed nasi are both heavier and longer than soldiers with vestigial mandibles and well-developed nasi, *Armitermes* once again occupying an intermediate position.

Complete taxonomic descriptions for *Grigiotermes metoecus*, *Armitermes euamignathus*, *Cortaritermes silvestri*, *Velocitermes paucipilis*, and *Orthognathotermes gibberorum* can be found in Mathews (1977). *Procornitermes araujo* is fully described in Emerson (1952). Samples of *Cornitermes cumulans* collected during the study in Brasilia were identified following Emerson (1952). Although the general head and mandible forms were consistent with the published description, head length and width measurements were much lower than those previously described for this species. However, Emerson indicated that there is considerable variation in mean measurements between colonies from different localities. The samples from Brasilia were compared with various other species in the Museu Zoologia de Universidade de São Paulo (MZSP). The most closely related species was *C. villosus* which was clearly different in that it had a greater number of setae and differently shaped mandibles. As a result of this divergence the best classification appears to be *C. cumulans*. Specimens from Brasilia have been deposited in the MZSP and the Museum of Comparative Zoology, Harvard University.

Samples of *Nasutitermes* sp. collected from the Distrito Federal were compared extensively with material in the MZSP but differed from all species examined. *N. coxipoensis* most resembled the *Nasutitermes* we studied but differed in being smaller and in having a more oval shaped head. Further studies on these two forms are necessary to determine whether these differences are sufficient to warrant calling it a new species.

B. Weights

Fresh weights were measured on a Mettler balance. Fifty workers and fifty soldiers from each of three different nests were weighed, except for *Syntermes* for which only fifteen individuals of each caste

from the three nests were weighed and *Nasutitermes* for which five nests were sampled. The results are presented in Table 1 and are ordered from heaviest soldiers to lightest soldiers. *Syntermes dirus* has workers and soldiers much heavier than the next heaviest species, *Cornitermes*. The termite species with soldiers possessing strong or long mandibles are heavier than those termites whose soldiers have vestigial mandibles, and well developed nasi. These latter soldiers are also lighter than their workers, a relationship reversed in the other termite species.

Table 1. Individual wet weights of termites (measurements expressed in micrograms; mean with standard deviation in parentheses).

Species	Workers	Soldiers
<i>Syntermes dirus</i>	42.75a (2.34)	117.3 (11.1)
<i>Cornitermes cumulans</i>	9.30 (0.36)	19.83 (1.07)
<i>Orthognathotermes gibberorum</i>	6.91 (0.75)	19.09b (0.69)
<i>Procornitermes araujoi</i>	6.63 (0.76)	8.26 (0.40)
<i>Grigiotermes metoecus</i>	6.27 (0.95)	—
<i>Armitermes euamignathus</i>	3.48 (0.15)	4.19 (0.52)
<i>Cortaritermes silvestri</i>	3.23 (0.12)	2.08 (0.20)
<i>Nasutitermes</i> sp.	3.46c (1.06)	1.56 (0.42)
<i>Velocitermes paucipilis</i>	2.52c (0.55)	1.31b (0.09)

a Equal number of all three morphs weighed.

b Only major soldiers weighed.

c Mixture of two worker types weighed.

C. Morphology of Soldiers

The positions of measurements taken on soldier heads are indicated in Figure 2 (adapted from Coles 1980). Total body length was measured from tip of mandible or nasus, whichever extended further, to the end of the abdomen. The figures presented in Table 2 are the averages of 15 individual soldiers and are ordered from greatest to least mandible length. As can be seen, these five morphological measurements are, on the whole, positively correlated with each other, with total body length and with weight (Table 1). The major exception is *Orthognathotermes*, which has mandibles and a nasus of a different shape than the other species.

D. Worker-Soldier Ratios

Worker-soldier ratios were calculated by counting all of the workers and soldiers in a piece of termite mound. The piece was rapidly removed from the surrounding mound so as to prevent a change in the normal worker-soldier ratio. For all species except *P. araujoi*, *A. euamignathus*, *S. dirus* and *C. silvestri*, five pieces of mound from at least three different mounds were counted. The result obtained from a piece of mound was not used if the piece contained less than 600 individuals. Because of the large variation obtained in the first five counts for *P. araujoi*, an additional three pieces were counted. The fifth count used for *A. euamignathus* was an average of 45 samples and was taken from Domingos (1980). Only four counts were taken for *C. silvestri*.

The large diffuse mounds inhabited by *S. dirus* and the rapid retreat of soldiers and workers made it impossible to obtain worker-soldier ratios from populations within the mound for this species. Instead, the value presented in Table 3 is an average of counts made on eleven foraging parties. The method used (Coles 1980) was to plug the exit at least one hour after foraging had begun. After spraying with pyrethrin aerosol insecticide all soldiers and workers were collected and counted. Table 3 presents the data on worker-soldier ratios ordered from greatest to least percent soldiers.

Those termite species with soldiers having chemical-based defensive systems have fewer workers per soldier than the other termite species. In fact, for these species, *Velocitermes*, *Nasutitermes* and *Cortaritermes*, there is little variation between species in this worker-soldier ratio. Similarly, *Cornitermes* and *Procornitermes*,

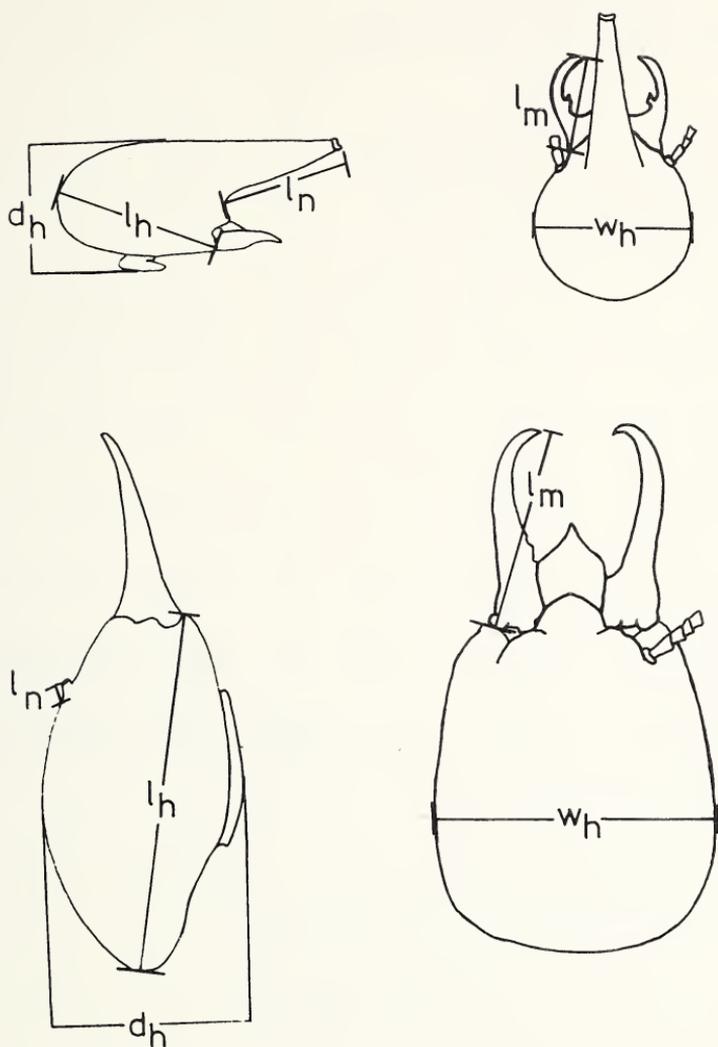


Figure 2. Positions of morphological measurements of soldier heads: lh = Lateral head length; ln = nagus length; lm = mandible length; Wh = maximum head width; dh = head depth including postmentum.

Table 2. Morphological measurements of soldiers (measurements expressed in millimeters; mean with standard deviation in parenthesis).

Species	Mandible Length	Nasus Length	Lateral Length of Head	Maximum Head Width	Head Depth	Total Body Length
<i>Orthognathotermes gibberorum</i>	2.96 (0.11)	0 —	3.06 (0.08)	2.09 (0.06)	1.83 (0.05)	9.25 (0.40)
<i>Syntermes dirus</i>	2.45 (0.11)	0.16 (0.02)	5.20 (0.19)	5.15 (0.15)	3.17 (0.14)	15.57 (0.65)
<i>Cornitermes cumulans</i>	1.36 (0.78)	0.36 (0.03)	3.90 (0.11)	2.67 (0.09)	1.95 (0.07)	9.55 (0.42)
<i>Procornitermes araujo</i>	1.14 (0.05)	0.45 (0.03)	2.46 (0.03)	1.98 (0.04)	1.57 (0.05)	7.47 (0.21)
<i>Armitermes euamignathus</i>	0.58 (0.02)	0.91 (0.05)	2.05 (0.05)	1.10 (0.04)	1.04 (0.05)	5.35 (0.20)
<i>Nasutitermes</i> sp.	0.17 (0.03)	0.63 (0.02)	1.65 (0.64)	1.05 (0.35)	0.82 (0.34)	4.32 (0.14)
<i>Velocitermes paucipilis</i>	0.15 (0.18)	0.80 (0.03)	1.65 (0.64)	1.05 (0.35)	0.82 (0.34)	4.32 (0.14)
<i>Cortaritermes silvestri</i>	0.15 (0.02)	0.61 (0.03)	1.64 (0.06)	1.08 (0.06)	0.80 (0.06)	3.95 (0.25)

Note: *Grigiotermes* is excluded for it has no soldiers.

two similar species have very similar workers-soldier ratios. *Armitermes* occupies an intermediate position while *Orthognathotermes* has a large number of workers per soldier.

II. THE MOUNDS

A. Mound size and form

Table 4 presents data on mean heights, widths and lengths of ten mounds for each of the nine species of termites. Figure 3 (a-r) consists of two photographs of each species mound, one of an entire mound and the other of a mound in transverse cross-section. As can be seen from the data and the photographs, the shapes of these mounds range roughly from an inverted cone (*Cornitermes*) to a low dome (*Orthognathotermes*).

Table 3. Proportion of workers in nests (mean with standard deviation in parentheses).

Species	Worker-Soldier	% Soldiers
<i>Velocitermes paucipilis</i>	4.00 (0.72)	25.80 (4.23)
<i>Nasutitermes</i> sp.	4.06 (0.83)	25.50 (5.56)
<i>Cortaritermes silvestri</i>	5.12 (1.64)	21.20 (6.90)
<i>Syntermes dirus</i> *	9.66 (2.72)	11.10 (3.02)
<i>Armitermes euamignathus</i>	13.82 (3.79)	7.68 (2.57)
<i>Procornitermes araujoi</i>	30.12 (18.30)	5.10 (3.76)
<i>Cornitermes cumulans</i>	30.23 (7.61)	3.48 (3.14)
<i>Orthognathotermes gibberorum</i>	80.75 (18.18)	1.30 (0.32)

*Figures derived from foraging parties. See text, *Grigiotermes* excluded as it has no soldiers.

The nature and form of individual mounds vary greatly and the characteristics listed below are generalized descriptions of mounds found in the Distrito Federal and Emas Park.

Cornitermes cumulans (Fig. 3 a,b): The mound has a very hard outer shell of soil surrounding a soft inner core of carton (fecal material, communitated plant material and bits of soil) which often extends below ground as much as 40 cms. The galleries are large and unlined.

Nasutitermes sp. (Fig. 3 c,d): The mound is domed with the outer several centimeters softer than the inner core (as in arboreal *Nasutitermes* and *Constrictotermes*) and often extends 25 cms underground. The internal structure consists of thin-walled, convoluted,

Table 4. Dimensions of the epigeal portion of termite mounds (measurements expressed in centimeters; mean with standard deviation in parentheses).

Species	Height	Length	Width
<i>Cornitermes cumulans</i>	91.6 (16.7)	92.8 (17.1)	79.5 (14.5)
<i>Nasutitermes</i> sp.	78.1 (14.3)	100.1 (18.2)	85.9 (16.4)
<i>Syntermes dirus</i>	51.7 (19.4)	173.0 (26.5)	150.7 (20.5)
<i>Velocitermes paucipilis</i>	31.2 (4.5)	27.3 (7.0)	22.6 (5.8)
<i>Grigiotermes metoecus</i>	2.96 (4.5)	60.2 (7.9)	47.2 (7.2)
<i>Procornitermes araujoi</i>	28.8 (12.0)	69.5 (33.9)	60.0 (34.4)
<i>Armitermes euamignathus</i>	26.7 (5.1)	59.5 (8.8)	52.8 (8.1)
<i>Cortartiermes silvestri</i>	15.8 (4.7)	24.8 (3.2)	20.5 (2.6)
<i>Orthognathotermes gibberorum</i>	15.0 (3.0)	35.9 (11.3)	40.4 (13.6)

irregular galleries with a mottled black and soil-colored lining of fecal origin.

Syntermes dirus (Fig. 3 e,f): This species builds low-domed termitaria, the major parts of which are below ground level (often to depth of 1.5 m.). The galleries are large and diffuse, often containing grass stores and are lined with regurgitated soil in which individual pellets are clearly visible.

Velocitermes paucipilis (Fig. 4 g,h): The mounds are pyramidal, very soft, crumbly and are generally built around a grass tussock. They often extend several centimeters underground in a series of very diffuse galleries which are lined with a discontinuous layer of black material of fecal origin. Large amounts of cut plant material are found inside the mound.



Figure 3. Mounds of the termite species studied; external view and longitudinal section: a and b, *Cornitermes cumulans*; c and d, *Nasutitermes* sp.; e and f, *Syntermes dirus*.

Grigiotermes metoecus (Fig. 4 i,j): These medium-sized domed mounds are often occupied by other species of termites and ants. The galleries are distinguished by smooth, shiny soil-colored floors and by small pieces of stone incorporated into the 'ceilings.' Individual deposits of fecal material used in construction are visible on the mound surface.

Procornitermes araujoii (Fig. 4 k,l): These medium-sized, rounded mounds are often characterized by a thin layer of loose soil covering the outer shell. These mounds are quite brittle and homogenous and have galleries with a mottled lining of black soil and colored particles, probably of fecal origin. They rarely extend below ground.

Armitermes euamignathus (Fig. 5 m,n): This species builds very characteristic slightly domed mounds. The walls are very hard but the mound itself is only loosely held to the substratum with a cavity frequently occurring between it and the soil. The internal structure consists of large irregular chambers connected by very small galleries. During the alate flight season mounds of this species are characterized by earthen turrets several centimeters high built on the outer surface and serving as 'launching platforms' for alates.

Cortaritermes silvestri (Fig. 5 o,p): This species builds soft, low rounded mounds with large irregular galleries. The mounds are frequently built around grass tussocks and extend several centimeters underground as in *Velocitermes*.

Orthognathotermes gibberorum (Fig. 5 q,r): The low mounds built by this species are covered with loose soil and bound together by living grass stems. The galleries are regular and homogenous throughout. The mound frequently extends several centimeters underground but can be separated easily from surrounding soil when pried up.

B. Mound hardness and nest material

The 'hardness' of a mound was measured using a soil penetrometer which measures the force necessary to push a metal cone into the soil. The resistance to penetration is obtained by dividing the load of penetration (force applied) by the area at the base of the cone, which was 637.939 mm². The resistance to penetration was taken as a measure of hardness of the mound surface.

A termite mound is not a solid structure but consists of a complex system of galleries and chambers. The outer wall is often thick enough for penetration of the whole cone. However, at times, the

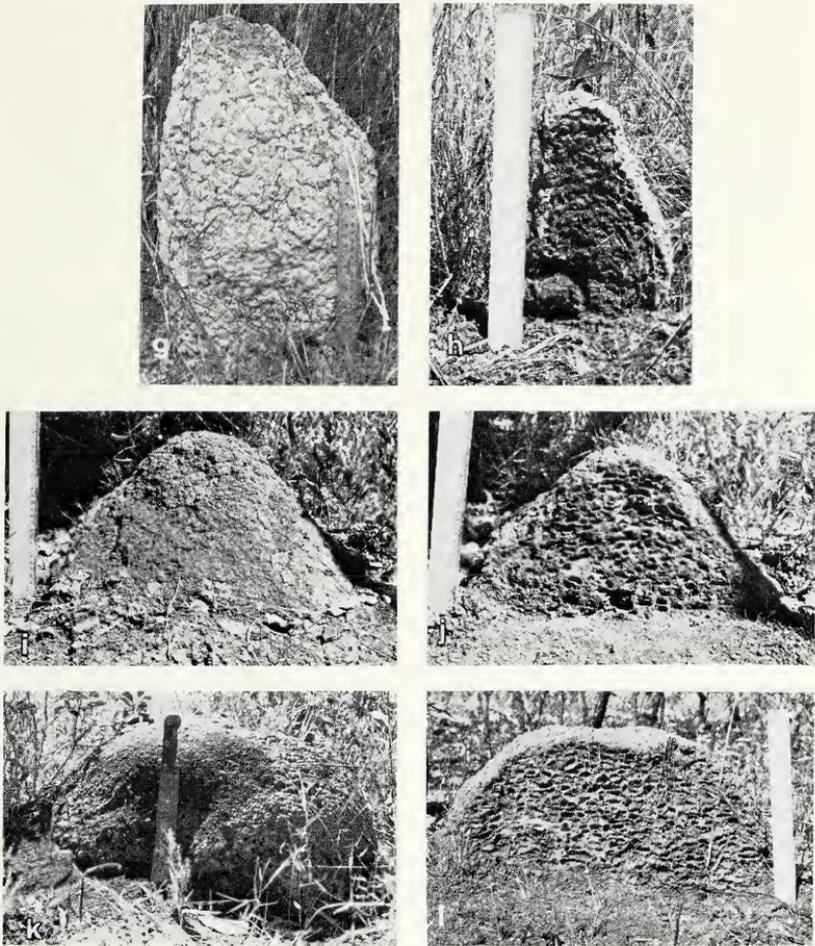


Figure 4. Mounds of the termite species studied; external view and longitudinal section: g and h, *Velocitermes paucipilis*; i and j, *Grigiotermes metoecus*; k and l, *Procornitermes araujo*.

cone pushed into a gallery and a low reading was obtained. In order to obtain a representative figure for the whole mound ten measurements were taken, each from different positions, e.g. base, middle, top.

The hardness of any mound varies considerably throughout the year with the amount of rainfall. To reduce these variations all the



Figure 5. Mounds of the termites species studied; external view and longitudinal section: m and n, *Armitermes euamignathus*; o and p, *Cortaritermes silvestri*; q and r, *Orthognathotermes gibberorum*.

measurements were made in one month (April) at the end of the rainy season. Some variation in hardness occurs from day-to-day and so on any one day of recording, one mound from each of the eight species was examined. Ten mounds from each species were examined and ten measurements were made from each mound. Care was taken to select approximately the same size of mound for the ten mounds of any one species.

The mean values for the hardness of termite mounds in each species are shown in Table 5. As the range is large (15.24–0.11 Newtons/mm³) the data were transformed (\sqrt{x}) and the differences

Table 5. "Hardness" of outer mound and materials used in mound construction (In column 1, any two means not followed by the same letter are significantly different at $p = 0.05$. In columns 3 through 6, ++ = usually used; + = occasionally used).

Species	Resistance to Penetration (Newtons mm ³)		Nest Construction Material			
	Termite Mound	Soil at Base	Soil	Regurgitated Soil	Fecal Material	Saliva
<i>Velocitermes paucipilis</i>	0.11a (0.05)	0.48 (0.16)	++	++		
<i>Nasutitermes</i> sp.	0.25b (0.05)	0.42 (0.15)		++	++	++
<i>Cortaritermes silvestri</i>	0.25b (0.04)	0.44 (0.18)	++		++	
<i>Procornitermes araujoii</i>	0.36b (0.11)	0.42 (0.14)	++	++	++	++
<i>Orthognathotermes gibberorum</i> *	0.48 (0.15)	— —	++		++	
<i>Syntermes dirus</i>	0.57c (0.13)	0.42 (0.14)	+	++		+
<i>Grigiotermes metoecus</i>	1.25d (0.17)	0.70 (0.18)	+		++	
<i>Armitermes euamignathus</i>	4.66e (1.08)	0.36 (0.10)	++		+	
<i>Cornitermes cumulans</i>	15.24f (5.36)	0.37 (0.16)	+	++		++

*Determined for only 4 mounds so no statistics performed.

between these means tested for significance using Hartley's multiple range test. The ranking obtained from this analysis is shown in Table 5 with the mean values of the raw data. *Velocitermes*, *Nasutitermes*, *Cortaritermes* and *Procornitermes* had the softest nests while *Cornitermes* had the hardest nest, 140 times harder than the softest, *Velocitermes*.

The composition of material used to build mounds was determined by direct observation of workers. Observations were made on at least ten mounds per species, at different times of the day and year. The results are presented in Table 5. Four types of material

were observed to have been used by termite workers in nest construction: soil, regurgitated soil, fecal material and saliva. In some cases, such as *Procornitermes* nests, all four were used. Soil and/or regurgitated soil were always the most common forms of building material.

C. Distribution and Abundance of Nests

Information on the distribution and abundance of termite mounds in each vegetation type was collected from a variety of sources and the results are presented in Table 6. Different sampling methods can produce different results, depending on the spatial distribution of the termite mounds, the size of area sampled and the number of areas sampled. It is often difficult to interpret figures on termitaria densities because investigators do not report whether all termitaria examined contained the mound-building species. Thus, the specific methods used to obtain each of the densities reported in Table 6 are detailed below.

Method a: (Coles 1980); *method b* (Domingos 1980); *method c* (Coles de Negret et al. in prep.).

Blocks of 50 × 50 meters were selected randomly in each of the four vegetation types studied in the Distrito Federal. As some of the termite species in the present study were occasionally found in mounds built by other species, in these methodologies, all the epigeal mounds in the area were completely excavated. The abundance of each species was thus expressed in numbers of nests per hectare. In order to exclude sites with only foraging termites, a "nest" was defined as a structure in which termite nymphs and larvae were present.

Method d: (Redford in prep.).

Twelve separate transects, each of 100 by 20 meters were marked out in the campo limpo vegetation of Emas National Park, Goiás. All the mounds built by *Cornitermes cumulans* in each transect were counted. The figure in Table 6 is the mean calculated from these twelve transects (standard deviation = 16.1).

Method e: (Brandão in prep.).

Two blocks, 100 by 100 meters were marked out in separate areas of campo sujo and two others, of the same size, in areas of cerrado vegetation in the Distrito Federal. All the *Syntermes dirus* mounds present in each area were counted. As this species frequently constructs small soil domes, apparently for storing food, nests were

Table 6. Distribution and densities of termite nests/mounds per hectare in four vegetation types (Letters correspond to different sampling methods—see text for details).

Species	Campo Limpo	Campo Sujo	Cerrado Senu Stricto	Cerradão
<i>Grigiotermes metoecus</i>	40a	28a	24a 4c	48a
<i>Armitermes euamignathus</i>	84a 236b	112a 116b 41f	116a 152b 156c	124a 120b
<i>Cornitermes cumulans</i>	0a 58d	12a	32a 0c	0a
<i>Cortaritermes silvestri</i>	40a	12a	4a	0a
<i>Nasutitermes</i> sp.	48a	32a	0a 16c	0a
<i>Procornitermes araujoi</i>	4a	12a	52a 12c	4a
<i>Syntermes dirus</i>	4a	20a 33e 54e	0a 0e 8e	0a
<i>Velocitermes paucipilis</i>	40a	96a 101f 27g	32a 24c	0a
<i>Orthognathotermes gibberorum</i>	12a	0a	16a	4a

again defined as structures in which termite nymphs and larvae were present.

Method f: (Curado et al. in prep.).

All the mounds built by *Armitermes euamignathus* and *Velocitermes paucipilis* in an area of campo sujo (100 by 100 meters) in the Distrito Federal were sampled and counted.

Method g: (internal report, University of Brasilia).

Mounds of *Velocitermes paucipilis* present in a transect 230 by 10 meters extending from campo limpo to campo sujo in the Distrito Federal were counted.

III. FEEDING HABITS AND FORAGING BEHAVIOR

Feeding habits were deduced from field observations, examination of worker mandibles and gut contents, information in the literature and in some cases, from laboratory food preference experiments. Results are summarized in Table 7. Details of foraging behavior, methods of investigation and food sources are given below.

Grigiotermes metoecus

Field observations and examinations of worker mandibles and gut contents indicate that this species is entirely geophagous. It excavates subterranean galleries in the soil surrounding its mound and is also frequently found in old, disused termite workings, presumably rich in organic material.

Armitermes euamignathus

In the cerrado and cerradão vegetations foraging workers can be found under the bark of living trees and sound, dead trees. However, this species also occurs with equal frequency in campo limpo where few or no woody shrubs exist. Field observations on the foraging behavior of 100 colonies of this species show that in the absence of woody vegetation they can exploit the root systems of grasses (Domingos 1980). Laboratory food preference experiments carried out by the same author on five colonies of *A. euamignathus* indicates that when presented with a range of food sources, all colonies selected wood in preference to bark, litter and grass roots. Further field observations confirmed that this species selects dead, sound wood in preference to live and to dead, decomposed wood. The workers forage diurnally and reach the food source via subterranean galleries. On average, mounds are 0.4 and 0.3 meters from their food sources in cerrado and cerradão respectively and 1.2 and 1.0 meters in campo sujo and campo limpo, respectively (Domingos op. cit.).

Cornitermes cumulans

Field observations on foraging parties indicate that workers of this species feed on living and dead grasses and herbs, which they reach through subterranean tunnels, occasionally foraging under a fine layer of soil-sheeting. Small pieces of grass are cut from standing grass tussocks and carried to the mound. Feeding *in situ* has been observed occasionally. Preliminary food preference experi-

Table 7. Modal feeding habits (++ = commonly consumed; + = occasionally consumed).

SPECIES	FOOD SOURCE			
	Humus	Sound Wood	Decomposing Wood	Grass & Herbaceous Litter
<i>Grigiotermes metoecus</i>	++			
<i>Armitermes euamignathus</i>		++		+
<i>Cornitermes cumulans</i>				++
<i>Cortaritermes silvestri</i>	+(?)			+(?)
<i>Nasutitermes</i> sp.n.		+	+	++
<i>Procornitermes araujoii</i>				++
<i>Syntermes dirus</i>				++
<i>Velocitermes paucipilis</i>				++
<i>Orthognathotermes gibberorum</i>	++(?)			

ments carried out on laboratory colonies showed that workers collect dead grass in greater amounts than live. When presented with only dead roots or dead grass blades, they fed more on the latter.

Cortaritermes silvestri

Field observations made in the Distrito Federal and information presented in Mathews (1977) indicate that this species feeds in grass tussocks among the roots and stems. It is not clear, however, whether it feeds on the organic residues in the soil or on the grass roots themselves.

Nasutitermes sp.

These termites have not been observed foraging in the open and rarely construct runways over the ground as do many other species in this genus. It is probable that they excavate underground tunnels to their food source, the exact nature of which is not known. Recent

experiments on laboratory colonies have shown that this species can feed on a range of plant material including sound wood and both living and dead grass.

Procornitermes araujo

Field observations have been made on above-ground foraging parties in the open and under soil sheeting. Workers cut and collect grass litter, generally at night, but occasionally on dull, humid days.

Syntermes dirus

This species forages above ground in the open, at night, and crepuscularly. Workers and soldiers leave the tunnels from small exit holes which are plugged with several millimeters of soil during inactive periods. These foraging holes may be on the mound or at distances of up to 20 meters from it. The above-ground foraging parties consist of major workers and soldiers. At the end of a particular trail the workers spread out over several centimeters and start cutting grass. Some climb up stands of vegetation and cut long pieces of grass which drop to the ground. Other workers cut these into smaller pieces and carry them to the nest. Consumption *in situ* has not been observed.

Velocitermes paucipilis

These termites feed on grass and surface litter which they collect at night in the open. The workers form trails to the food source where they spread out to cover a large area, cut small pieces of grass and leaves, and return with them to the nest. The workers are flanked at regular intervals by soldiers oriented with their raised heads pointing outwards.

Orthognathotermes gibberorum

Examination of worker mandibles and gut contents together with information from Mathews (1977) suggests that this species feeds on organic residues in the soil. Observations of foraging behavior have not been made.

Food sources were divided into four categories: humus, sound wood, decomposing wood, and grass and herbaceous litter. The few termites eating sound wood and the many eating grass and herbaceous litter probably reflect the fact that most of the vegetation types included in this study were open with few trees. Examination of the termite fauna within the gallery forests would reveal many

more wood-eating species. The predominance of grass-eating termites is understandable because of the large biomass and rapid turnover of their food source.

Of the 54 species of termites in the cerrado vegetation of the Distrito Federal (excluding gallery forests) only nine mound-building species were examined in this study. Many of the other species do not build mounds and are found instead living within mounds built by one of these nine species. It is probable that many of these non-mound-building species will be found to be geophagous or humivorous, feeding in or near the mounds they inhabit.

DISCUSSION

The cerrado vegetation of the Distrito Federal, Brazil has a diverse termite fauna with at least 54 species present (excluding those found in gallery forest vegetation) (Coles 1980). Estimates of the termite density in savanna areas in other continents are much lower with only 19 species in the Sahel, Senegal, 19 in northern Guinea, Nigeria, 23 in southern Guinea, Nigeria and 36 in savannas of the Ivory Coast (Wood and Sands 1978).

A survey by Coles (1980) indicated that most cerrado species were present in all the physiognomic vegetation types; however, in terms of abundance, certain species were more common in one particular type of vegetation. This is clearly illustrated by the data in Table 6. Nests of *Nasutitermes* sp., *Velocitermes paucipilis*, *Cortaritermes silvestri*, *Syntermes dirus* and *Cornitermes cumulans* were all more abundant in the open vegetation types (campo limpo and campo sujo). *Grigiotermes metoecus* and *Armitermes euamignathus* were equally common in all types while *Procornitermes araujo*i was more common in woodland areas. *Orthognathotermes gibberorum* had an irregular distribution being less common in the cerrado *sensu strictu* of the Distrito Federal but more common in the campo limpo of Emas Park. These preferences for particular vegetation types can, to some extent, be related to the feeding habits of each species (Table 7); however, abundance of a species is also influenced by other species present. In some areas conditions were particularly favorable for one species, an example of which was found in Emas National Park where populations of *Cornitermes cumulans* were exceptionally high, with other species much less common.

The variation in abundance of a species in different regions can be

accompanied by variations in mound form and size. Howse (1979) gives several different examples of termite species which build very different mounds in different regions. *Macrotermes subhyalinus* in western Uganda builds mounds with very thick walls and no openings but on the Serengeti Plains, where the soil is volcanic ash, the mounds are low with many pit-like openings. In the semi-arid regions of eastern Africa they are different again, being steeple-shaped and constructed around a central chimney. Even though regional differences can exist, the characteristics of mounds investigated in this study showed a remarkable consistency throughout the cerrado region reinforcing observations by Emerson (1938).

In constructing a mound, galleries are excavated within the soil by the termites and particles are often transported from considerable depth and incorporated in the epigeal portion of the mound. This not only increases aeration of the soil but can also alter its chemical composition (Lee and Wood 1971). Soil used in building is reinforced with excreta and in some instances wood and other plant material.

Studies on the chemical composition of termite mounds in the cerrado have recently been started in Brasilia. Preliminary results indicate that both *Velocitermes* and *Armitermes* mounds have much higher concentrations of calcium, phosphorus, potassium and aluminum than the soil surrounding the mound (Curado et al. in prep.). However, an analysis of Table 5 shows that the materials used in mound building are not directly related to the hardness of the outer layer of the mound. Such factors as the way in which the material is deposited by the workers at the actual site of construction as well as the size and arrangement of galleries and the thickness of walls also contribute to the overall hardness of the mound.

The mounds are constructed entirely by the worker caste. This caste takes little active role in the defense of the mound, a role performed by the soldier caste. The proportion of these two castes varies with the species and is apparently finely regulated by pheromones produced by the queen and the soldiers (Lüscher 1961). Haverty (1977), in a comprehensive work, summarized the data available on the relative proportion of workers and soldiers in 112 species of termites. Unfortunately, many of these data, gathered by different investigators, are not strictly comparable because of differences in sampling techniques and types of groups sampled. The

homogeneity in methodology used in calculating worker-soldier ratios in this study allows for precise comparison between species within the limits of accuracy of this method. The worker-soldier ratios were found to vary greatly between nests in some species (i.e., *Procornitermes*) and remain quite constant in others (i.e., *Velocitermes*).

The behavior of nasute soldiers, which respond to a break in the nest by rapidly recruiting to the break, can greatly alter the worker-soldier ratio calculated. As an example of this, on one occasion the number of soldiers counted from a piece of *Nasutitermes* mound, which had been excised from the surrounding mound but left in place for 30 seconds, was almost half again the number of soldiers counted from a piece taken from the same mound but removed immediately following excision. Although comparison can be made between the nine species of termites it must be noted that these data were taken during one period of the year and present a static picture of the proportions of workers and soldiers in given nests. It seems probable that in the species examined, as in other species (Sands 1965), the worker-soldier ratio varies seasonally and possibly also with the age and size of the nest.

It is evident from the data that some species have proportionally many more soldiers than other species. Even though the proportion of soldiers in a colony varies, in all cases (when there is a soldier caste) the soldier caste is largely responsible for the defense of the colony and has morphological features which allow it to do this. The type of defense used by soldier termites tends to be based on chemicals, mechanical defense or a combination of both. The soldier type using a chemical-based defense has vestigial mandibles (Table 2), is lighter than its workers (Table 1), and produces potentially toxic and repellent secretions which are ejected from the tip of a long tube or nasus at the front of the head (Nutting et al. 1974, Eisner et al. 1976; Howse 1975; Prestwich 1979). Of the termites studied in this work, *Velocitermes*, *Nasutitermes* and *Cortaritermes* fall into this category. The soldier type using a mechanical-based defense rarely produces defensive secretions and has a large head, and strong, sharp mandibles. *Orthognathotermes* is the only species within those here studied that has no development of the nasus, relying solely on its mandibles for defense. *Syntermes*, *Cornitermes* and *Procornitermes* all have strong mandibles which can pierce human skin, drawing blood, together with a greatly reduced level of

chemical defense (see 'nagus length' Table 2 as one indicator of the extent to which chemicals are used in defense). *Armitermes* stands in an intermediate position between the principally chemical and the principally mandibulate type soldiers, with a long nasus and mandibles which can pierce human skin but not draw blood. *Grigiotermes* is very interesting in that it has no soldiers; the workers however produce a large drop of liquid on either side of the abdomen when disturbed, which may serve a defensive purpose.

Termites are probably the dominant form of animal life in many areas of central Brazil, both in number of species and biomass. They play major roles in herbivory, decomposition, soil formation and alteration, and as an important source of food for other animals. Ants are probably the major predators of termites, but in central Brazil mammals are common and important predators as well. The aspects of termite biology reported in this study are all important in defense by termites against mammalian predators. The small size of termites, the type of soldier defense and the proportion of soldiers to workers are all factors influencing feeding by mammals once the termite mound has been opened. The shape, size and hardness of a mound influence the ways in which a mammalian predator can break into a nest while the distribution and abundance of nests are a measure of the spatial availability of termites as a food source. Lastly, the feeding habits of termites are important in determining when, and if, termites are available outside of the mound. Food preference tests with large and small mammalian predators and observation of wild giant anteaters (Redford in prep.) have shown that all of these aspects of termite biology interact in determining which species of termites are preferred as food and how available they actually are to mammalian predators.

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THE LIFE HISTORY OF THE JAPANESE CARRION
BEETLE *PTOMASCOPUS MORIO* AND THE ORIGINS OF
PARENTAL CARE IN *NICROPHORUS* (COLEOPTERA,
SILPHIDAE, NICROPHORINI).*

BY STEWART B. PECK

Department of Biology, Carleton University,
Ottawa, Ontario, K1S 5B6, Canada

INTRODUCTION

The subject of the origin and evolution of sociality in insects has a rapidly growing literature. Most of this pertains to the Hymenoptera. Within the Coleoptera, presocial or subsocial parental care and division of labor are known in at least nine families (Wilson, 1971). The most advanced form of parental care known in beetles is that of the *Nicrophorus* carrion or burying beetles (tribe Nicrophorini). This generalization is based on the study of six European species by Pukowski (1933, 1934) which has since been abstracted and popularized by many (e.g., Balduf, 1935; Milne and Milne, 1944, 1976; Wilson, 1971, 1975). Briefly, a male and female form a conspecific pair at a carcass of a mouse or other small vertebrate. They work cooperatively to exclude competitors, to bury the carcass, and to shape it into a ball in a crypt. The male leaves after oviposition but the female tends the developing larvae, calling them to the carrion by stridulation, and repeatedly feeds them by regurgitation. Such behaviors do not exist in the other tribe of silphid carrion beetles, the Silphini.

The only work on the life cycle of a North American *Nicrophorus* is a short note by Leech (1934) on *N. defodiens* (under the name *N. conversator*). Thus, it is not really known how general or widespread is the phenomenon of parental care in the genus, nor if all species are equally advanced behaviorally. There are about 20 species in the New World, and at least 65 species in all the world, in several lineages within the genus.

As part of a series of studies on the comparative biology and evolution of silphid beetles, I undertook a study of the life history of *Ptomascopus morio* Kraatz of Japan, to learn something of the

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origin of parental care in *Nicrophorus*. *Ptomascopus* is the only other genus in the tribe Nicrophorini and contains only two Asian species, *P. morio* being more common and widespread than *P. plagiatus* Menetries (Hlisnikowski, 1942). It is illustrated in many general Japanese insect books such as Esaki *et al.* (1932, 1956), Nakane *et al.* (1963), and Nakane (1980). The larvae are illustrated by K. Kurosa in Kawada (1959).

The genus shares with *Nicrophorus* many derived morphological characters relative to the Silphini: adults with stridulatory files, reduced second antennal segment, fused gular sutures, sexually dimorphic membranous antclypeus; larvae with abdominal parantotal projections and cuticular sclerotization reduced, and with only one pair of ocelli.

The main morphological characters in which *Ptomascopus* is more primitive than *Nicrophorus* are in its possession of a normally clavate antennal club, rather than with a strongly capitate club formed from the last four segments, and in its less fossorial tibiae.

METHODS AND MATERIALS

Four pairs of *P. morio* were collected in August, 1980, at carrion baits in a warm-temperate mixed mesophytic forest in the Omogo Valley of Mount Ischizuchi Quasi-National Park, Shikoku, Japan. They were brought to Ottawa, Canada, and placed in culture at 18° C, with a normal daylight regime, from September to December. The pairs were kept in separate seven cm deep boxes of clear plastic, floored with five cm of coarse damp sand. Two cm cubes of chicken neck were given as carrion food at required intervals. Observations were made daily. The data gained are variable in quantity and quality and are usually not abundant enough for tests of significance. Only simple means, sample sizes, and ranges are reported, but these are sufficient for comparative purposes.

RESULTS

Both sexes dug irregular tunnels in the sand but not in direct association with the carrion. Most of their time was spent in these tunnels. They fed at the carrion and sporadically dug under it, but there was no direct indication of digging with the intention of burying the food, or of manipulating the food into a food ball, or of forming a crypt for it. Mating was observed occasionally but no indication of a courtship ritual was noted.

Eggs were laid singly in the sand several cm to the side of the carrion. A mean of 13 eggs ($N = 9$, $r = 9-16$) were laid per female in 6 days ($N = 9$, $r = 5-8$), and a new clutch was started after a refractory period of 6 more days ($N = 8$, $r = 5-8$). The eggs hatched in 5 days ($N = 30$, $r = 4-7$). Frequent adult attempts to fly and leave the culture containers after the egg clutch was laid may indicate that post-mating (for the male) or post-oviposition dispersal is normal, and that the adults are normally not present with their young.

The larvae fed together under and directly on the carrion. There was no indication of parental attendance to, or feeding of, the larvae. The adults and larvae may feed on fly larvae or other insects associated with carrion in nature, but carrion alone is adequate for complete development of larvae in culture. There were 3 larval instars; the first lasted 1 day ($N = 30$, $r = 1-2$), the second 2 days ($N = 30$, $r = 2-3$). The third instar larvae fed for 7 days ($N = 30$, $r = 6-9$) before crawling away from the carrion and burrowing into the sand to form pupal cells. In total, over 300 larvae were produced, of which about 50 were preserved for morphological study.

Prepupae had a high mortality due to a fungal contamination. The prepupal phase seems to be about 30 days in duration ($N = 7$, $r = 28-40$). The pupal phase also seems to last about another 30 days before emergence of the adult ($N = 2$, $r = 25-35$). At culture temperatures the parental generation adults died by early December, for a longevity of at least four months. This could be considerably different in the field depending on their sensitivity to cool fall temperatures and whether or not they overwinter as adults.

DISCUSSION

There was no indication of any subsocial or other behavioral association between the larvae and the adults as known in *Nicrophorus*. The brood size, reduced fecundity, and shorter larval developmental times are similar to those reported in *Nicrophorus*, but otherwise the life cycle characteristics are generally similar to those reported for the carrion-feeding Silphini (Balduff, 1935; Brewer and Bacon, 1975; Cole, 1942; Cooley, 1917; and Ratcliffe, 1972). It should be noted that some Silphines appear to have derived feeding characteristics, being strict predators and phytophages. How this may have changed behavior and life cycle characteristics is not known.

The results were verified by Dr. Kazuyoshi Kurosa of Tokyo (pers. comm.) who reared the beetle some 30 years ago in Oita Prefecture, Japan, but did not publish the results. He found no parental care, no sign of burying the food, and no parental attendance on the larvae, which grew well on fresh beef. Still, further observations with a natural forest soil substrate and natural food items like mouse or shrew carcasses would be desirable. How the beetles survive and "partition resources" in the face of what seemed to me to be severe competition from the diverse fauna of Japanese carrion beetles remains unknown.

CONCLUSIONS

It appears that the origin of parental care of larvae did not occur in an ancestor common to *Ptomascopus* and *Nicrophorus*, but seemingly in *Nicrophorus* itself, after the differentiation of the genus. If the origin was sometime after that of the genus itself we may expect a wider range of parental care and related behaviors in *Nicrophorus* than is generally assumed in the recent literature on these beetles. A greater number of *Nicrophorus* species should be studied to investigate the questions of the origin and evolution of sub-sociality within the genus, and the results should be evaluated with reference to a cladistic (phylogenetic) analysis of the evolution of morphological characters.

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TERGAL AND STERNAL GLANDS IN MALE ANTS*

BY BERT HÖLLDOBLER AND HILTRUD ENGEL-SIEGEL

Department of Organismic and Evolutionary Biology,
MCZ-Laboratories, Harvard University,
Cambridge, Massachusetts.

Introduction:

Several recent morphological investigations have uncovered a variety of hitherto unknown or neglected exocrine glandular structures in ant workers (Hölldobler and Haskins 1977; Hölldobler and Engel 1978; Kugler 1978; Jessen et al 1979; Hölldobler et al 1982; Hölldobler 1982; Jessen and Maschwitz in press). The behavioral functions of several of these glands have already been determined (For review see Hölldobler 1982).

These studies dealt almost exclusively with ant females and except for the results of Janet's (1902) classical histological investigations of the internal anatomy of males of *Myrmica rubra*, nothing is known about exocrine glandular structures in the gaster of ant males. Since we consider this information important not only for a further analysis of the behavior of ant males, but especially for our understanding of the evolution of pheromone glands and chemical communication in ants, we have undertaken a histological study of exocrine glandular structures in ant males. In this paper we present a survey of the abdominal glands not directly associated with the gonads. The purpose of this paper is not to give detailed descriptions of each gland found, but rather to present a comparative account of abdominal glands detected in representative species in the different subfamilies.

Materials and Methods:

For histological investigations live specimens were fixed in alcoholic Bouin or Carnoy (Romeis 1948), embedded in methyl methacrylate, and sectioned 8μ thick with a D-profile steel knife on a Jung Tetrander I microtome (Rathmayer 1962). The staining was Azan (Heidenhain). Especially small objects were embedded in a water soluble plastic (JB-4 embedding kit, Polysciences, Inc., Pennsyl-

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vania) and sectioned 4–6 μ thick with glass knives on a rotary microtome. In this case the staining was Hematoxylin-Eosin (triple strength). The SEM pictures were taken with an AMR 1000 A Scanning Electron Microscope. In a few cases only specimens were available which had been preserved in 70% ethanol.

Results:

The major results are summarized in table I. In the following we will discuss some of the details of our findings.

Penis and subgenital plate glands:

Janet (1902) described in males of the myrmicine species *Myrmica rubra* two major glandular structures directly associated with the copulatory apparatus. (1) The first comprise the penis glands, paired clusters of glandular cells located inside the penis valves (Fig. 1). Each cell sends a duct through a membrane into the lumen formed by the valves (sperm gutters). This gland was also detected in males of *Formica rufa* (Clausen 1938) in *Conomyrma brunnei* and *Forelius sp.* (Marcus 1953; cit. in Forbes 1954), in *Camponotus pennsylvanicus* (Forbes 1954), in *Neivamyrmex harrisi* (Forbes & Do-Van-Quy 1965) and we found it in representative species of all major subfamilies of ants. The size of the paired penis gland clusters (which are also called aedeagal gland, Forbes 1954) varies greatly among different species. In some it is a major gland (Fig. 1). In others it is represented only by a few glandular cells, and sometimes we were unable to identify the opening of the glandular ducts. (2) The other major gland, associated with the copulatory apparatus is located in the 9th sternite, which together with the coxopodites comprise the subgenital plate (Weber 1954). We therefore named these paired clusters of glandular cells "subgenital plate gland". Each glandular cell sends a duct through the intersegmental membrane into the ventral part of the genital chamber (Fig. 1,2). The subgenital plate gland was found in representative species of all subfamilies studied.

Tergal glands:

In his study of the workers and males of *Myrmica rubra*, Janet (1898, 1902) discovered a pair of clusters of a few glandular cells under the 6th abdominal tergite. Each cell is drained by a duct that penetrates the intersegmental membrane between the 6th and 7th

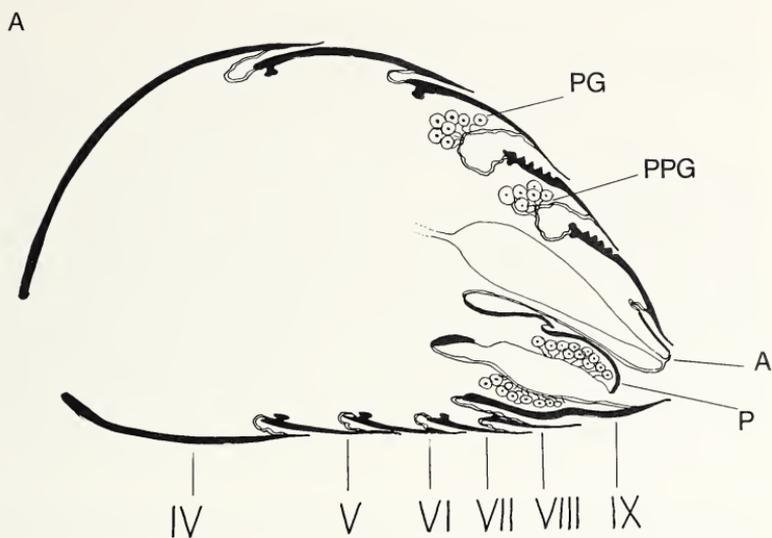


Fig. 1 A. Schematic drawing of a longitudinal section through the gaster of a *Novomessor* ♂. B. Longitudinal section through 6th, 7th, 8th and 9th abdominal segments of a *Novomessor albisetosus* ♂. A=anus; P=part of penis with penis gland; PG=pygidial gland; PPG=post-pygidial gland; SPG=subgenital plate gland.

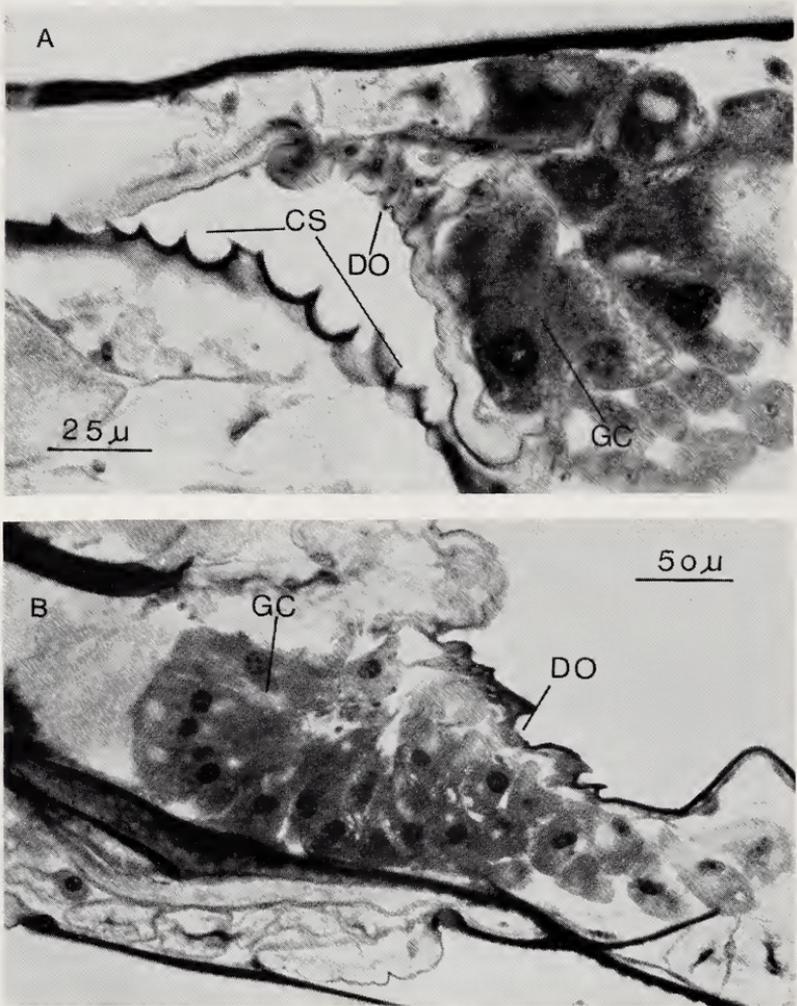


Fig. 2 A. Longitudinal section through pygidial gland of *Novomessor albisetosus* ♂. B. Longitudinal section through subgenital plate gland of *N. albisetosus* ♂. CS= cuticular structure; GC=glandular cells; DO=openings of glandular ducts.

abdominal tergites. In recent investigations this gland was found in workers of representative species belonging to all subfamilies, except in the Formicinae. Although the structure and size of the gland varies greatly, its wide distribution led us to conjecture that this gland might be a primitive monophyletic trait in ants generally, perhaps reaching back to the typhioid (or mutilloid) wasp ancestors of ants. In fact, we have recently found first indications that this gland is also present in some living typhiid wasps.

Since this gland is anatomically closely associated with the last exposed tergite in female ants (7th abdominal tergite = pygidium) Kugler (1978) suggested that it be called the *pygidial gland*. Of the several tergal glands recently discovered, the pygidial gland appears to be the most frequent in occurrence. Moreover, in several species its secretions have been found to serve as pheromones (Hölldobler et al 1976; Hölldobler and Haskins 1977; Maschwitz and Schönege 1977; Kugler 1979; Hölldobler and Traniello 1980 a,b; Traniello and Jayasuriya 1981). The pygidial gland seems to be homologous with the "anal glands" of the dolichoderine ants described by Pavan and Ronchetti (1955). As we pointed out previously (Hölldobler and Engel 1978) the term "anal gland" is misleading, because the gland does not exit from the anal or cloacal opening of the gaster, but between the 6th and 7th abdominal tergites. We therefore suggested to refer the dolichoderine structure to the pygidial gland. Recently Jessen and Maschwitz (in press) proposed to name the pygidial gland in honor of its discoverer Charles Janet. Thus we have now three names for this tergal gland: anal gland, pygidial gland and Janet's gland.

Because the anatomical designation of the organ in ant workers (a criterion we prefer) has been used in several recent publications, we will continue to call the tergal gland opening between the 6th and 7th abdominal tergites *pygidial gland*.

Table 1. (Following pages) List of species that were investigated histologically, and of the types of tergal and sternal glands found. When the histological series was incomplete and we could not make a definite statement, or when we could not clearly identify glandular ducts, the column is marked with a "?". r=with reservoir; c=with cuticular structure.

TABLE I

<i>Subfamily/species</i>	Collector and Locality
MYRMECIINAE	
<i>Myrmecia pilosula</i>	B. Hölldobler, Brindabella Ranges, Australia
PONERINAE	
<i>Diacamma australis</i>	B. Hölldobler, Townsville, Qld., Australia
<i>Ectatomma ruidum</i>	J. Traniello, BCI, Panama
<i>Ectatomma tuberculatum</i>	J. Traniello, BCI, Panama
<i>Leptogenys diminuta</i>	B. Hölldobler, Kuranda, Qld., Australia
<i>Pachycondyla apiacalis</i>	J. Traniello, BCI, Panama
<i>Pachycondyla obscuricornis</i>	J. Traniello, BCI, Panama
<i>Paltothyreus tarsatus</i>	B. Hölldobler, Shimba Hills, Kenya
<i>Rhytidoponera metallica</i>	B. Hölldobler, Brindabella Ranges, Australia
DORYLINAE	
<i>Eciton</i>	A. Aiello, R. Silberglied, BCI, Panama
<i>Neivamyrmex</i>	A. Aiello, R. Silberglied, BCI, Panama
PSEUDOMYRMECINAE	
<i>Pseudomyrmex pallidus</i>	P. Ward, Texas, USA
MYRMICINAE	
<i>Catalacus intrudens</i>	B. Hölldobler, Shimba Hills, Kenya
<i>Leptothorax (Macromischa) alardycei</i>	B. Cole Florida Keys, USA
<i>Novomessor albisetosus</i>	B. Hölldobler, Arizona, USA
<i>Novomessor cockerelli</i>	B. Hölldobler, Arizona, USA
<i>Orectognathus versicolor</i>	B. Hölldobler, Eungella, Queensland, Australia
<i>Pogonomyrmex barbatus</i>	B. Hölldobler, Arizona, USA
NOTHOMYRMECIINAE	
<i>Nothomyrmecia macrops</i>	R. W. Taylor, Eyre Peninsula, Australia
ANEURETINAE	
<i>Aneuretus simoni</i>	Anula Jayasuriya, Sri Lanka
DOLICHODERINAE	
<i>Iridomyrmex purpureus</i>	B. Hölldobler, Canberra, Australia
<i>Liometopum apiculatum</i>	B. Hölldobler, Arizona, USA
FORMICINAE	
<i>Formica perpilosa</i>	B. Hölldobler, Arizona, USA
<i>Myrmecocystus mendax</i>	B. Hölldobler, Arizona, USA
<i>Oecophylla longinoda</i>	B. Hölldobler, Shimba Hills, Kenya

Intersegmental tergal glands

Intersegmental sternal glands

IX/ VIII	VIII/ VII	VII/ VI	VI/ V	V/ IV	IV/ III	IX/ VIII	VIII/ VII	VII/ VI	VI/ V	V/ IV	IV/ III
	+	+									
		r									
	+	+									
	?	+									
+	+	r				+	+				
		+					r				
	?	r,c									
	+	+									
	+	r									
	+	+				+		+	+		
		+									
	+	+									
		+	+	+	+			+	+	+	+
		r	r	r	r				r	r	r
		+	+	+	+			+	+	+	+
		r	r	r	r				r	r	r
		+									
		r									
+	+	+									
		+									
	+	+									
	r,c	r,c									
	+	+									
	r,c	r,c									
	?	+									
	+	+									
		r									
	+	+									
	r										
	?										
	+	+	+								
	+	r									
		+									
		r									

+

TABLE 1 (continued)

<i>Subfamily/species</i>	Other tergal glands
MYRMECIINAE	
<i>Myrmecia pilosula</i>	
PONERINAE	
<i>Diacamma australis</i>	glandular cells in 7th and 8th segment ducts open dorsally into genital chamber
<i>Ectatomma ruidum</i>	
<i>Ectatomma tuberculatum</i>	
<i>Leptogenys diminuta</i>	
<i>Pachycondyla apiacalis</i>	
<i>Pachycondyla obscuricornis</i>	
<i>Paltothyreus tarsatus</i>	IXth tergite; ducts open into genital chamber
<i>Rhytidoponera metallica</i>	
DORYLINAE	
<i>Eciton</i>	IIIrd
<i>Neivamyrmex</i>	IIIrd
PSEUDOMYRMECINAE	
<i>Pseudomyrmex pallidus</i>	
MYRMICINAE	
<i>Catalacus intrudens</i>	
<i>Leptothorax (Macromischa)</i> <i>alardycei</i>	
<i>Novomessor albisetosus</i>	postpetiole gland opens between IIIrd tergite and postpetiole postpetiole gland
<i>Novomessor cockerelli</i>	
<i>Orectognathus versicolor</i>	
<i>Pogonomyrmex barbatus</i>	
NOTHOMYRMECIINAE	
<i>Nothomyrmecia macrops</i>	
ANEURETINAE	
<i>Aneuretus simoni</i>	
DOLICHODERINAE	
<i>Tridomyrmex purpureus</i>	
<i>Liometopum apiculatum</i>	
FORMICINAE	
<i>Formica perpilosa</i>	
<i>Myrmecocystus mendax</i>	
<i>Oecophylla longinoda</i>	

As mentioned before Janet found this gland not only in workers of *M. rubra* but also in males. Ant males differ from the workers in having one more exposed segment (8th segment); often even part of the 9th segment is visible. Thus in ant males the pygidial gland does not open at the last exposed tergite (Fig. 1).

As can be seen from tab. 1 we found a pygidial gland in species of the subfamilies Myrmeciinae, Ponerinae, Dorylinae, Pseudomyrmecinae, Myrmicinae, Nothomyrmeciinae and Dolichoderinae. In *Aneuretus simoni* (Aneuretinae) we detected a few glandular cells, but we could not clearly see glandular ducts. In the males, as in the workers, there exists a considerable variation in the morphology of the pygidial glands, even within a single subfamily. In some species large clusters of glandular cells are associated with a special cuticular structure on the 7th tergite (Fig. 1, 2, 6c). Some species possess more or less developed reservoirs, composed of an invagination of the intersegmental membrane (Fig. 3). In other species there are only a few glandular cells that send dorsolaterally ducts through the intersegmental membrane.

In ant males a post pygidial gland is almost as common as the pygidial gland (Fig. 1). It also consists of paired clusters of glandular cells that open through the intersegmental membrane, but between the 7th and 8th tergites (Tab. 1). This gland is especially well developed in *Nothomyrmecia macrops* males, where the intersegmental membrane forms a large reservoir. There it closely resembles the pygidial gland found in workers. Interestingly, the males of this species have only a few glandular cells between the 6th and 7th tergites. Thus in comparison with *Nothomyrmecia* females (including queens) the major tergal gland in the males is shifted one segment posteriorly. In most other ant species examined, however, the gland between the 6th and 7th tergites (pygidial gland) is the major tergal gland in both workers and males.

The doryline males are a remarkable exception. They, too, have large pygidial glands, consisting of paired complex glands and a large reservoir. But the same structure is present in the next 3 segments anteriorly (6th–5th; 5th–4th; 4th–3rd) (Fig. 4, 5). In addition, intersegmental glandular cells were found between the 7th and 8th tergites. In the 3rd tergite we also found paired groups of glandular cells, the ducts of which penetrate the sclerotized cuticle of the 3rd tergite dorsolaterally.

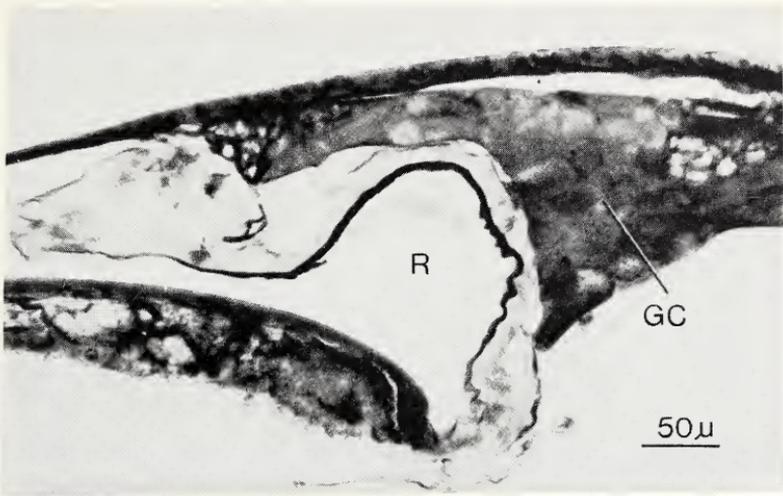


Fig. 3 Longitudinal section through pygidial gland of *Pogonomyrmex barbatus* ♂. GC=glandular cells; R=reservoir.

Sternal glands:

More than in any other subfamily, the males of the doryline ants are also richly endowed with sternal glands (Tab. 1; Fig. 4). We found major complex glands with intersegmental reservoirs between the 3rd and 4th, 4th and 5th, 5th and 6th sternites. Glandular clusters are also present between the 6th and 7th sternites—but without a pronounced reservoir. In addition, clusters of glandular cells whose ducts penetrate the sclerotized cuticle were found in the 3rd sternite, they are also strongly developed in the 8th and 9th sternites (Fig. 4). Similar sternal glands were found in the 8th sternite of males of *Myrmecia pilosula*, *Pachycondyla apiacalis* and *P. obscuricornis*. In both *Pachycondyla* species the glandular ducts open in bundles into cuticular cups located in the 8th sternite (Fig. 7a).

In the ponerine species *Leptogenys diminuta* the males possess a huge intersegmental sternal gland between the 7th and 8th sternites. This gland consists of large paired clusters of glandular cells. Each cell sends a duct into wider collecting channels which lead into a paired large reservoir, consisting of ventro-lateral invaginations of the intersegmental membrane (Fig. 6). There is a second paired sternal gland between the 8th and 9th sternite; but this gland is

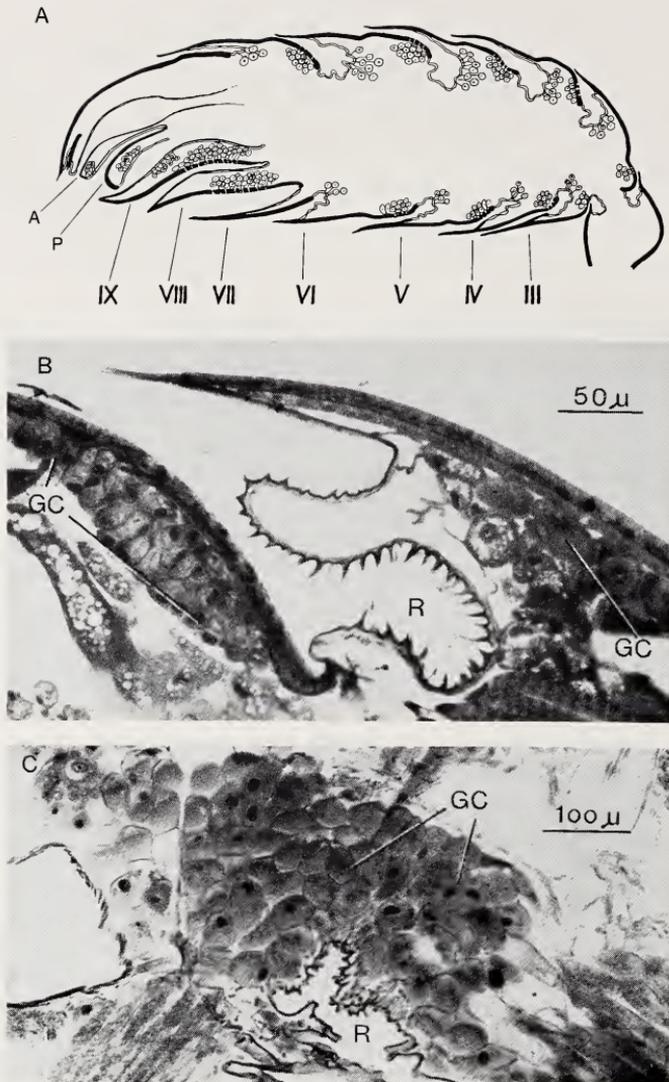


Fig. 4 A. Schematic drawing of a longitudinal section through the gaster of a *Neivamyrmex* spec. ♂, illustrating the segmental glandular structures. B. Longitudinal section through a intersegmental complex-gland (between IVth and Vth tergites). C. Longitudinal section through a intersegmental sternal gland of *Eciton* spec. ♂. A=anus; GC=glandular cells; P=part of penis with penis gland; R= reservoir.

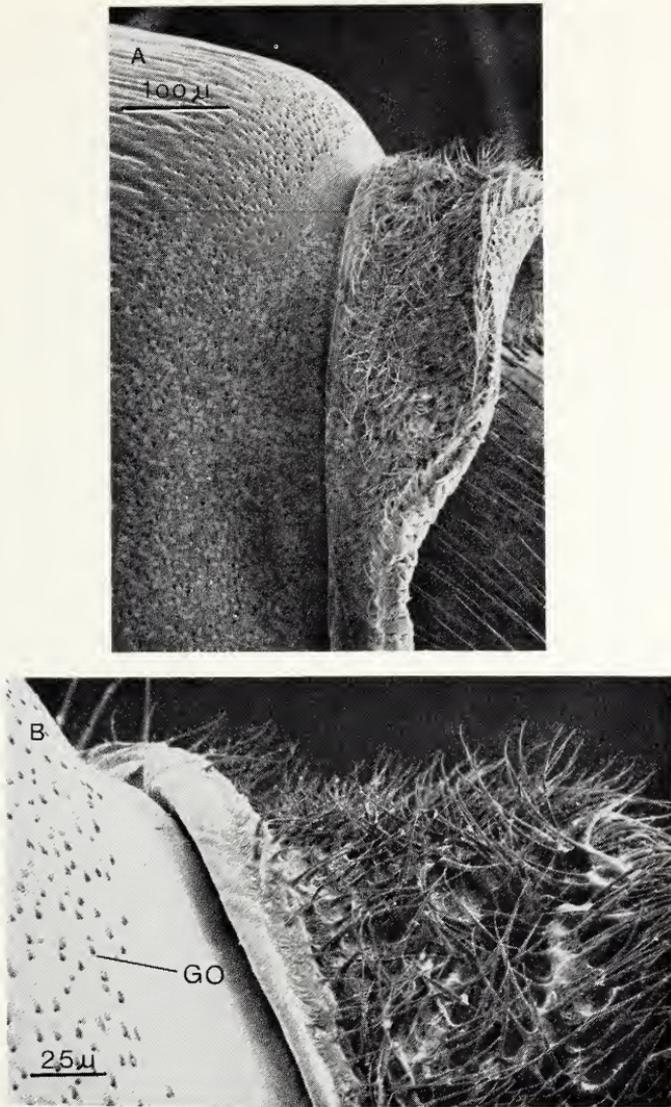


Fig. 5 A. SEM micrograph of the tergite with the attached intersegmental membrane of a *Neivamyrmex* ♂. B. Larger magnification showing clearly the glandular duct openings in the cuticle (GO) and the intersegmental membrane which consists of a mat of bristle-like structures. This mat-membrane forms the intersegmental glandular reservoir. See also Fig. 4B.

much smaller, and no pronounced reservoir could be detected. *Leptogenys* workers have two well developed sternal glands between the 5th and 6th, and the 6th and 7th sternites respectively (Hölldobler and Engel 1978; Jessen et al 1979). *Leptogenys* males lack these structures but do possess sternal glands in the 7th and 8th sternites. In males of the ponerine ant *Paltothyreus tarsatus* we found large paired clusters of glandular cells in the 8th sternite. The glandular ducts open through the intersegmental membrane between the 8th and 9th sternites. In addition *Paltothyreus* males possess unpaired intersegmental sternal glands, similar to those found in *Paltothyreus* workers (Hölldobler and Engel 1978), but smaller, between the 5th and 6th, and 6th and 7th sternites.

Other abdominal glands:

As indicated in table 1 we found several other abdominal glands in males which cannot directly be assigned to the group of tergal or sternal glands. In a few species (*Novomessor*, *Leptogenys*) we detected glandular cell clusters in the petiole. In *Ectatomma*, *Diacamma*, *Paltothyreus* we found small tergo-sternal glands. The ducts of the glandular cells composing them open laterally through the pleural membrane. We found similar small glandular cell bunches in males of *Pachycondyla* and *Rhytidoponera*, but we could not clearly identify the glandular ducts. These tergo-sternal glands resemble closely similar structures described by Jessen et al (1979) in workers of several ponerine species. Finally we found small groups of glandular cells directly at the anus of males in *Pachycondyla*, *Ectatomma*, *Neivamyrmex*, *Eciton*, *Myrmecocystus* and *Liometopum* (Fig. 7b). These anus glands vary considerably in size, and it is possible that they are present in more species than we were able to document. We first found them in workers of *Dorylus* (Hölldobler and Engel 1978). The anus glands should not be mistaken for the rectal gland, an invagination of a glandular epithelium of the rectum, recently discovered in *Oecophylla* workers by Hölldobler and Wilson (1978). It is interesting to note that males of *Oecophylla* also possess a small rectal gland.

Discussion:

Except for the glands associated with the ovipositor and sting apparatus, which the males lack, ant males are as richly endowed with exocrine glands as the females. In many species of ants the males have well developed mandibular glands, pro- and post-

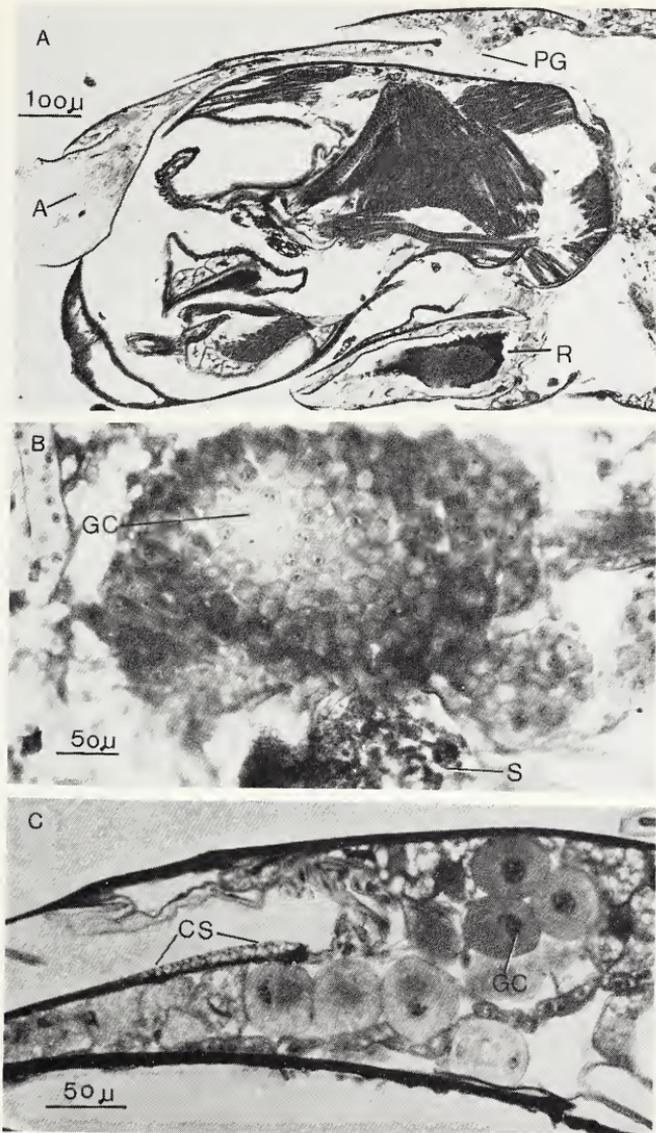


Fig. 6 A. Longitudinal section through gaster of a *Leptogenys diminuta* ♂, showing the reservoir (R) of the large sternal gland between 7th and 8th sternites. A=anus. B. Section through the large cluster of glandular cells of the sternal gland, opening into the reservoir between 7th and 8th sternite. S=secretion in reservoir. C. Longitudinal section through the pygidial gland of *Leptogenys diminuta* ♂. Note that the glandular cells (GC) are considerably larger than the glandular cells of the sternal gland (Fig. 6B). CS=cuticular structure

pharyngeal glands, maxillary glands, salivary glands, and meta-pleural glands, although the size of these various structures can vary considerably between the female castes and males. In this paper we surveyed specifically the abdominal sternal and tergal glands in ant males.

In almost all species studied we encountered two major glandular structures that Janet (1907) had already described in *Myrmica rubra*, the penis glands and the subgenital plate glands. Also quite generally present in males (except in the Formicinae) are the pygidial glands. The males share these organs with the females, although less well developed in some species. An interesting case is *Nothomyrmecia*: here the males have a rudimentary pygidial gland but a well developed postpygidial gland (between the 7th and 8th tergites).

The males of the doryline ants are unusually well endowed with abdominal glands, in which they differ markedly from the workers. Although doryline workers have well developed pygidial- and postpygidial glands (Hölldobler and Engel 1978), the males have massive glandular structures in each segment. In this context the findings by Whelden (1963) are of considerable interest. Whelden described a series of exocrine glands in the gaster of *Eciton* queens as follows: "Each of the segments of the gaster, including those telescoped together in the posterior part, contains a pair of these glands which are smaller in the anterior segment than those in the following segments". We were not yet able to section a doryline queen and therefore cannot compare the queen organs with those we found in males. It appears, however, that the males possess a glandular equipment very similar to that of the queens. Presumably in doryline queens these massively developed exocrine glands play an important role in the queen's chemical control of the worker ants and in her high attractiveness to workers, (Watkins and Cole 1966). We hypothesize that the males imitate queen pheromones, which might enable them to penetrate a foreign colony in order to get access to the wingless virgin female reproductives (Franks and Hölldobler unpublished). In fact, this might also be the function of the massively developed sternal gland in *Leptogenys* males. In this genus, as in the dorylines ergatoid reproductive females presumably mate in the nest, so that males flying in from other nests have to penetrate a foreign colony.

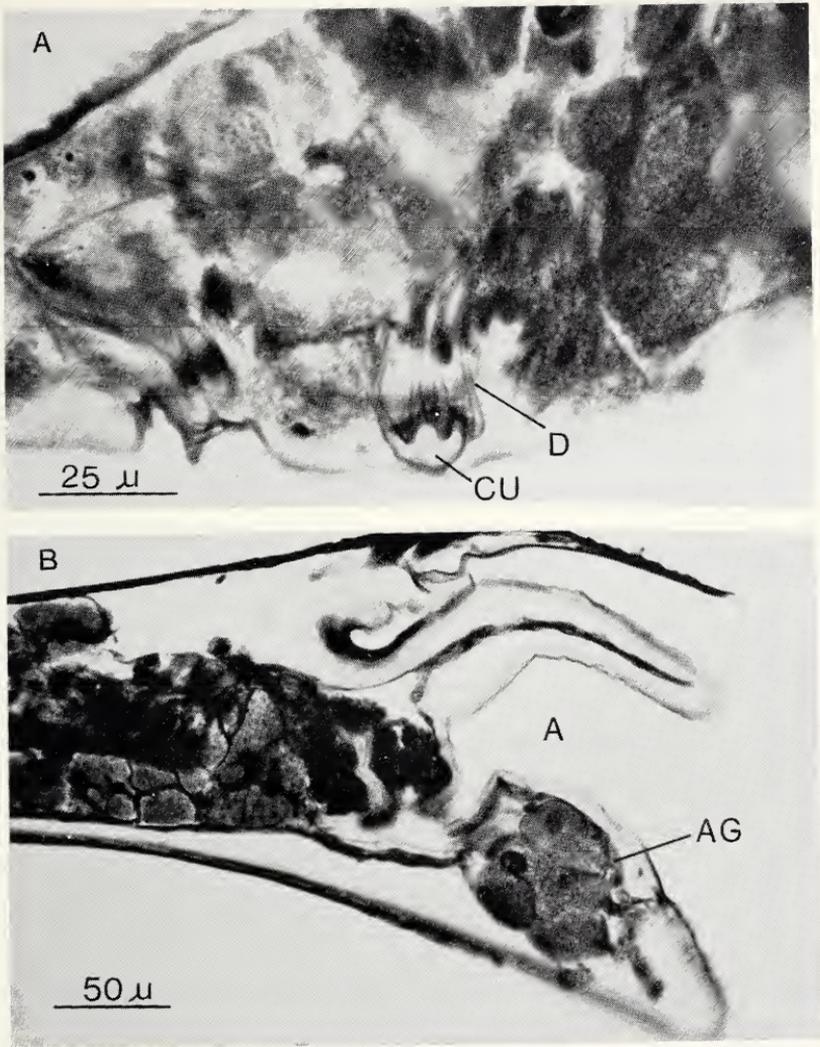


Fig. 7 A. Longitudinal section through sternal gland in 8th sternite of a *Pachycondyla apiacalis* ♂. D=glandular duct; CU=cuticular cup. B. Longitudinal section through 8th tergite of a *Ectatomma ruidum* ♂. A=anus; AG=anus gland.

But these are speculations. We know nothing about the function of the abdominal glands in ant males. Jessen and Maschwitz (in press) suggested that some of the numerous intersegmental glands they discovered in workers of the ponerine *Pachycondyla tridentata* might function as lubrication glands, reducing the friction between the segments when the workers bend the gaster during the act of stinging. In ant males some of the intersegmental glands could produce lubricants in order to keep the abdomen flexible during mating behavior or to assist the extrusion of the copulatory apparatus. On the other hand some of the well developed tergal and sternal glands seem almost certainly to produce allomones or pheromones. The recent morphological investigations of glandular structures in ants have opened a new phase in the study of chemical communication in ants.

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TERMITE-TERMITE INTERACTIONS: WORKERS AS AN AGONISTIC CASTE*

BY BARBARA L. THORNE
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138

Termite soldiers are a defensive caste. Their heavily sclerotized head capsules can be equipped with hard mandibles capable of crushing, pinching, piercing, or slashing predators. Soldier castes of many phylogenetically advanced species have well-developed frontal glands and are capable of exuding or spraying chemical secretions. Such chemical armaments are toxic, irritable, or oily fluids which can impair physiological, sensory and/or mechanical faculties of the recipient (Prestwich, 1979). Termite soldiers are thus formidable opponents for ants and vertebrate predators. Soldiers are fed by workers and their behavior within the colony is generally limited to signaling alarm, participating in defense, and organizing foraging expeditions (Stuart, 1969; Traniello, 1981).

Despite their specialization, however, soldiers are not the only defensive caste in a termite colony: worker termites of some species (from four families) are known to be able fighters in termite-termite aggressive interactions [Kalotermitidae (Grassi and Sandias, 1896–1897; Dropkin, 1946); Hodotermitidae (Nel, 1968); Rhinotermitidae (Pickens, 1934; Clément, 1978); Termitidae (Dudley and Beaumont, 1889a,b; Andrews 1911)]. This paper explores intra- and interspecific agonistic encounters among termites, and focuses on the roles of workers and soldiers in such conflicts.

The report is presented in two sections, corresponding to two sets of experiments on this topic. Section A describes a field manipulation inducing intraspecific encounters among colonies of *Nasutitermes corniger* in Costa Rica. Section B presents data on laboratory experiments examining intra- and interspecific interactions among four species of Panamanian termites.

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A. INTRASPECIFIC FIELD EXPERIMENT: *NASUTITERMES CORNIGER*

Nasutitermes corniger (Motschulsky) is a common arboreal termite ranging through much of Central and northern South America (Thorne, 1980). Large carton nests contain up to 800,000 termites (Thorne and Noirot, 1982) and, with the addition of foragers, total colony size may exceed a million individuals. Distinct foraging trails, covered by carton galleries, are visible issuing from a nest and proceeding along tree branches, trunks, and the ground surface. The termites also travel underground and in galleries located within trees or fallen logs. *N. corniger* foraging trails can radiate many meters from the parent colony.

Given the density of *N. corniger* colonies in primary forest (7.0 ± 1.8 per hectare in the Hubbell Plot of Barro Colorado Island, Panama, $N = 4$ hectares) and in areas of young second growth (27 in one hectare in Frijoles, Panama) (Thorne, unpub. data), it is likely that, at least occasionally, foraging parties from different colonies encounter one another in the midst of exploring or exploiting a local food source. Observation of a natural inter-colony encounter would be difficult. It would require tracking single foraging trails, which would undoubtedly result in disturbance as one cleared away the forest litter to locate foragers. Even if trails could be accurately followed without disruption, it would be rare to view simultaneous interception with an active trail known to be from a second colony. Because the odds of witnessing such a natural event are low, I forced an encounter through a transplant experiment.

METHODS

On the morning of 18 August, 1978 three *Nasutitermes corniger* nests were collected from separate areas of second growth near Sirena headquarters of Corcovado National Park, Osa Peninsula, Costa Rica. The nests measured 29.8, 52.7, and 41.9 cm in height and 26.0, 29.8, and 26.0 cm in diameter, respectively. Nests were sawed from their host trees and hand-carried to the experimental site. Each colony was suspended on a wire from one of two branches of a large tree (Fig. 1). The nests were hung in an equilateral triangle such that the distance from their base to the ground was 60 cm, the distance from the edge of each colony to each neighbor was 50 cm, and the original compass orientation of each colony was main-

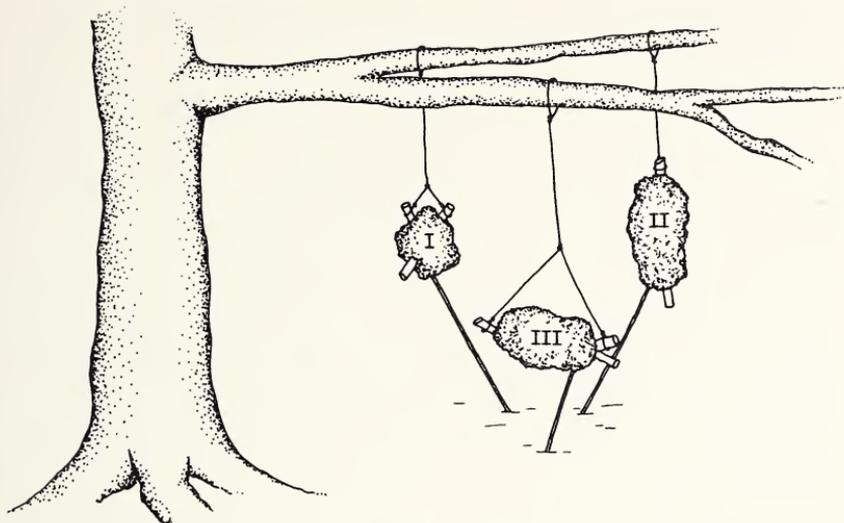


Figure 1. Field set-up for intraspecific encounter experiment involving Costa Rican *Nasutitermes corniger*.

tained. A coat of tanglefoot was placed at the base of each wire strand (near the point of attachment to nest support branches) to prevent termites from crawling up the wires. A 3.5×3.5 m² plot beneath the nest triangle was completely cleared of leaf litter, forest debris and herbaceous plants so that movement patterns of the termite trails could be monitored. At 7:30 p.m. that evening stick "ramps" (90 cm in length, 1 cm in diameter) were installed to connect the nests to the ground. The tips of the sticks were shallowly inserted into both the nest carton and ground surface for support. Bases of the ramps also ended in vertices of an equilateral triangle on the ground, 20 cm from tip to tip.

RESULTS

Hanging above the ground from a single strand of wire, each nest was an island in mid-air: no escape routes were open for the termites. By dusk of the day of collection, soldiers and workers from all colonies were crawling over the peripheries of their nests. This activity gained participants and momentum: at 7:30 p.m. each nest was a seething mass of termites. The stick ramps were embedded to

connect the nests to the ground. Immediately following implantation termites swarmed onto the ramps, soldiers in the lead followed by a mixture of soldiers and workers. Only four white immatures were seen leaving the nests throughout the experimental period.

As they reached the ground groups fanned out: termites from a single colony divided into several ribbons heading in different directions. Because of the close proximity of the ramp exits, it was inevitable that encounters occur between trails from different colonies. The meetings were not passive. Soldiers oriented towards (and apparently squirted) termites from other colonies, but this did not seem much of a deterrent to recipients. The major defense stemmed not from the soldiers, but from the *Nasutitermes* workers.

Workers from different colonies grabbed each other with their mandibles and locked in one-on-one conflict. Pairs of workers squirmed and bent with vigor, often until the death of both. Occasionally a third or fourth worker would join the engagement, but usually only temporarily. Workers avidly attacked soldiers as well, grabbing at the legs and occasionally biting the abdomen.

The next morning worker carcasses littered the arena over an area of approximately 1,500 cm², with some battle "patches" as far as 1.5 m from the center of the ramp triangle. The density of bodies was often quite high (25–50 dead in a 4.0 cm² area). Surviving termites did not appear to cannibalize the dead. Ants, flies, staphylinid beetles, and wasps began scavenging the termite carcasses.

How were foraging trail routes influenced by the intersection battles? Agonistic confrontations were instigated when at least one colony was in the process of establishing or changing a foraging route, i.e. in a scouting phase. Preliminary observations (Fig. 2) suggest that both colonies' foraging pathways were displaced by encounters — trails were repulsed from the meeting site following battles lasting 10–30 minutes. One colony may maintain a trail tangential to the "battle field", but I did not see one continuing through an area of dead termites.

It is difficult to determine the effect of agonistic encounters on final foraging path location. In isolation a colony establishes foraging routes by scouting in a broad network, but several hours later this highly branched fan collapses into a single actively travelled ribbon with few side trails. Thus the fact that termites have traversed a given area in no way assures that route as the path of a final

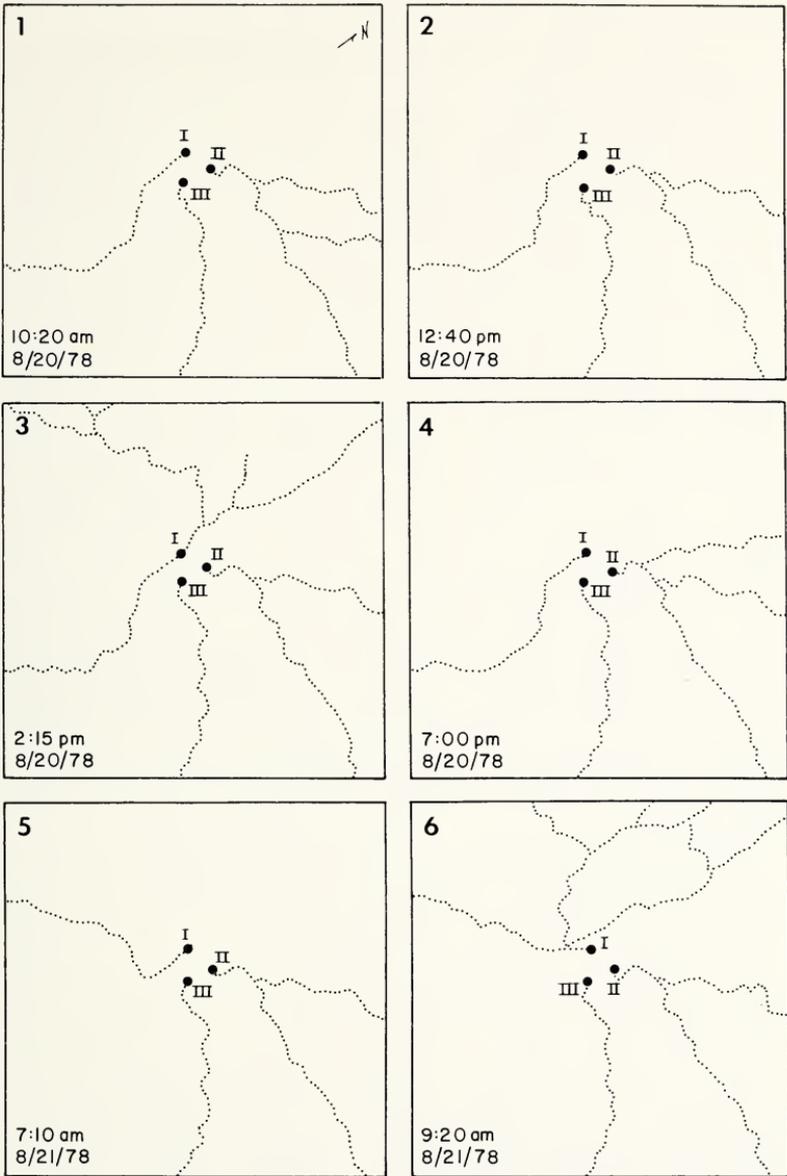


Figure 2. Periodic maps of ground foraging trails departing from the tips of exit ramps attached to suspended *Nasutitermes corniger* colonies (Section A). Central dots indicate positions of the ramps. Maps are 3.5×3.5 m².

foraging trail. Battles may be a deterrent to formation of a given path, but their influence is difficult to assess independently.

Foraging path trajectories from the three nests were monitored for two and one half days following initiation of the experiment (see Fig. 2 for the final 24 hour period). Once a scouting fan condensed into a single pathway the positions were relatively stable. Minor adjustments in path locations did occur periodically, and activity on specific trails varied from day to day and even hour to hour. Occasionally (usually in the evening) new scouting parties would emanate from the ramp tip or as a tributary of the main trail network.

Construction of trail covers varied from colony to colony. Colony III began covering both its ramp and ground trails quickly (a total of 64 cm of trail covered by 7 a.m., 20 August). In contrast, Colonies I and II had only 19 cm and 3.2 cm of covering, respectively, at 7 a.m. on 20 August. These same relative speeds were repeated when the initial experiment was replicated from 21 to 22 August. Building behavior also showed distinct inter-colony variation, mainly in the amount of advance siding deposited before the trails were roofed.

To replicate the first nights' encounters, I removed the three ramps and scraped clean the entire $3.5 \times 3.5 \text{ m}^2$ grid at noon on 21 August. This caused attrition of those individuals on the ground and out foraging, but the established trails had to be destroyed to induce active scouting. New ramps (90 cm long) were installed at 6:30 p.m., with ends touching the ground in an equilateral triangle of side length 25 cm.

Members of Colony I came down their ramp fairly rapidly and began three major paths from its tip, one to the southeast, one to the north, and one due west. At 7 p.m. termites from Colony II began coming down their ramp and immediately began to fight with Colony I's southeast-bound foragers. When the first workers from Colony III came down their ramp and encountered foreigners, they rapidly reversed direction and returned *en masse* to the mouth of their nest, after which a large group of Colony III termites stormed down the ramp. The possibility of worker recruitment in these circumstances should be investigated. The battle between Colonies I and III was vehement for 20 minutes; after 30 minutes Colony I's southeast trail was abandoned. Colony III established a new trail 180° away from the direction of original interference with Colony I.

Table 1: Comparative Size Measurements and Percentage of Soldiers Per Colony

		BODY LENGTH (INCLUDING HEAD) ^a (mm)	HEAD WIDTH ^a (mm)	DRY WEIGHT ^b (μ gms)	APPROXIMATE PERCENTAGE SOLDIERS
<i>Anitermes bequaioni</i> (Termitidae, Termitinae)	SOLDIER	3.8 \pm 0.1	0.87 \pm 0.03	0.33	
	WORKER	3.3 \pm 0.2	0.85 \pm 0.02	0.34	7-9% ^c
<i>Anitermes chagresi</i> (Termitidae, Nasutitermitinae)	SOLDIER	4.3 \pm 1.3	1.23 \pm 0.02	1.03	
	WORKER	3.8 \pm 0.1	0.84 \pm 0.02	0.83	7-8% ^c
<i>Nasutitermes corniger</i> (Termitidae, Nasutitermitinae)	SOLDIER	3.6 \pm 0.1	0.95 \pm 0.05	0.34	18% ^d
	WORKER	3.8 \pm 0.2	1.15 \pm 0.07	0.60	(range: 8-27%)
<i>Nasutitermes ephratae</i> (Termitidae, Nasutitermitinae)	SOLDIER	3.3 \pm 0.4	0.90 \pm 0.04	0.39	15% ^d
	WORKER	3.7 \pm 0.2	1.16 \pm 0.08	0.65	(range: 6-23%)

a Measurements determined from 10 specimens in each category. Morphological measurements are known to vary among colonies of *Nasutitermes* (Thorne, unpub.); the figures given are from termites within a single colony. (Mean \pm S.D.)

b Determined by drying and weighing a number of termites, then dividing their cumulative weight by the number weighed to yield this "average" per individual weight.

c From samples of termites captured while foraging.

d Calculated as the average percentage (arcsin transformed) of soldiers in the neuter population (excluding immatures) of 12 colonies, chosen at random and quantitatively dissected. The range among the 12 colonies is also given.

In these and several other encounters that night, aggressive interactions among colonies were similar to those described earlier.

B. INTRA- AND INTERSPECIFIC LABORATORY EXPERIMENTS:
TERMITE-TERMITE INTERACTIONS AMONG FOUR
PANAMANIAN SPECIES

To examine conflicts among colonies and species of sympatric termites I staged laboratory encounters in pairwise tests: soldiers vs soldiers, soldiers vs workers, and workers vs workers. Characteristics of the four species used in these experiments are summarized in Table I. *Amitermes beaumonti* soldiers have curved mandibles; *Armitermes chagresi* soldiers have long, curved mandibles and a prolonged nasus; and soldiers of *Nasutitermes corniger* and *N. ephratae* are nasutoid with vestigial mandibles (Fig. 3).

METHODS

Experimental trials were conducted in March and April, 1981 in the Smithsonian Tropical Research Institute laboratory on Barro Colorado Island (BCI), Panama (9° 09' N, 79° 51' W). All *Amitermes beaumonti* and *Armitermes chagresi* were collected from nests on BCI; samples of *Nasutitermes corniger* and *N. ephratae* were from colonies in Frijoles, Panama (4 km east of BCI). Pairwise encounters were staged in petri dish arenas (4.6 cm diameter) lined with moist filter paper. Equal numbers of termites, soldiers or workers, from each colony were introduced to an arena simultaneously. Dishes were then covered and left undisturbed in darkness for 12 hours. After the interaction period survivors were counted: conspicuously injured individuals were considered as dead. Most worker-worker trials involved 50 individuals from each colony (only large workers (♀) were used from *Nasutitermes* colonies; *Amitermes* and *Armitermes* have monomorphic worker castes). When soldiers of *Amitermes* or *Armitermes* were involved in a trial, and in occasional trials involving *Amitermes* or *Armitermes* workers, fewer individuals were available so experiments proceeded with less than 50 termites from each colony. In Table II the number of individuals from each colony used in each trial is indicated in parentheses following the survival percentages. A minimum of three trials were conducted for each intra- and interspecific interaction. Each such



Figure 3. Termite-termite interactions (Section B). a. *Nasutitermes corniger* workers (dark heads) vs *Armitermes chagresi* soldiers (light heads). b. *N. corniger* soldiers vs *Amitermes foreli* workers. c. *N. corniger* intraspecific worker-worker encounter. d. *Amitermes foreli* soldier vs *N. ephratae* worker. e. *Armitermes chagresi* soldier vs *N. ephratae* worker.

trial pitted termites from different colonies. After the 12 hour encounter all dead termites from selected trials were collected and examined for injuries under a dissecting microscope.

RESULTS

Survival percentages of termites involved in each trial are presented in Table II. For conspecific interactions among members of a single caste (soldier vs soldier or worker vs worker), it was not possible to differentiate colony affiliation so a single survival percentage is indicated. These figures indicate whether or not a fight ensued, although it is impossible to determine if one colony suffered more or less mortality than the other.

Variability within and between blocks of Table II is high. Among some replicates mortality is low for both groups of interacting termites (signified by a '-' at the base of the block). Some encounters suggest consistent "victors", represented by an arrow pointing in the direction of that party. Other groups of interactions indicate agonistic behavior on both sides ('+'), without clear assignment of a "winner" or "loser".

All interspecific worker-worker encounters resulted in a fight, often with a trend suggesting a "dominant" species but with sufficient variation among trials to prevent assigning a "winner". Such variation may result from relative differences in individual colony nutrition, age, health, and history. For example, an interaction between two strong colonies may be quite different from a similar encounter between members of a weak and a strong colony. It should be noted that soldiers are absent during worker-worker trials, which may affect the excitability and response of workers.

Intraspecific worker-worker engagements demonstrated variable aggression within *Nasutitermes corniger* and *N. ephratae*, and no lethal attacks in any of the *Amitermes* or *Armitermes* trials. Fighting among conspecific *Nasutitermes* colonies is variable and apparently influenced by as yet uninvestigated factors. In these experimental trials, aggressive interactions generally occurred, although in all but one *N. corniger* trial well over half of the workers survived the 12 hour meeting. I have previously observed both extremes in conspecific *Nasutitermes corniger* encounters: 100% mortality and 100% survival, even among colonies from distant locations. Dudley & Beaumont (1889a,b) report that mixing two *N. corniger* colonies

resulted in lethal fights. Variance in response may be due to experimental protocol, particularly isolation of a colony's soldiers and workers. Under natural conditions a colony's soldiers and workers may interact with one another in recognition of and response to foreign termites. The soldier secretion has been demonstrated an alarm pheromone in *N. exitiosus*, although workers showed little reaction to fresh secretion presented on an applicator (Eisner *et al.* 1976).

In these experiments soldiers and workers from different *N. corniger* or *Amitermes chagresi* colonies did not fight, while soldier-worker conflict did occur in *N. ephratae* and *Amitermes beaumonti* conspecific encounters. In the field manipulation involving Costa Rican *N. corniger* (Section A), soldier-worker battles were observed.

Summarizing other general trends, *N. ephratae* workers scored relatively well in worker-worker inter-specific encounters, although they were not consistent victors over *Amitermes* workers. Both *Amitermes* and *Armitermes* soldiers fared relatively well in most encounters while *Nasutitermes* soldiers were less successful. In intraspecific *Armitermes chagresi* interactions, only soldier-soldier conflict was observed; among *Amitermes beaumonti*, only meetings between soldiers and workers stirred fighting. Such patterns imply species differences in communication, meaning, and recognition of any colony-specific odors.

Injuries suffered by the dead during the interaction experiments were scored for several trials, and are summarized in Table III. Presence or absence of damage to the abdomen was scored, though no analysis of extent of abdominal injury was recorded because the exact number of wounds or punctures was difficult to assess. The percentage of dead with abdominal wounds is generally high.

Table II (Following pages): Survival Percentages of Panamanian Termites in Paired Laboratory Encounters

Paired encounters were staged matching equal numbers of termites (number of individuals from each colony given in parentheses following trial results). The total percentage of individuals surviving the 12 hour meeting is given for intraspecific soldier-soldier and worker-worker interactions: inability to identify colony affiliation prevented comparative percentages. All other trials report the survival percentage of the termites listed to the left over that of termites listed on top. Arrows at the base of a block point in the direction of a consistent "winner"; arrows in parentheses note a less pronounced tendency, '-' indicates few deaths on either side (no fight); '+' signifies lethal interactions among the termites but with no consistent trend toward a victor.

<i>Nasutitermes</i>						
<i>corniger</i>	100% survival (50)	100%/100% (50)	100%/100% (50)	100%/100% (50)	46%/42% (50)	
soldiers	100% survival (50)	100%/100% (50)	100%/100% (50)	100%/100% (50)	0%/78% (50)	
	100% survival (50)	100%/100% (50)	100%/100% (50)	100%/100% (50)	2%/94% (50)	
					0%/90% (50)	
<i>Nasutitermes</i>						
<i>corniger</i>	100% survival (50)	98%/86% (50)	98%/86% (50)	98%/86% (50)	28%/84% (50)	
workers	48% survival (50)	92%/56% (50)	92%/56% (50)	92%/56% (50)	6%/80% (50)	
	69% survival (50)	90%/0% (50)	90%/0% (50)	90%/0% (50)	12%/74% (50)	
	66% survival (50)	94%/2% (50)	94%/2% (50)	94%/2% (50)	22%/0% (50)	
	83% survival (50)	82%/4% (50)	82%/4% (50)	82%/4% (50)	14%/28% (50)	
					6%/50% (50)	
					(-)	
<i>Nasutitermes</i>						
<i>ephratae</i>	99% survival (50)	99% survival (50)	99% survival (50)	99% survival (50)	52%/66% (50)	
soldiers	98% survival (50)	98% survival (50)	98% survival (50)	98% survival (50)	96%/80% (50)	
	99% survival (50)	99% survival (50)	99% survival (50)	99% survival (50)	94%/72% (50)	
					94%/86% (50)	
					90%/90% (50)	
					100%/98% (50)	
					100%/98% (50)	
						+
<i>Nasutitermes</i>						
<i>ephratae</i>	59% survival (50)					
workers	86% survival (50)					
	98% survival (50)					

Table II: Survival Percentages of Panamanian Termites in Paired Laboratory Encounters

	<i>Anitermes bequaerti</i>		<i>Armitermes chagresi</i>		<i>Nasutitermes corniger</i>		<i>Nasutitermes ephratae</i>	
	soldiers	workers	soldiers	workers	soldiers	workers	soldiers	workers
<i>Anitermes bequaerti</i> soldiers	100% survival (8)	33% / 17% (6)	20% / 60% (5)	80% / 60% (5)	20% / 80% (10)	50% / 17% (12)	100% / 100% (5)	40% / 20% (10)
<i>Anitermes bequaerti</i> workers	100% survival (8)	80% / 80% (5)	0% / 80% (5)	67% / 50% (6)	100% / 60% (5)	90% / 1% (10)	100% / 100% (5)	83% / 0% (6)
	93% survival (7)	80% / 80% (5)	20% / 80% (5)	33% / 17% (6)	83% / 67% (6)	83% / 17% (6)	100% / 100% (5)	100% / 20% (5)
	-	+	-	-	+	-	-	-
<i>Armitermes bequaerti</i> soldiers	100% survival (50)	0% / 100% (6)	0% / 6% (50)	8% / 2% (50)	78% / 86% (50)	20% / 56% (50)	90% / 100% (20)	24% / 2% (50)
<i>Armitermes bequaerti</i> workers	100% survival (50)	0% / 100% (6)	8% / 2% (50)	73% / 83% (50)	56% / 62% (50)	22% / 36% (50)	100% / 100% (50)	16% / 36% (50)
	100% survival (50)	0% / 100% (5)	73% / 83% (50)	90% / 90% (50)	96% / 34% (50)	22% / 6% (50)	100% / 100% (50)	10% / 22% (50)
					68% / 0% (50)	4% / 20% (50)		14% / 32% (50)
						0% / 22% (50)		10% / 26% (50)
	-	-	+	+	+	+	-	(-)
<i>Armitermes chagresi</i> soldiers		42% survival (6)	100% / 100% (5)	20% / 40% (10)	86% / 0% (7)	75% / 75% (8)	100% / 0% (7)	
<i>Armitermes chagresi</i> workers		70% survival (5)	100% / 100% (5)	67% / 0% (3)	80% / 0% (5)	80% / 80% (5)	100% / 0% (7)	
		80% survival (5)	100% / 100% (5)	100% / 14% (7)	67% / 0% (3)	50% / 0% (10)	100% / 0% (10)	
				60% / 40% (5)	83% / 17% (6)			
				50% / 50% (4)				
<i>Armitermes chagresi</i> soldiers		100% survival (50)	0% / 42% (50)	92% / 92% (50)	96% / 86% (50)	56% / 10% (50)		
<i>Armitermes chagresi</i> workers		100% survival (50)	10% / 0% (50)	4% / 8% (50)	96% / 100% (50)	76% / 68% (50)		
		100% survival (50)	14% / 0% (50)	22% / 0% (50)	88% / 74% (50)	70% / 82% (50)		
				36% / 0% (50)	0% / 38% (50)	73% / 24% (41)		
			-	+	+	+	+	
<i>Nasutitermes corniger</i> soldiers				100% survival (50)	100% / 100% (50)	100% / 100% (50)	46% / 42% (50)	
				100% survival (50)	100% / 100% (50)	100% / 100% (50)	0% / 78% (50)	
				100% survival (50)	100% / 100% (50)	100% / 100% (50)	2% / 94% (50)	
							0% / 90% (50)	
<i>Nasutitermes corniger</i> workers					100% survival (50)	98% / 86% (50)	28% / 84% (50)	
					48% survival (50)	92% / 56% (50)	6% / 80% (50)	
					69% survival (50)	90% / 0% (50)	12% / 74% (50)	
					66% survival (50)	94% / 2% (50)	22% / 0% (50)	
					83% survival (50)	82% / 4% (50)	14% / 28% (50)	
						6% / 50% (50)		
							(-)	
<i>Nasutitermes ephratae</i> soldiers						99% survival (50)	52% / 66% (50)	
						98% survival (50)	96% / 80% (50)	
						99% survival (50)	94% / 72% (50)	
							94% / 86% (50)	
							90% / 90% (50)	
							100% / 98% (50)	
							100% / 98% (50)	
<i>Nasutitermes ephratae</i> workers							59% survival (50)	
							86% survival (50)	
							98% survival (50)	

Table III: Analysis of Injuries for 7 Paired Worker-Worker Interactions

	Percentage of Individuals with Abdominal Wounds	Antennal	Legs	Heads	Mean Number of Non-Abdominal Wounds Per Individual
<i>Armitermes chagresi</i> (10 of 12) vs <i>Nasutitermes ephratae</i> (16)	100%	5	6	1	1.20
<i>Armitermes chagresi</i> (20 of 21) vs <i>Nasutitermes ephratae</i> (43)	—	3	13	3	1.00
<i>Nasutitermes ephratae</i> (8) vs <i>Nasutitermes corniger</i> (41)	87.5%	7	6	2	0.94
<i>Nasutitermes ephratae</i> (12) vs <i>Nasutitermes corniger</i> (43)	—	41	61	0	2.37
<i>Nasutitermes ephratae</i> (37) vs <i>Amiterme</i> (38)	87.5%	2	6	1	1.12
<i>Nasutitermes ephratae</i> (46) vs <i>Amitermes beaumonti</i> (38)	78.0%	30	125	1	3.83
<i>Nasutitermes ephratae</i> (37) vs <i>Nasutitermes corniger</i> (37)	100%	3	13	0	1.25
<i>Nasutitermes ephratae</i> (46) vs <i>Nasutitermes corniger</i> (37)	90.7%	27	169	0	4.56
<i>Nasutitermes corniger</i> (19) vs <i>Amitermes beaumonti</i> (38)	65.6%	36	32	20	2.75
<i>Nasutitermes corniger</i> (37) vs <i>Amiterme</i> (38)	82.6%	39	46	0	1.85
<i>Nasutitermes corniger</i> (37) vs <i>Amitermes beaumonti</i> (39)	73.7%	12	25	1	2.05
<i>Nasutitermes corniger</i> (37) vs <i>Amitermes beaumonti</i> (39)	50.0%	24	35	19	2.05
<i>Nasutitermes corniger</i> (37) vs <i>Amitermes beaumonti</i> (39)	67.6%	47	113	0	4.32
<i>Nasutitermes corniger</i> (37) vs <i>Amitermes beaumonti</i> (39)	50.0%	24	35	19	2.05
<i>Nasutitermes corniger</i> (37) vs <i>Amitermes beaumonti</i> (39)	67.6%	47	113	0	4.32
<i>Nasutitermes corniger</i> (37) vs <i>Amitermes beaumonti</i> (39)	35.9%	28	53	16	2.51

Numbers in parentheses following species names are the number of individuals examined (killed). The colony with the fewest deaths is listed first for each interaction. Descriptions of the injury categories and criteria are described in text Section B under Results.

Damage to each antennae and leg was scored separately, and a pierced or decapitated head was scored as one head injury, even if multiple punctures were present. Thus for 10 dead termites, a maximum of 20 antennal, 60 leg, and 10 head injuries were possible. That number of cumulative injuries divided by the total number of termites examined yielded the mean number of non-abdominal injuries per individual. This index gives some indication of the intensity of attack.

The frequency of antennal, leg, and head injuries shows that *Amitermes beaumonti* heads appear relatively vulnerable (at least when faced by *Nasutitermes*), and that *N. corniger* was prone to numerous leg injuries.

DISCUSSION

Worker termites of some species join in aggressive encounters with members of other colonies and are often adept fighters, particularly against other workers. Intensity and outcome of agonistic encounters is variable depending on the species, colonies, and castes involved. Soldiers also participate in termite-termite conflicts. This study suggests that mandibulate soldiers are more effective one-on-one inter-specific antagonists than are *Nasutitermes* soldiers, although nasute soldiers are generally present in higher numbers per colony and may be more effective in groups.

Research on termite-termite encounters has not been extensive, but is of interest because the recognized defensive caste, the soldiers, are not the sole participants, and may not join in such interactions at all. After viewing the attack of an introduced *Termes* worker by nymphs and larvae in a *Calotermes* colony, Grassi and Sandias write in their 1896-1897 account (p. 283), "...similar observations have been made several times, and show... that the soldiers purposefully reserve themselves for more important foes." Pickens (1934) noted that workers of established *Reticulitermes hesperus* colonies will attack and kill founding pairs and incipient colonies which settle nearby.

Andrews (1911) did an extensive series of intra-specific interaction experiments with *Nasutitermes rippertii*. Nearly all staged encounters resulted in immediate conflict involving both soldiers and workers, although occasionally two colonies were completely docile towards each other. Andrews also came to the conclusion

that "different communities (colonies) have different grades of hostility" (p. 218). Studying *Coptotermes acinaciformis*, Howick and Creffield (1980) similarly report inter-colony variance in degree of aggression.

The mechanism by which termites recognize non-colony members, and the associated stimuli for aggressive response, are not understood. Termites of some species quickly discriminate between colony-mates and foreigners; other species seem oblivious to "aliens". Certain treatments have been shown to interfere with recognition or aggressive behaviors: water washes (Andrews 1911), chilling termites to immobilization (Dropkin 1946; Howick & Creffield 1980), and laboratory rearing (Nel 1968). Unpigmented immatures of some species appear immune from attack (Andrews 1911, Sands & Lamb 1975). Dudley and Beaumont (1889a) postulated that colony members bear like "odors", and that they can thereby differentiate colony-mates from foreigners. This idea of what is now termed colony-specific recognition pheromones is still viable (reviewed by Stuart 1970), perhaps involving cuticular hydrocarbons as recognition cues (Howard et al. 1978, Blomquist et al. 1979). The degree of intraspecific pheromone variation, the environmental components of response, and the mode of aggressive stimulus remain unknown.

Workers may be particularly useful as a capable, defensive unit in termite-termite encounters because they are the numerically dominant caste and although they are accompanied by soldiers on foraging forays, they are vulnerable to predation and competition while foraging. Termite mounds and arboreal nests have few exposed openings, and any which exist are guarded, usually by soldiers. In contrast, worker foragers cannot rely on nest protection, and their armada of soldier escorts may be insufficient to stay competitors. Mandibulate soldiers are normally in low proportion relative to workers (Haverty 1977). The ratio of termite soldiers to workers in *Nasutitermes* is relatively high (Haverty 1977), but the soldiers have vestigial mandibles and their chemical sprays are apparently not a complete defense against other termites. Soldiers may be especially proficient at repelling ant and vertebrate attacks (although workers may assist, eg. Eisner *et al.* 1976), while worker castes are adept at joining with soldiers to defend resources against other termites.

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TYPE DESIGNATIONS AND SYNONYMIES FOR NORTH AMERICAN SILPHIDAE (COLEOPTERA)

BY STEWART B. PECK¹ AND SCOTT E. MILLER²

The purpose of this paper is to provide type data and lectotype and neotype designations for North American Silphidae described by J. L. LeConte, Thomas Say, M. H. Hatch, and J. W. Angell, and new synonymies of other species. We are engaged in ongoing revisionary work on North American silphids (e.g. Miller and Peck, 1979) and have found considerable nomenclatural confusion because of varying interpretations of poor descriptions and names not fixed to types. Publication of these data is also necessary for their inclusion in the forthcoming fascicle on this family in "A Catalog of the Coleoptera of America North of Mexico", U.S. Dept. Agric. Handbook 529 (J. M. Kingsolver, editor-in-chief). Improved identification keys and characterizations of all United States and Canadian silphids are given in Peck (1982a).

In the LeConte and Horn collections of the Museum of Comparative Zoology (MCZ), Harvard University, the specimens that bear "type" labels have not been formally validated, and these were placed on the assumed types (supposedly the first in each series) during routine curation early in this century. The Say neotypes were selected from the LeConte collection because it is generally agreed that the original Say material is lost, and that LeConte had the opportunity to compare his specimens with those in Say's collection (see Lindroth and Freitag, 1969; Miller and Peck, 1979). The specimens designated do not differ in characters from the original published descriptions.

Primary types from the Hatch collection have been deposited by Oregon State University in the United States National Museum of Natural History (USNM).

Types have recently been designated for *Silpha aenescens* Casey, *Silpha ramosa* Say, *Agyrtes longulus* LeConte, and *Necrophilus pettitii* Horn (Miller and Peck, 1979; Peck, 1974 and 1982b).

¹Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6.

²Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Herman (1964) has shown that the correct spelling of the genus of the sexton or burying beetles is *Nicrophorus* Fabricius, 1775, and not *Necrophorus* Thunberg, 1789 (see Madge, 1980).

TYPE SPECIMENS OF NOMINAL SPECIES

Nicrophorus lunatus LeConte 1853: 277. LECTOTYPE (here designated), a male with a yellow disc and a red square label with white dorsal margin "Type 3144" and white label "N. sayi Lap/lunatus Lec.," and our designation label, in MCZ. The yellow circle in LeConte's code is supposed to mean "Central Valley or Western States (Ohio, Illinois, Indiana, Missouri, Western Tennessee, Kentucky, Iowa, and southern Great Lakes)". However, the species localities were published by LeConte as New York and Georgia. The name is a junior synonym of *Nicrophorus sayi* Laporte, 1840; and a junior homonym of *Nicrophorus lunatus* Fischer, 1842, of Eurasia. Harold (1868) supplied *Nicrophorus luniger* as a replacement name for *Nicrophorus lunatus* LeConte.

Nicrophorus confossor LeConte 1854: 20. Described from a single specimen, the HOLOTYPE: a male with a dark blue disc (indicating Oregon and Washington), and a red square label with white dorsal margin "Type 3146" and white label "N. confossor/Cooper Lec.," and white label "maratimus 4", in MCZ. The published type locality is Prairie Paso, which is in Washington. The species is a synonym of *Nicrophorus investigator* Zetterstedt, 1824.

Nicrophorus pollinator LeConte 1854: 19. LECTOTYPE (here designated) a male with dark blue disc (meaning Oregon and Washington), red label with white dorsal margin "Type 3145", white label "N. pollinator/Cooper Lec.", white label "vespilloides 9", and our designation label, in MCZ. Accompanied by male paralectotype with blue disc, red label with white dorsal margin "Type/2/3145" and white label "vespilloides 10" and male paralectotype with blue disc and red label with white dorsal margin "Type/2/3145" and white label "vespilloides 11", both in MCZ. The published distribution is from Fort Vancouver to the Yokolt Plain. The species is a synonym of *Nicrophorus defodiens* Mannerheim, 1846, and a junior homonym of *Nicrophorus pollinator* Mannerheim, 1853 (which is a synonym of *Nicrophorus investigator* Zetterstedt, 1824).

Necrophorus orbicollis Say 1825: 177. NEOTYPE (here designated), a male in LeConte collection with white label "N. orbicollis/Say/Hallii Kirby", and our designation label, in MCZ. Published localities are from "the N.W. Territory" (which at the time meant Ohio, Indiana, Illinois, Wisconsin, and Michigan), and "very rare in the Middle States", and "one specimen from Dr. T. W. Harris of Milton, Massachusetts". The Harris collection is preserved in the MCZ and was examined but no specimens of the species were found that would help to validate Say's species concept.

Necrophorus hecate immaculosis Hatch 1957: 15. The name was validated by this use as a subspecies, not by its earlier use as an aberration (Hatch 1927: 362) according to Article 10b of the ICZN. The holotype, which we have not seen, is a specimen from "California" in the Institut für Pflanzenschutzforschung Zweigstelle Eberswalde, East Berlin (formerly Deutsches Entomologisches Institut). Our examination of much west coast material (and unpublished data of R.S. Anderson) shows that *immaculosis* represents part of a range of variation in elytral patterning within *N. hecate* Bland 1865, and, furthermore, that *hecate* represents a portion of variation within *N. guttula* Motschoulsky 1845. We therefore propose *immaculosis* as a NEW SYNONYM of *hecate*, and *hecate* as a NEW SYNONYM of *guttula*.

Necrophorus maritimus Eschscholtz, in Guerin-Meneville 1835, Iconographie, plate 17, fig. 8. This name was last used by Hatch (1957: 14) as *Necrophorus investigator maritimus*, for material mostly from coastal islands of British Columbia with reduced elytral fascia. It was originally described from Sitcha Island, Alaska, but we have not seen authentic type material. Our examination (and unpublished data of R. S. Anderson) of much west coast material shows this to be one part of variation, which is not geographically coherent, of *N. investigator* Zetterstedt 1824, and we therefore propose *maritimus* as a NEW SYNONYM.

Necrophorus grandior Angell 1912: 307. LECTOTYPE (here designated), a male with labels "California", "Janson", "Original/type", "Necrophorus / grandior / Angell", "Necrophorus / grandior / 2917 Ang./Det. M. H. Hatch 1925", "Necrophorus/germanicus/ab. bipunctatus/♂ Kr./M. H. Hatch-1926" and our designation label, in USNM. Hatch (1927) cited this as the "type" (holotype), but it was published as a syntype. The species is a synonym of *Nicro-*

phorus germanicus (Linnaeus), 1758. The location of the second syntype, a specimen of *N. humator* (Gleditsch) 1767 (according to Hatch 1927) is unknown. It is not in the Hatch collection at Oregon State University (G. L. Peters, pers. comm.).

Silpha truncata Say 1823: 193. NEOTYPE (here designated), a male with dark green disc (meaning New Mexico) and white label "S. truncata Say.", and our designation label, in MCZ. The published locality is "Arkansa" and "near the Rocky Mountains", which we take to mean the upper reaches of the Arkansas River in eastern Colorado. Say collected the single specimen while he was a naturalist on Major Long's 1819 party exploring the upper reaches of the Platte, Arkansas, Canadian, and Red Rivers, of the southern Great Plains and foothills of the Rockies (Weiss and Ziegler, 1931). The species is now *Thanatophilus truncatus* (Say).

Silpha bituberosa LeConte 1859b: 6. Described from a single specimen, the HOLOTYPE: a female with pale green disc (meaning Nebraska, Kansas, North Dakota, South Dakota, Oklahoma, Colorado, Wyoming, and Montana), and red label with white dorsal margin "Type 8952" and white label "S. bituberosa/Drexler Lec.", in MCZ. The published type locality is "near Fort Bridger", now in SW Wyoming. The species is now in the genus *Aclypea* (in some literature as *Blitophaga*), but the former name is given priority, following Seidlitz (1888: 311) as the first reviser in accordance with article 24 (a) (i) of the International Code of Zoological Nomenclature.

Silpha caudata Say 1823: 192. The species was described from material collected by Thomas Nuttall "on the upper Missouri" River and by Say from "near the Rocky Mountains." LeConte (1859c) recognized this species as a synonym of *Silpha lapponica* Herbst, now *Thanatophilus lapponicus* (Herbst), and this has been accepted ever since. We do not designate a neotype for this name, for it is not necessary in the interests of stability of nomenclature.

Necrophilus tenuicornis LeConte 1859a: 84. Described from a single specimen, the HOLOTYPE: a female with dark blue disc (meaning Oregon and Washington), and red label with white dorsal margin "Type 3147" and white label "N. tenuicornis/P. Sound Lec." and white label "Pt./tenuicorne/(Lec)". in MCZ. The published type locality is Puget Sound, Washington. The species is now *Apteroloma tenuicorne* (LeConte).

NEW SUBGENERIC SYNONYMY

Our studies, as well as those of R. S. Anderson, R. B. Madge, and A. F. Newton (all unpublished), have not provided data to support retention of the monotypic subgenus *Necrocharis* Portevin 1923 for *Nicrophorus carolinus* (Linnaeus 1771). Therefore we consider *Necrocharis* a NEW SYNONYM of *Nicrophorus* Fabricius 1775.

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We thank A. F. Newton (MCZ), T. J. Spilman (USDA c/o USNM), M. D. Schwartz and G. L. Peters (both Oregon State University) for their courtesy in allowing study of specimens under their care. A. F. Newton and R. B. Madge reviewed the manuscript and have provided much helpful advice throughout our silphid studies. R. S. Anderson (and his unpublished Masters thesis at Carleton University on distribution and biology of Silphidae in Canada and Alaska) helped clarify questions of species identities. Miller's work was done while at the Santa Barbara Museum of Natural History and the Smithsonian Institution.

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CHEMICAL MIMICRY AS AN INTEGRATING MECHANISM
FOR THREE TERMITOPHILES ASSOCIATED WITH
RETICULITERMES VIRGINICUS (BANKS)^{1,2}

BY RALPH W. HOWARD,^{3,4} C. A. MCDANIEL,⁵
AND GARY J. BLOMQUIST⁶

INTRODUCTION

The mechanisms by which termitophiles integrate themselves into the social life of termite colonies have long intrigued entomologists (Kistner, 1979). Various authors have suggested that plausible integration mechanisms might include the using of "appeasement chemicals" (Wilson, 1971), passing as morphological mimics (Kistner, 1968), or engaging in behavioral mimicry (Kistner, 1979). We recently reported (Howard et al., 1980a) that the host-specific, highly integrated termitophile *Trichopsenius frosti* Seevers associated with *Reticulitermes flavipes* (Kollar) possesses the same complex mixture of cuticular hydrocarbons as its termite host. We suggested that this was an example of chemical mimicry which functioned to integrate this beetle into the termite society.

Reticulitermes virginicus (Banks) is sympatric with *R. flavipes* throughout much of its range and, as predicted (Howard et al., 1978; Blomquist et al., 1979), the two species possess distinctly different cuticular hydrocarbons which function as species recognition cues (Howard et al., 1982). They also have different termitophilous cohorts. Thus, *T. frosti* is associated only with *R. flavipes* whereas *T. depressus* Le Conte, *Xenistusa hexagonalis* Seevers (both Staphylinidae: Trichopseniinae), and *Philoterme howardi* Kistner and Gut (Staphylinidae: Aleocharinae) are associated only with *R. virginicus*. We now report that the three *R. virginicus* staphylinids also appear to use chemical mimicry as an integrating mechanism; i.e.,

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²Isoptera: Rhinotermitidae.

³Forestry Sciences Laboratory, Southern Forest Experiment Station, P. O. Box 2008
GMF, Gulfport, MS 39503.

⁴Author to whom correspondence should be addressed.

⁵National Monitoring and Residue Analysis Laboratory, USDA Animal and Plant
Health Inspection Service, P. O. Box 3209, Gulfport, MS 39503.

⁶Department of Biochemistry, University of Nevada-Reno, Reno, NV 89557

they have the same complex mixture of cuticular hydrocarbons as their host termite. In addition, we report that at least one of these beetles (*X. hexagonalis*) biosynthesizes its hydrocarbons.

METHODS AND MATERIALS

Portions of several colonies of *R. virginicus* were collected in 1979 from pine logs in Harrison, Jackson, and Stone Counties, Mississippi. The beetles were separated from the termites, counted by species, and stored at -20°C until used. A total of 230 beetles was collected: 10 *P. howardi*, 140 *T. depressus*, and 80 *X. hexagonalis*. Cuticular hydrocarbons from pooled samples (by species) were isolated and separated as previously described (Howard et al., 1978). Hydrocarbons were characterized by gas-liquid chromatography (GC) retention times and by electron impact (EI) and chemical ionization (CI) mass spectrometry (Howard et al., 1980b; Jackson and Blomquist, 1976). Double bond stereochemistries were determined by comparison with standards using argentation thin-layer chromatography (AgNO_3 -TLC) (Kates, 1972).

In vitro biosynthesis experiments were conducted as previously described (Howard et al., 1980a) using 60 *X. hexagonalis* collected from a single colony of *R. virginicus* in September 1979.

Radioactivity was assayed by liquid scintillation counting for 10 minutes at about 85 percent counting efficiency. All counting was done with a standard deviation of less than 5 percent. A portion of the isolated hydrocarbons was assayed for total radioactivity. The remainder of the material was separated by AgNO_3 -TLC into saturated, monounsaturated, and diunsaturated components, which then were assayed for radioactivity.

RESULTS

The retention times of all peaks present in the GC profile of cuticular hydrocarbons from *R. virginicus* (Fig. 1) match those from the GC profile of the cuticular hydrocarbons of *P. howardi* (Fig. 2), *T. depressus* (Fig. 3), and *X. hexagonalis* (Fig. 4). Confirmation of the chemical identity for each of the hydrocarbon components in most of the GC peaks was obtained by EI and CI mass spectrometry (MS). In every instance, the GC-MS retention times and mass spectra of the beetle hydrocarbon components were identical to those

previously obtained from *R. virginicus* cuticular hydrocarbons (Howard et al., 1982). Likewise, concurrently obtained AgNO₃-TLC retention values (R_f) were identical for all beetle derived alkenes and *R. virginicus* alkenes. Components which were identified include n-alkanes, 2-, 3-, 11-, 13-, and 15-methylalkanes, 11,15-dimethylalkanes, Z-9-alkenes, Z,Z-7,9-dienes, and E/Z-6,9-dienes ranging in carbon number from C₂₁ to C₄₀ (Table 1). Double bond location and stereochemistries of the beetle derived alkenes were inferred solely from GC and GC-MS retention time data, and AgNO₃-TLC R_f data, since insufficient sample was available for infrared analysis and methoxymercuration-demercuration (Blomquist et al., 1980). Early eluting components not identified by a number in Figures 1 to 4 are unidentified, but have retention times consistent with a homologous series of n-alkanes.

The relative abundance of individual hydrocarbon components varied from species-to-species, but no more so than that of their termite host, whose percent composition varies considerably by caste (Howard et al., 1982).

The *in vitro* radioisotope incorporation experiment was conducted with *X. hexagonalis* to determine if this species can biosynthesize its cuticular hydrocarbons *de novo*. Howard (1978) reported that this species engages in frequent allogrooming with its termite host, with the resulting possibility of acquiring host hydrocarbons by mechanical transfer rather than by *de novo* biosynthesis. A combination of these two alternatives is also possible. After 2 hours of incubating beetle cuticular tissues with 10 μCi of [1-¹⁴C]-acetate, 19.6 ± 8.8 pmole (mean ± SD) of [1-¹⁴C]-acetate was incorporated into hydrocarbon. About 87.8 ± 5.3 percent of the radioactivity was in the alkane fraction, 10.2 ± 4.0 percent was in the alkene fraction, and 1.9 ± 1.3 percent was in the alkadiene fraction. This closely approximates the distribution of alkanes and olefins in *X. hexagonalis*, suggesting that this species can *de novo* biosynthesize its cuticular hydrocarbons. *In vitro* biosynthesis experiments were not conducted with *T. depressus* and *P. howardi* because we were unable to collect enough beetles simultaneously.

DISCUSSION

The striking mimicry of hydrocarbon components observed among these three beetles (representing two subfamilies) and their

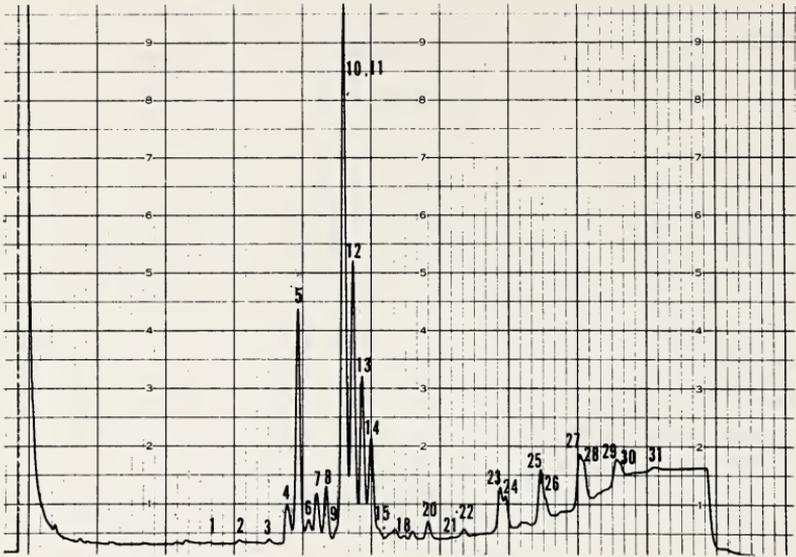


Fig. 1. GC trace of total cuticular hydrocarbons of *Reticulitermes virginicus*. GC conditions: 1.83 m \times 3 mm i.d. Stainless steel column packed with 3 percent (w/w) SP-2100 on 100/120 mesh Supelcoport; temperature programmed from 150° to 325° C at 5° C/min.

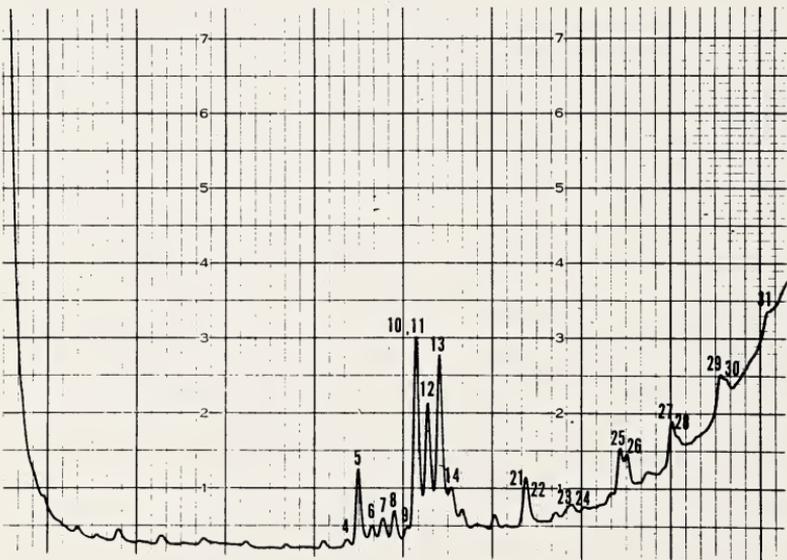


Fig. 2. GC trace of total cuticular hydrocarbons of *Philotermes howardi*. GC conditions same as for Fig. 1.

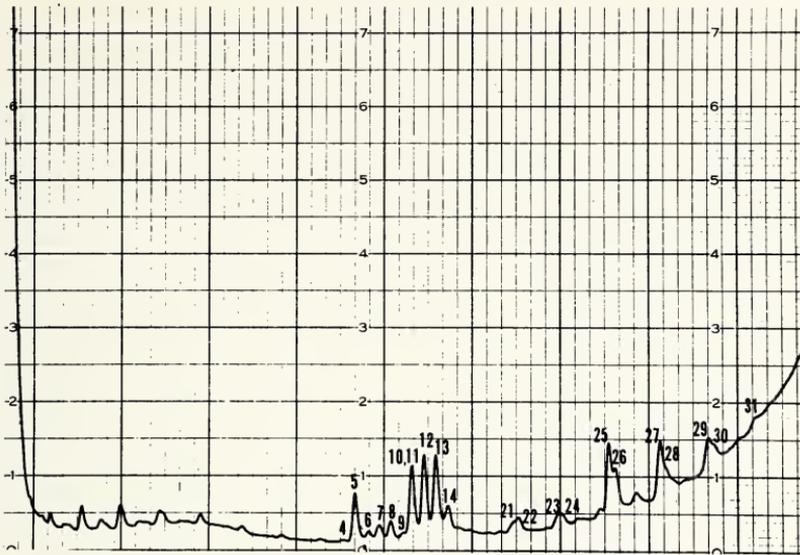


Fig. 3. GC trace of total cuticular hydrocarbons of *Trichopsenius depressus*. GC conditions same as for Fig. 1.

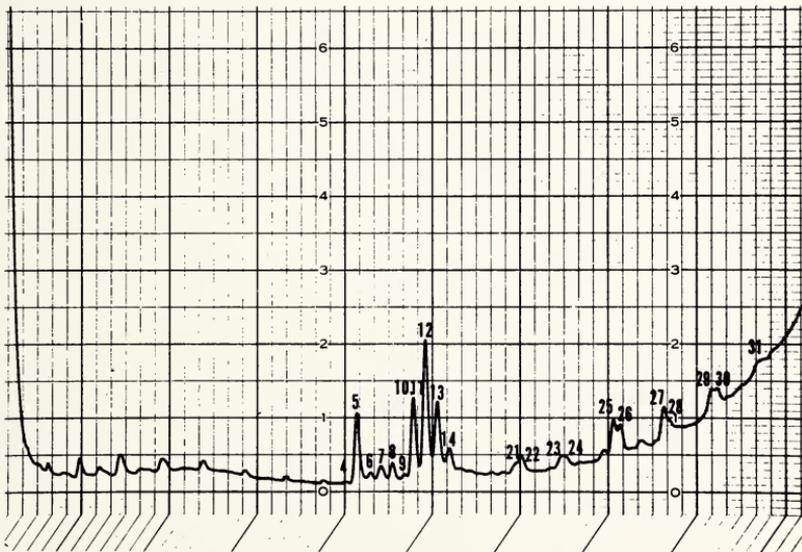


Fig. 4. GC trace of total cuticular hydrocarbons of *Xenistusa hexagonalis*. GC conditions same as for Fig. 1.

termite host is strongly suggestive for their role as integrating factors. It also supports our earlier hypothesis that cuticular hydrocarbons may serve as species recognition cues (Howard et al., 1978; Blomquist et al., 1979; Howard et al., 1980a; Howard et al., 1982). Behavioral evidence for this interpretation comes from the finding (Howard, unpublished observations) that live *T. depressus* placed into laboratory colonies of *R. flavipes* were killed by the termites within a 24-hour period (five observations). Similarly, the placing of live *T. frosti* into laboratory colonies of *R. virginicus* results in their being killed (five observations). Beetles can be freely exchanged among different colonies of their hosts however. These two *Trichopsenius* spp. are nearly identical morphologically and behaviorally, but differ markedly with respect to cuticular hydrocarbons. Similar transplants of workers or soldiers of *R. flavipes* or *R. virginicus* into colonies of the other species also resulted in the death of the alien individual (five observations). Transplants of conspecific termites into different colonies did not produce agonistic interactions (five observations). As with the beetles, the two termite species are morphologically and behaviorally quite similar. We have shown that *R. virginicus* workers are antagonistic towards neutral, critical-point dried (CPD) conspecific workers treated with *R. flavipes* cuticular hydrocarbons (Howard et al., 1982), but are not aggressive toward CPD workers treated with *R. virginicus* cuticular hydrocarbons. While we cannot exclude the possibility of other biochemical differences among either the beetles or their host termites, GC comparisons of total body extracts revealed none.

The termitophiles associated with *R. virginicus* (in common with other termitophiles) possess many epidermal glands (Kistner, 1979) which have often been postulated to be a source of chemicals which in some manner aids in the integration of the beetles into the termite society. While we cannot rule out this interpretation, we would like to suggest an alternative hypothesis for the function of these glandular products. Termitophiles are never found in great abundance (Wilson, 1971; Kistner, 1979), and the nature of termite nest-galley systems is such as to present substantial problems in the location and recognition of conspecifics. Perhaps these glands are producing pheromones directed at conspecifics rather than kairomones directed at their host. Since pheromones are usually produced in extremely

small amounts, such an interpretation would explain the lack of GC evidence to date for beetle derived biochemicals different from those of their termite host. An experimental test of this hypothesis must await the development of suitable bioassays.

Reticulitermes virginicus and its termitophiles have been co-evolving for a long period of time (Kistner, 1968, 1979). The beetles are totally integrated into the social life of the colony and appear to be chemically indistinguishable from the termites (chemical mimicry) vis-à-vis their cuticular hydrocarbons. Most known termite-termitophile associations, however, occur within the family Termitidae (Kistner, 1979). These associations are characterized by termitophiles ranging in status from nonintegrated to totally integrated. If our hypothesis is correct regarding the integrating role of cuticular hydrocarbons then a corresponding spectrum of congruences of hydrocarbon profiles would be predicted among the termitophiles of these communities. We are presently testing this hypothesis.

Many species of ants are known to haveinquilines associated with them, but unlike termitophiles, these myrmecophiles are seldom host specific (Wilson, 1971). In addition, myrmecophiles seem to show a wider range of integration (or lack thereof) than do termitophiles. A correspondingly greater range of integrating mechanisms might therefore be expected, and have been found. These include body color, appeasement substances, trichomes, unicellular epidermal glands, physogastry, exudatoria and grandular antennae. All have been superbly reviewed by Wilson (1971) and Kistner (1979). The most recent addition to this plethora of mechanisms is the finding that the scarab beetle *Myrmecaphodius excavaticollis* (Blanchard) associated with various *Solenopsis* spp. ("fire ants") has a cuticular hydrocarbon composition which closely mimics that of its current ant host (Van der Meer, personal communication in Howard and Blomquist, 1982). The mechanism by which the beetles achieve this is unknown. Each of the four ant hosts that the scarab beetles is found with, however, has a unique hydrocarbon profile. Perhaps ants, like subterranean termites, also use cuticular hydrocarbons as species-recognition cues. Clearly a great deal remains to be learned before we achieve an adequate understanding of the diversity of relationships between social insects and their guests.

Table 1. Cuticular hydrocarbons of *Reticulitermes virginicus*, *Philotermes howardi*, *Trichopsenius depressus* and *Xenitusa hexagonalis*.

GC Peak ¹	Component	Carbon number ²	Diagnostic MS ions ³
1	n-C ₂₁	21	296
2	n-C ₂₂	22	310
3	11-MeC ₂₂	23	168/169, 182/183, 324
4	Z-9-C ₂₃	23:1	322
4	E/Z-6,9-C ₂₃ ⁴	23:2	320
5	n-C ₂₃	23	324
6	11-MeC ₂₃	24	168/169, 196/197, 338
7	2-MeC ₂₃ + 3-MeC ₂₃	24	294/295, 322/323, 338, 280/281, 308/309, 338
8	n-C ₂₄	24	338
9	11-Me + 13-MeC ₂₄	25	168/169, 210/211, 352; 182/183, 196/197, 352
10	2-MeC ₂₄	25	308/309, 336/337, 352
11	E/Z-6,9-C ₂₅	25:2	348
11	Z-9-C ₂₅	25:1	350
12	n-C ₂₅	25	352
13	11-Me + 13-MeC ₂₅	26	168/169, 224/225, 366; 182/183, 210/211, 366
13	Z,Z-7,9-C ₂₅	25:2	348
14	2-Me + 3-MeC ₂₅	26	322/323, 350/351, 366; 308/309, 336/337, 366
15	n-C ₂₆	26	366
16	11-Me + 13-MeC ₂₆	27	168/169, 238/239, 380; 182/183, 210/211, 380

Table 1. Continued

GC Peak ¹	Component	Carbon number ²	Diagnostic MS ions ³
17	2-Me + 3-MeC ₂₆	27	336/337, 364/365, 380; 322/323, 350/351, 380
18	n-C ₂₇	27	380
19	11-Me + 13-MeC ₂₇	28	168/169, 252/253, 394; 182/183, 224/225, 394
20	n-C ₂₈	28	394
21	11-MeC ₂₈	29	168/169, 266/267, 408
22	n-C ₂₉	29	408
23	11-MeC ₂₉	30	168/169, 280/281, 408
	11-Me + 13-Me + 15-MeC ₃₁	32	168/169, 308/309, 450; 182/183, 280/281, 450; 224/225, 252/253, 450
24	11,15-diMeC ₃₁	33	168/169, 238/239, 252/253, 322/323
25	11-Me + 13-MeC ₃₃	34	168/169, 322/323; 182/183, 294/295
26	11,15-diMeC ₃₃	35	168/169, 238/239, 280/281, 350/351
27	11-Me + 13-Me + 15-MeC ₃₅	36	168/169, 350/351; 182/183, 308/309; 224/225, 280/281
28	11,15-diMeC ₃₅	37	168/169, 238/239, 308/309, 378/379
29	11-MeC ₃₇	38	168/169, 378/379
30	11,15-diMeC ₃₇	39	168/169, 238/239, 336/337, 406/407
31	11-MeC ₃₉	40	168/169, 406/407

¹See Figures 1 to 4.²Determined from CI-MS where (M - 1)⁺ is always the base peak.³EI-MS.⁴E/Z-6,9-C₃₃ indicates E/Z-6,9-tricosadiene, where the slash indicates that one double bond is cis (Z) and one is trans (E), but which is which, is unknown. The diene in peak 11 is named correspondingly.

SUMMARY

The three highly integrated staphylinid termitophiles (*Philotermes howardi* Kistner and Gut, *Trichopensius depressus* Le Conte, and *Xenistusa hexagonalis* Seevers) associated with *Reticulitermes virginicus* (Banks), possess the same cuticular hydrocarbons as their host. This congruence is hypothesized to be a form of chemical mimicry and is postulated to function as a major way these beetles achieve integration into the termite society.

ACKNOWLEDGEMENT

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PARATARUMA, A NEW GENUS OF NEOTROPICAL
CRABRONINI (HYMENOPTERA, SPHECIDAE)*

BY LYNN S. KIMSEY

Department of Entomology,
University of California, Davis, CA, 95616, USA

Crabronini are a diverse group of wasps that are found world wide. Typical members of this tribe can be recognized by the single forewing submarginal cell, large cuboidal head and ventrally converging eyes.

The new genus, *Parataruma*, is found in lowland neotropical forest in widely separated localities. This distribution can probably be explained in several ways. Most of the neotropical lowland forest has been poorly collected, and much of it has been destroyed. In addition, these wasps are small and darkly colored, making them difficult to observe.

Specimens were obtained from the following institutions: British Museum of Natural History, London (BMNH); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Entomology Museum, University of California, Davis (UCD), and the U.S. National Museum, Washington, D.C. (USNM).

***Parataruma* Kimsey, new genus**

Generic diagnosis

Head (figs. 3, 4): Eyes asetose, inner orbits converging strongly below; scapal basin smooth or finely sculptured, laterally margined by carinae; genal carina well-developed, following ocular margin to vertex; orbital foveae absent; occipital carina well-developed, flanged and foveate; antennal sockets touching each other and ocular margin; male flagellomeres II–III modified; palpal formula 6:4; mandibles with a tooth on inner margin and single apical notch; ocelli large, 1.5 times as wide as antennal sockets, forming an isolateral triangle.

Thorax (fig. 1): Pronotal collar with transverse anterior and posterior carinae, sharply angulate laterally; scutum longitudinally

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ridged without anterior transverse carina; notauli indicated by carinae; admedian lines absent; scutellum with deep prescutellar sulcus; metanotum simple; postspiracular carina well developed; omalus well-developed, continuous with acetabular carina; verticaulus short, ending in a ventral depression; hypersternaulus and mesosternaulus absent; forewing recurrent vein joining submarginal cell almost medially; jugal lobe subequal in length to submedial cell; legs simple; propodeum finely sculptured, dorsal enclosure limited by foveate sulcus, lateral propodeal carina present.

Abdomen: Sessile; female pygidium forming a sharp, straight medial ridge, with deep submedial notch, terminating in a sharp process, surrounded by stout setae (figs. 7-9).

Genotype: *Parataruma leclercqi* Kimsey, original designation.

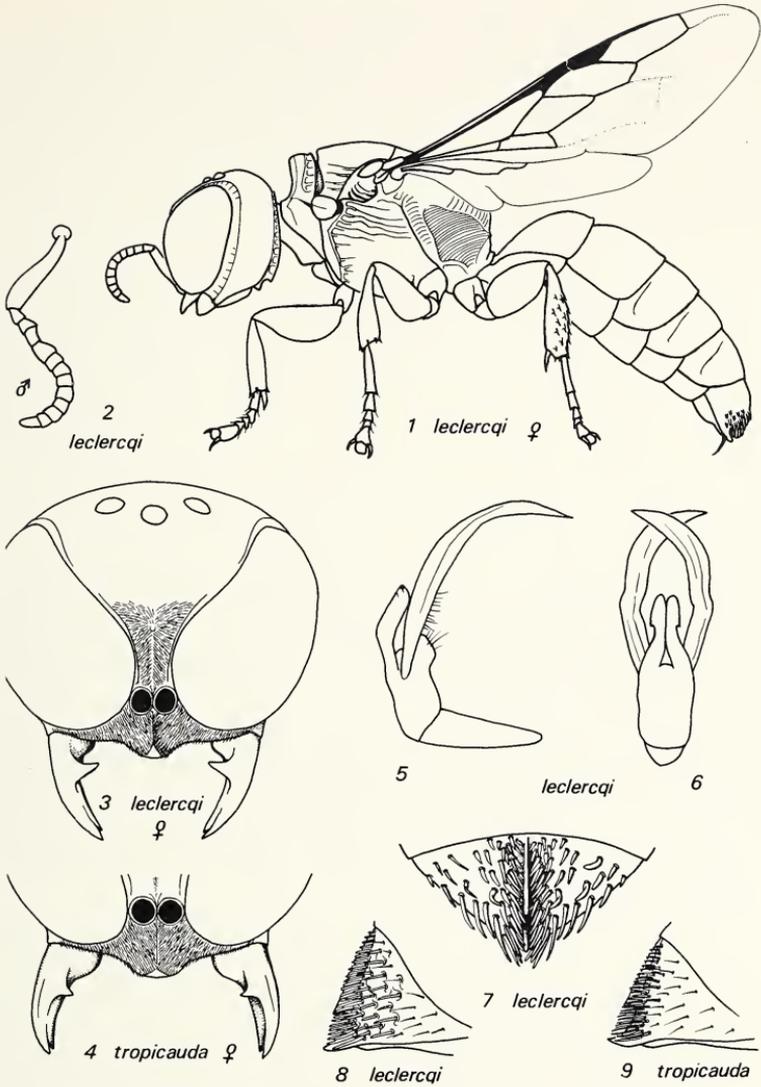
Discussion.

Parataruma most closely resembles *Foxita* and *Taruma*, based on the carinate scapal basin, wing venation, narrow female pygidium, apically notched mandible and absence of the sternaulus. In fact, this genus will key out to *Taruma* in Bohart and Menke (1976:374). However, several characteristics of *Parataruma* are unusual and immediately distinguish members of this genus from all other crabronines, including *Foxita* and *Taruma*. These characteristics are the well-developed genal and scapal carinae, the lack of any transverse carinae on the face and the peculiar female pygidium, which has been reduced to a narrow convex ridge and pointed apical projection surrounded by papillae-like setae.

***Parataruma leclercqi* Kimsey, new species**

Figures 1-3, 5-8

Holotype female: Length 5 mm; head finely and densely punctate, except along occipital and genal carinae; face with bulging brow, scapal basin punctation obscured by pubescence; clypeal margin medially produced into a rounded lobe subtended beneath by a tuft of setae on either side; flagellomeres I-II 1.3 times as long as wide; flagellomere III as long as wide; flagellomeres IV-IX wider than long; flagellomere X 1.5 times as long as wide; mandible with tooth on inner margin longer than diameter of antennal socket (fig. 3); pronotum foveate along anterior and posterior carinae; scutum finely punctate-striate with medial and lateral carinae and raised



Figs. 1-3, 5-8 *Parataruma leclercqi*. Figs. 4, 9. *Parataruma tropicauda*. Fig. 1. Lateral view of female. Fig. 2. Male antenna. Figs. 3-4. Complete and partial front view of female face. Figs. 5-6. Lateral and dorsal views of male genital capsule. Figs. 7-9. Female pygidium, dorsal (7) and lateral (8, 9) views.

notauli; scutellum punctate-striate with anterior margin foveate, posterior margin with 13 evenly spaced ridges; mesopleuron with fine punctures, 1–2 puncture diameters apart, upper half with 9 longitudinal ridges; hypoepimeron ridged; propodeum finely striate laterally, enclosure with deep medial groove, foveate above, punctate-striate medially, transversely ridged and foveate below; terga I–V densely and finely punctate, punctures 0.5 puncture diameter apart or less; tergum VI with large, contiguous, almost foveate punctures; pygidial ridge sharp, abruptly notched submedially, terminating in a sharp apical projection, nearly obscured by dense papillae-like setae (figs. 7, 8); sternum I integument rough, irregular; sternum II punctures about 1 puncture diameter apart laterally, almost impunctate medially, sterna III–V impunctate, except transverse subapical punctate strip; sternum VI triangular, basal half impunctate, apical half densely punctate. Body black, except yellow scape, flagellum beneath, medial mandibular spot, pronotal lobe and sublateral dorsal spots, scutellum laterally, metanotum medially, T–II lateral spot, apices of fore and mid-femora, most of tibiae and tarsi. Pubescence sparse and pale, except dense silvery appressed pubescence on clypeus, scapal basin and gena on both sides of carina.

Male: Length 4.5 to 5.5 mm; same as female, except F–I slightly wider than long; flagellomere II slightly longer than wide, deeply indented beneath; flagellomere III about as long as wide (fig. 2); scutum with longitudinal ridges, densely punctate; sterna closely punctate, punctures 1 puncture diameter apart or less. Male genitalia as in figs. 5–6.

Holotype female: Barro Colorado Island, Zona del Canal, Panama, August 30, 1978, R.B. and L.S. Kimsey (USNM). Paratypes, 13 females: same data as type, except July 17, 1976 (UCD), September 12, 1978 (UCD) and C. and M. Rettenmeyer, April 20, 1963 (UCD); Costa Rica, Turrialba (MCZ, USNM); Colombia, Magdalena, 10–15 km e Santa Marta, November 26, 1974, M. Cooper (BMNH); Venezuela, Zulia, Rosario, June 14, 1976, A.S. Menke and D. Vincent (USNM); Trinidad: St. George, St. Augustine, June and August 1976, F.D. Bennett and J.S. Noyes (BMNH); St. Andrew, Oropuche, June 28, 1976, J.S. Noyes (BMNH). Two males, which I am not designating as paratypes, were from: Brazil, São Paulo, Ribeirao Preto, January 7, 1968. G.E. Bohart (UCD);

and Mexico, Oaxaca, Oaxaca, April 22, 1959, H.E. Evans (UCD).

The diagnostic features of this species are the yellow female antennae; yellow spots on the mandibles, metanotum and tergum II; extensive silvery appressed setae on the scapal basin, gena and mesopleuron; large tooth on the inner margin of the mandibles and the dense setae obscuring the pygidial ridge. In addition *leclercqi* tends to be slightly larger than *tropicauda*, 5–7 mm versus 4.5–5.0 mm for *tropicauda*.

I have named this species after Jean Leclercq for two reasons: first, to acknowledge the tremendous amount of work he has done on the Crabronini. Second, and most important, because he sent me 10 specimens of this genus to describe even though he recognized them as new.

***Parataruma tropicauda* Kimsey, new species**

Figures 4 and 9

Holotype female: Only diagnostic characteristics are listed below. Length 5 mm; scapal basin coarsely and irregularly punctate; mesopleuron with 5 or more longitudinal ridges, polished with sparse punctures; mandible with tooth on inner margin shorter than diameter of antennal socket. Body black, with yellow on: underside of scape; pronotal lobes, two pronotal dorsal spots; scutellum lateral spots; fore and midfemora apically; tibiae apically, basally and inner surfaces; tarsi. Pubescence sparse and pale, except silvery appressed setae on clypeus and ocular side of genal carina.

Holotype female: 10–15 km e Santa Marta, Magdalena, Colombia, November 26, 1974, M. Cooper (BMNH). Paratype female: same data as type (BMNH).

This species can be distinguished from *leclercqi* by the lack of yellow markings on the mandibles and metanotum, half black scape and dark flagellum; the sparse or absent silvery pubescence on the scapal basin and mesopleuron and sparse setae surrounding the pygidial ridge.

The species name *tropicauda*, “ridge-tail”, refers to the peculiar pygidial ridge of the female.

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SUPPLEMENTARY STUDIES ON ANT LARVAE: FORMICINAE (HYMENOPTERA: FORMICIDAE)¹

BY GEORGE C. WHEELER² AND JEANETTE WHEELER²

Introduction

This article describes formicine larvae received since the preparation of our most recent supplement (1980). The larva of *Proformica* has not been previously described. Also included are references to formicine larvae in the literature and a discussion of the status of *Colobopsis*.

The terms describing body profile and mandible shape are explained in our 1976 monograph. Our own contributions are cited by year and page only.

TRIBE 4. FORMICINI

Genus ACANTHOMYOPS Mayr

The larvae are very active and can quickly change their posture from circular to linear or reverse.

Genus FORMICA Linnaeus

Alpert and Ritcher 1975:289. Adults of the scarabaeid beetle *Cremastochilus armatus* feed on larvae of *Formica fusca* and *Formica obscuripes*.

Genus LASIUS Mayr

Lasius sitkaensis Pergande

Akre and Hill 1973. The pselaphid beetle *Adranes taylori* Wickham possesses trichomes (tufts of golden hairs) on the abdomen, tips of elytra and venter. These trichomes are highly attractive to half-grown or smaller ant larvae, less so to larger larvae and workers. The beetles are fed by the larvae through trophallaxis and obtain other nutrients by feeding on dead larvae and workers. Beetles are often seen walking about with larvae actively holding on to the trichomes with their mouthparts; Fig. 4 (p. 531) shows a larva so attached.

¹Manuscript received by editor June 10, 1982.

²Adjunct Research Associates, Desert Research Institute, Reno, NV; present address: 326 Laurel Ridge Road, San Antonio, TX 78253.

Genus MYRMECOCYSTUS Wesmael

Snelling (1976:22) quoted our characterization (1968:211) of the genus and compared the larvae of this genus with those of *Lasius*. Page 23: "I provided some erroneous identifications to the Wheelers. These may be corrected: '*lugubris*'=*creightoni*; '*mojave*'=*testaceus*; '*semirufus*'=*kennedyi* (Calif.) and *depilis* (Ariz.)"

Page 7: "These data, albeit fragmentary, seem to indicate that protein, such as that derived from the tissues of other insects is essential for larval development." Page 6: "The insect fragments are placed among the larvae and these must fend for themselves. I have seen no indication that larvae of these species are fed by trophallaxis."

Page 8: Larvae are subject to desiccation; hence they are to be found in the upper chambers of the nest only in the evening and early morning. When the surface begins to warm up the brood is removed to deeper chambers.

Genus PROFORMICA Ruzsky

Profile pogonomymecoid. Integument of venter of anterior body somites and of portions of labium, maxilla and labrum papillose. Body hairs mostly with bifid tip. Antenna large. Head hairs few, with 2- or 3-branched tip. Labrum large and subrectangular. Mandible ectatommoid, with one medial tooth.

The specialization index is 18.

Proformica ferreri Bondroit

Length (through spiracles) about 3.7 mm. Profile pogonomymecoid (i.e., diameter greatest near middle of abdomen, decreasing gradually toward anterior end and more rapidly toward posterior end, which is rounded; thorax more slender than abdomen and forming a neck, which is curved ventrally). Anus posteroventral and with a small posterior lip. Leg, wing and gonopod vestiges present. Spiracles small and decreasing in diameter posteriorly. Integument of venter of anterior somites papillose; dorsal surface of posterior somites sparsely spinulose, the spinules minute and in short to long transverse rows. Body hairs sparse, moderately long (0.024-0.07 mm), with simple, bifid or multifid tip. Cranium suboctagonal, slightly broader than long. Antenna large, with 3 (or 2) sensilla, each bearing a spinule. Head hairs few, short (0.013-0.04 mm long), unbranched or with bifid tip. Labrum large, subrectangular, slightly

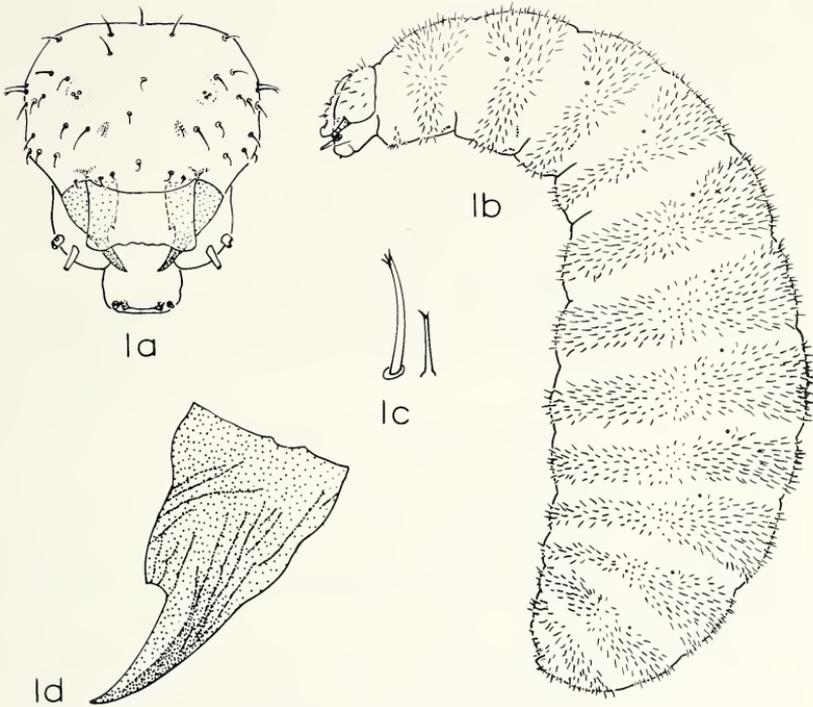


Figure 1. *Proformica ferrari*. a, Head in anterior view, X100; b, larva in side view, X33; c, two body hairs, X320; d, left mandible in anterior view, X320.

broader than long, with ventral border erose; anterior surface with 12 sensilla; with minute papillae near ventral border; ventral surface papillose and with 6 sensilla; posterior surface densely spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with about 6 sensilla. Mandible large; ectatomoid (i.e., subtriangular; with a medial blade arising from the anterior surface and bearing a small medial tooth; apex curved medially to form a tooth); anterior and posterior surfaces with longitudinal rugae. Maxilla rather large; with paraboloidal apex; integument papillose, the papillae bearing minute spinules; palp a short rounded knob bearing 5 (1 encapsulated and 4 bearing a spinule each) sensilla; galea digitiform with 2 apical sensilla. Labium prominent; integument papillose; with a dorsal transverse welt bearing minute spinules in transverse rows; palp a low knob with 5

(1 encapsulated and 4 bearing a spinule each) sensilla; an isolated sensillum medial to each palp; opening of sericteries wide and with a sclerotized projection at each side. Hypopharynx with minute spinules in transverse rows. (Masterial studied: 16 larvae from Huesca, Spain, courtesy of X. Espadaler.)

TRIBE 7. OECOPHYLLINI

Genus OECOPHYLLA F. Smith

Hinton 1951:169. The larvae of *Wurthia aurivillii* Kemner and *W. myrmecophila* Roepke (Pyrallididae) feed on the brood of ants of this genus.

TRIBE 9. PLAGIOLEPIDINI

Genus ACANTHOLEPIS Mayr

Acantholepis frauenfeldi Mayr

Tohmé and Tohmé 1975: 136-138. "Les 5 stades larvaires sont identifiés grâce à leur forme, leur dimension et surtout leurs poils." Fig. 3 (p. 136).

TRIBE 10. BRACHYMYRMECINI

Genus BRACHYMYRMEX Mayr

Brachymyrmex admotus Mayr

Length (through spiracles) about 1.6 mm. Very similar to *Brachymyrmex depilis* (1953:139) except in the following details. Type 2 body hairs twice as long (0.15 mm). Head hairs 2- or 3-branched: 0.038-0.075 mm long. Mandible with apical tooth slightly more curved medially. Palp and galea subequal in height; galea more slender. Labial palp taller. (Material studied: 6 larvae from Costa Rica, courtesy of Jack Longino.)

TRIBE 12. CAMPONOTINI

When we defined "praesaepium" (1953:180) we had overlooked the first description (without a name) of the structure by W. M. Wheeler and Bailey (1920:270-271): — "In a study undertaken by the senior author and Mr. George C. Wheeler of the larvae of a large number of other ant genera, no structure comparable to the Pseudomyrmine trophothylax has been found, except in certain species

of *Camponotus* of the subgenus *Colobopsis*. In all the species of the latter subgenus examined the larva is very hypocephalic and the ventral portion of the first abdominal segment projects considerably beyond the thoracic segments and presents a pronounced concavity or basin in the mid-ventral region precisely in the position of the trophothylax of the *Pseudomyrminae*. A feeble vestige occurs in many *Camponotus* larvae belonging to other subgenera. No solid pellet is deposited in the basin of *Colobopsis*, but it may, perhaps, be used to hold a supply of the liquid food regurgitated by the workers or of the saliva secreted by the larva itself for the benefit of its attendants." We later found pellets in the praesaepium of *Colobopsis* (1970:650).

Genus CAMPONOTUS Mayr

Camponotus rasilis W. M. Wheeler

Petralia and Vinson 1979. Venter—description and SEM.

Genus COLOBOPSIS Mayr

Colobopsis was established by Mayr in 1861 as a genus. In 1889 Emery "reduced it to a subgenus under *Camponotus*, owing to the existence of forms intermediate between these two groups and the relatively unimportant distinguishing characters of *Colobopsis*" (W. M. Wheeler 1904:139). And there it has remained through W. M. Wheeler's "Key to the Genera and Subgenera of Ants" (1922), Emery's "Genera Insectorum" (1925), Creighton's "The Ants of North America" (1950). Brown (1973:179) did not employ subgenera; so he had to synonymize it with *Camponotus* or raise it to generic rank; he chose the former.

However, we have noticed of late a tendency among myrmecologists to elevate *Colobopsis* to generic rank (e.g., Snelling 1981:404). Although we have some doubts about adult characters, we can certainly support the elevation by larval characters. In 1953:181 we wrote: "The genera of this tribe are so similar that we cannot distinguish them; hence we have not attempted to key them. *Colobopsis* is, however, exceptional; differences of generic magnitude separate it not only from the other subgenera of *Camponotus* but also from the other genera of Camponotini."

Tribe Camponotini

1. Posterior $\frac{1}{2}$ of venter of AII raised to form transverse welt, and, on either side ridges from the welt extend forward
2. Body hairs numerous
3. Body hairs of 5 types: (1) 2- to 6-branched; branches all in same plane, the most numerous type; (2) simple, short, slightly curved; (3) few, simple, long and whip-like; (4) few, denticulate (5) few, uncinata
4. Antenna small
5. Head hairs numerous, long

Colobopsis

1. Praesaepium formed from ventral surface of TIII and AI: anterior border of AII forms ventral wall; no side walls
2. Body hairs sparse
3. Body hairs of 3 types: mostly (1) simple or (2) bifid; few (3) very long and whip-like; none uncinata.
4. Antenna minute, peg-like
5. Head hairs moderately numerous, short

Colobopsis pylartes W. M. Wheeler
Petralia and Vinson 1979. Venter—description and SEM.

Genus POLYRACHIS F. Smith

Hinton 1951:169. The larvae of *Wurthia aurivillii* Kemner and *W. myrmecophila* Roepke (Pyralidae) feed on the brood of ants in this genus.

Polyrhachis dives F. Smith

Hinton 1951: 167. The larvae of *Batrachedra myrmecophila* Snell. (Cosmopterygidae) feed on the brood of this ant.

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MORPHOLOGICAL COMPARISONS BETWEEN THE
OBLIGATE SOCIAL PARASITE, *VESPULA AUSTRIACA*
(PANZER), AND ITS HOST, *VESPULA ACADICA* (SLADEN)
(HYMENOPTERA: VESPIDAE)¹

BY

HAL C. REED AND ROGER D. AKRE²

Department of Entomology
Washington State University
Pullman, WA 99164

INTRODUCTION

Obligate social parasites (inquilines) show a vast array of behavioral and morphological adaptations to their unique mode of life (Wilson 1971). The hazards of colony invasion, usurpation, and subsequent subjugation of members of the host colony (queen and/or workers) require special features in order to overcome colony defenses and to become integrated within the host's society. Not only do these species have adaptations for colony takeover, but they also lack certain social characteristics, the most notable being the absence of a worker caste.

Such traits are exemplified in the workerless ant inquiline, *Tel-eutomymex schneideri* Kutter, that has enlarged tarsal claws and a gaster with a concave venter which enables this parasite to ride on the dorsum of its host (Wilson 1971). Among the parasitic bumble bees (*Psithyrus* spp.) a number of characteristics, such as strong development of the sting and exoskeleton, are adapted for successful colony takeover, while other social traits, such as a pollen-collecting apparatus on the hind leg, are lacking (Alford 1975). Similarly, vespine inquilines are distinct from their hosts in possessing stronger exoskeletons, a closer fitting of their abdominal segments, stouter and more recurved stings, broader heads, more powerfully built mandibles, and sharp bidentate clypei (Weyrauch

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²Research Assistant and Entomologist, respectively, Department of Entomology, Washington State University, Pullman 99164.

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1937, Beaumont 1958). These traits are presumed to function in preventing sting penetration by host defenders and in facilitating stinging or injuring the hosts.

Investigators have noted these unique traits primarily among the European vespine inquilines and their hosts (Beaumont 1958, Bischoff 1931, Carpenter and Pack-Beresford 1903, Eck 1979, Robson 1898, and Weyrauch 1937). One of these inquilines, *Vespula austriaca* (Panzer), has only recently been found in colonies of a Nearctic species [*V. acadica* (Sladen) Reed et al. 1979] and behavioral interactions with members of the host colony have been documented (Reed 1982). Although researchers have discussed the external morphology of *V. austriaca* in relation to the European host, *V. rufa* (L.), no comparisons have been made between the Nearctic host and *V. austriaca*. Consequently, the objectives of this paper are: (1) a morphometric comparison between the *V. acadica* queen and the parasite; (2) descriptions of certain external features such as the stings, mandibles, femora, and abdominal sclerites; and (3) a survey of exocrine glands of the two species.

MATERIALS AND METHODS

Seven external body parts were measured in pinned specimens of the host queen and parasite using a dissecting microscope equipped with an ocular micrometer. These characters have been commonly used in other biometrical studies of vespid wasps (Blackith 1958, Eck 1979, Eickwort 1969). Specimens were obtained from local collecting sites (Reed 1982) and from several North American entomological museums (Acknowledgements). Measurements of the interocular distance, mesonotal length, hind tibial length, and forewing length followed the description and diagrams of Eck (1979). Also, the length of the front femur was measured from the base to the apex in the same manner as the hind tibial length, while the width was taken at its widest point. Head width was measured in dorsal aspect, behind the eyes along the vertex, and between the upper edges of the genae. The mesonotal length was measured along the midline from the anterior prescutal suture to the posterior transcutal suture. The length and midline width of the first gastral tergum were also determined in dorsal view.

Scanning electron micrographs (SEM) of the sting apparatus of the host and three parasite species were prepared. Dissected stings were

dehydrated in 100% ethanol, critical point dried, and then coated with gold. Photographs of femora and Dufour's glands, which had been preserved in ethanol, were taken using conventional macro-photographic techniques.

Exocrine glands and certain other internal features (e.g., ovaries, ganglia) were examined in specimens preserved for dissection by injecting Kahle's solution under an anterior abdominal tergum until the gaster swelled. Specimens were subsequently stored in 70% ethanol. Seven *V. acadica* queens and 19 *V. austriaca* females were examined to establish the occurrence and size of the 14 known vespine glands (Landolt and Akre 1979). Dissections were conducted using a binocular dissecting microscope equipped with an ocular micrometer. Gland size and condition were compared with previous measurements (Landolt and Akre 1979). In a few cases, exocrine glands were inspected in freshly killed specimens. Abdominal plates, mandibular features, and front femora were also studied in the preserved specimens.

RESULTS

The morphometric analysis of selected characters revealed that although both species are very similar in terms of overall body size (i.e., as indicated by the width of the mesonotum and gastral tergum I), certain body parts of *V. austriaca* are significantly larger than those of the host (Table 1). The head and interocular distance of the parasite is slightly wider than that of *V. acadica*. The mesonotum of the two species are comparable with only the mesonotal length being significantly larger in the parasite. Also, the length of the hind tibia and the forewing are longer than the corresponding parts in the host, although forewing length is extremely variable in both species. The first gastral tergum, like the mesonotum, only differs significantly in its length.

One of the more unique morphological differences is the larger front femora of *V. austriaca* (Fig. 1). This femur is consistently wider and longer in the parasite females than in host queens. Furthermore, the femur is quite robust in the parasite, while it is slender and more concave on the inner side in *V. acadica*.

Table 1. Measurements of seven external body parts of *V. acadica* queens (N = 57) and *V. austriaca* females (N = 44).

Body part	Mean and standard deviation (mm)	
	<i>V. austriaca</i>	<i>V. acadica</i>
Head width**	4.31 ± 0.14	4.09 ± 0.09
Interocular distance**	1.90 ± 0.08	1.78 ± 0.06
Mesonotum		
width	4.91 ± 0.19	4.86 ± 0.19
length**	3.80 ± 0.17	3.67 ± 0.19
Hind tibia		
length**	3.91 ± 0.16	3.45 ± 0.16
Forewing		
length**	13.6 ± 0.50	13.0 ± 0.56
Gastral tergum I		
width	4.48 ± 0.20	4.39 ± 0.19
length**	1.70 ± 0.11	1.41 ± 0.11
Front femur		
width**	0.89 ± 0.07	0.81 ± 0.06
length**	3.16 ± 0.10	2.78 ± 0.10

**Means are significantly different using the t test at 0.01 level of significance.

The mandibles of both species are roughly triangular when viewing the mesal (inner) face. The dimensions of the three sides are approximately the same in each species; however, the mandible of the parasite is more robust, especially at its base. This stoutness is apparent when viewing the ventral edge of the mandible. The ventro-basal area is distinctly wider in *V. austriaca*, and the mesal face lacks the concavity that is typical of the mandibles of the host queen. The mandibles of both species have three primary or marginal teeth along the truncated, cutting margin with two alternating, secondary teeth and a molar shelf behind the margin as is characteristic of vespines (Duncan 1979). Most yellowjackets (including *V. acadica*) also have a rounded projection immediately beyond the notch on the cutting margin (see Fig. 6 in Landolt and Akre 1979, Duncan 1939); however, this projection in *V. austriaca* is pointed and more tooth-like. Thus, the parasite actually has a fourth marginal tooth near the dorsal edge.

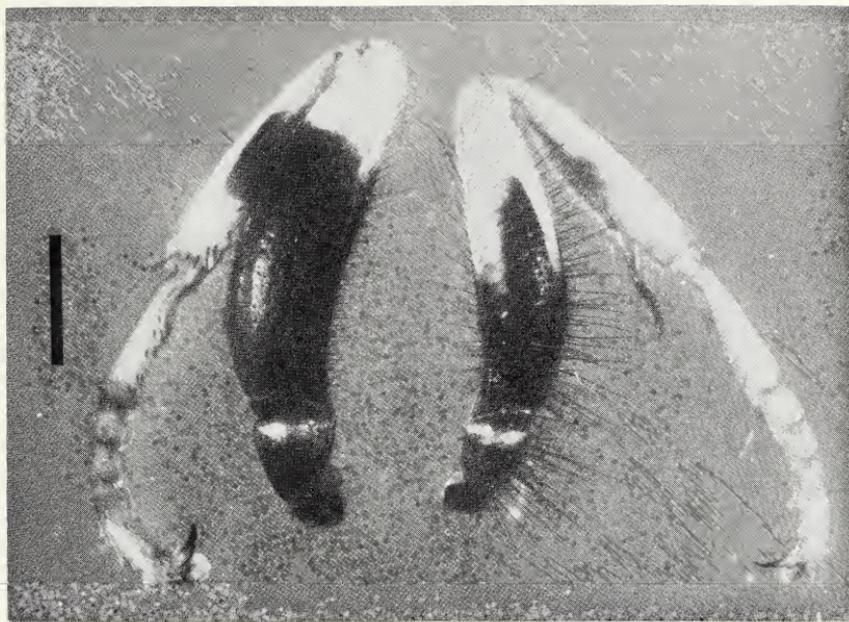


Figure 1. Front legs of a *V. austriaca* parasite (left) and *V. acadica* queen (right). The femur of the parasite is thicker and longer than that of the host queen. The black line indicates 1 mm.

The terga and sterna of the gaster of the parasite are more difficult to dissect apart than those of the host. This "tough armature" is often mentioned in regard to vespine parasites. The gastral sclerites appear to overlap very tightly which undoubtedly prevents sting penetration during usurpation attempts. However, the close fitting of the abdominal segments does not appear to be due to a reduction of intersegmental membranes or because of more sclerotization. Instead, *V. austriaca* has better developed muscles (i.e., larger bundles) in the abdominal sterna and terga than are present in the same segments of a *V. acadica* queen. For example, the three pairs of intersternal retractors (Duncan 1939) of a fat-laden, fall parasite are about 1.5 times as wide as these same muscles in a fall *V. acadica* queen. Consequently, this parasite should be able to retract the gastral sclerites more tightly than a host queen.

The stout, recurved sting of vespine parasites is one of the most important morphological adaptation to their mode of life. The two North American vespine inquilines, *V. austriaca* and *Dolichoves-*

pula arctica (Rohwer), have large and highly curved sting shafts in comparison with those of nonparasitic queens such as *V. acadica* (Fig. 2). However, a facultative social parasite, *V. squamosa* (Drury), does not have a recurved sting shaft, but has a large abrupt curve at the distal end (Fig. 2E). *V. austriaca* and *D. arctica* stylets have a similar configuration, except only the extreme tip of the stylet is abruptly hooked (Fig. 2C). However, this condition is entirely lacking in the *V. acadica* queen (Fig. 2D). Both parasite and host have barbs on the sting lancets.

In conjunction with the curved sting, the distal tip of the seventh abdominal sternum of *V. austriaca* turns down more sharply than does the same sternum of the *V. acadica* queen. In addition, this sternum has prominent lateral carinae on the ectal surface, whereas, this ridge is less developed in the host queen. The seventh sternum in *V. austriaca* is a *ca* 0.40 mm longer along the midline than that of *V. acadica*.

The exocrine glands of four late summer and two spring foundresses, and one fall *V. acadica* queen were examined and measured. Thirteen of the 14 known glands in *Vespula* were present, and their size and development fell within the ranges reported by Landolt and Akre (1979). The endostipal gland was lacking. In contrast, only 12 glands were located in two aged and 17 pre usurpation, summer parasites since the sixth sternal and endostipal glands were absent. The head glands, except for the hypopharyngeal, were comparable in size to those of *V. acadica* and other vespines (Landolt and Akre 1979). The two distinct clusters of cells of the hypopharyngeal gland were nearly in contact with each other in the center of the suboral plate of the labrum-epipharynx (see Fig. 5, Landolt and Akre 1979). The clusters were on the average larger than those in *V. acadica*, but were usually within the size range found in *V. pensylvanica* (Sausure) ($0.03 - 0.8 \text{ mm}^3$). However, two parasites had clusters about 0.12 mm^3 . The thoracic or salivary glands were also present in *V. austriaca* and were similar in size to those in nonparasitic queens.

Although the seventh sternal gland, eighth tergal gland, and poison gland reservoir are similar in size and development to those of other vespines, evident differences exist between the two species in the other gastral glands. The sixth sternal gland and the associated sternal brush (i.e., tuft of hairs) are absent in *V. austriaca*. This gland (but not the brush) is present in *V. acadica*, other members of

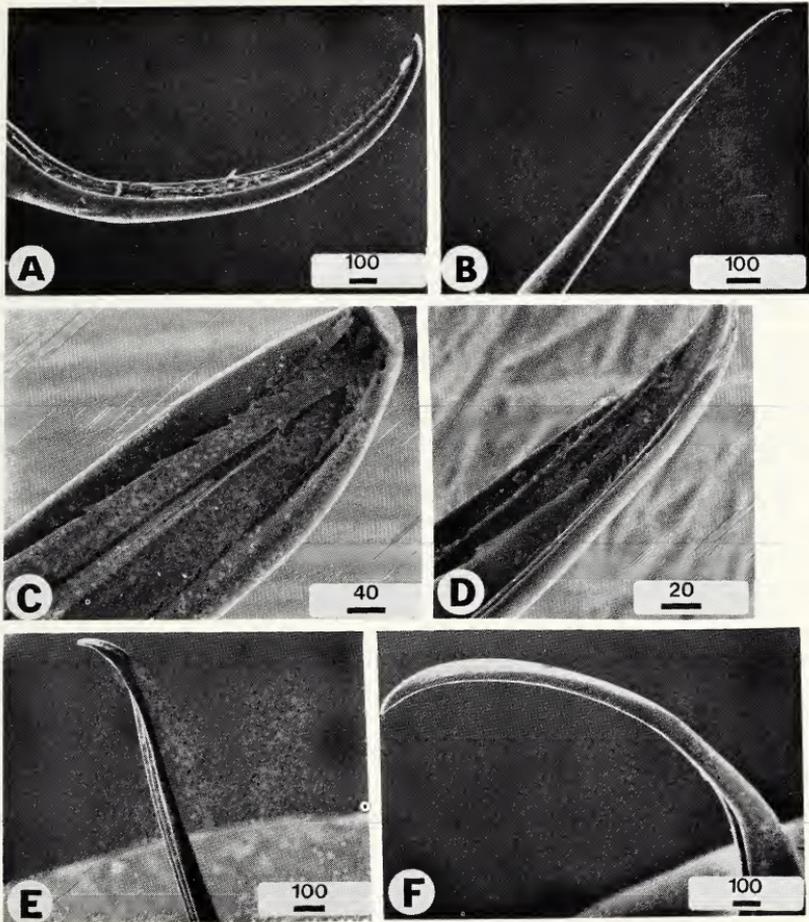


Figure 2. The sting shaft of three social parasites and one host species (*V. acadica*). The sting shaft of *V. austriaca* is larger and curved (A) as compared to the smaller, straight shaft of the host queen (B). In *V. austriaca* the distal tip of the stylet is distinctly curved (C, upper right) unlike the distal end of the stylet in *V. acadica* (D). The facultative, social parasite, *V. squamosa*, does not have a curved sting shaft, but it is sharply bent at the distal end (E). The other Nearctic inquiline, *D. arctica*, also has a recurved sting (F). The measurements are given in microns.

the *V. rufa* species group, and *V. squamosa*, but is absent in queens of *Dolichovespula* and the *V. vulgaris* group (Landolt and Akre 1979). The seventh sternal gland and associated brush are present and well developed in both species. The Dufour's gland of *V. austriaca* is considerably larger than in most other yellowjacket queens (Fig. 3) and averaged 5.8 mm long (range = 4.8 - 7.5 mm, N = 15) and 0.5 to 0.8 mm wide. In contrast, this gland was less developed in *V. acadica* (\bar{x} = 2.1 mm long, 0.3 - 0.5 mm wide) and other nonparasitic queens (Landolt and Akre 1979, 1.5 - 2.5 mm long). The same gland was found to be enlarged in the facultative social parasite *V. squamosa*, as it was ca. 0.2 mm wide and 6 mm long (Landolt and Akre 1979). However, the most well developed Dufour's gland is found in the other Nearctic vespine inquiline, *D. arctica*. One *D. arctica* female had a Dufour's gland 14 mm long and 0.3 mm wide (Landolt and Akre 1979) and in two parasites dissected by Jeanne (1977) this gland was 12.8 mm and 27.2 mm long. In this study three, early summer, *D. arctica* parasites were found to have very long glands (16.5, 20.0, 20.5 mm) greatly folded around themselves and the alimentary canal. In these three parasites and 16 other preurpation individuals the gland was flattened and did not contain any material in the lumen. In contrast, the gland was fully distended and filled with an oily substance in summer, preurpation *V. austriaca*. It was empty and flattened in new fall parasites, while in the aged parasites the gland was only partially full and appeared collapsed. The gland contained a yellow oily substance in preserved specimens, but instead had a clear, oil-like material in three *V. austriaca* specimens killed and immediately dissected.

The ovaries consist of 12 ovarioles as do most *Vespula* and *Dolichovespula* (Kugler et al. 1976). The ovaries did not fill the entire gaster in the two aged parasites as they did in later summer foundresses of *V. acadica*. Preurpation parasites and early summer host queens had a slight ovarian development with 1 to 6 eggs greater than 1.0 mm in length and thus probably ready to be laid. Both species have six gastral ganglia.

DISCUSSION

This study confirms the results of a previous morphometric analysis of *V. austriaca* (Eck 1979). Eck (1979) compared the inquiline with the European host, *V. rufa*, and found that although both were

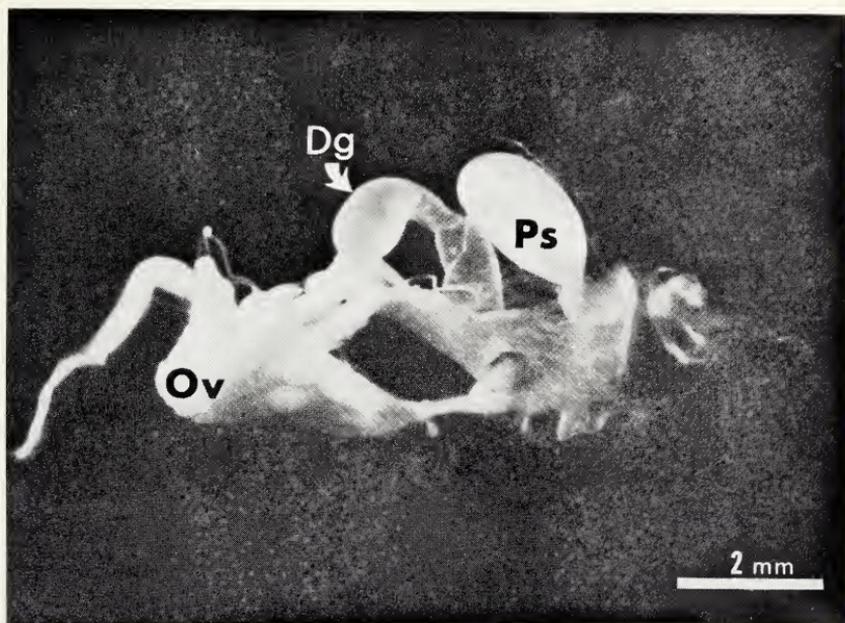


Figure 3. Reproductive organs of a pre-ovipositional *V. austriaca*. The Dufour's gland (Dg) is filled with a clear oil material and was 6.5 mm long when fully extended. Ov = ovaries, Ps = poison sac or poison gland reservoir.

nearly equal in overall body size, *V. austriaca* had a wider head and interocular distance, longer hind tibia, and longer forewing.

Some researchers (Beaumont 1958, Bischoff 1931, Weyrauch 1937) stressed the robust mandible of *V. austriaca*, while others (Bequaert 1916, Carpenter and Pack-Beresford 1903, Robson 1898) found only minor differences in size and did not consider the mandible of *V. austriaca* to be significantly larger. The mandible of *V. austriaca* is definitely robust as it is wider at the base than that of the host. Weyrauch (1937) discussed and diagrammed the robust nature of the mandible of the parasite *Pseudovespula ingriva* (Birula [= *D. ingriva* (Birula)]). He stated that the mandible of the inquiline was less triangular in shape than that of the host queen; a comparison that was not evident in this study. Weyrauch (1937) also illustrated the relatively pointed fourth marginal tooth in *P. ingriva*. The wider head and genae of *V. austriaca* and other vespine inquilines (Bischoff 1931, Weyrauch 1937) undoubtedly house larger mandibular muscles. These muscles in conjunction with the stout mandibles,

make these appendages a formidable, offensive weapon, probably as effective as the sting during colony invasions (Reed 1982). Indeed, Weyrauch (1937) concluded that the powerful mandibles of vespine inquilines were adapted for fighting with the host.

Another adaptation for combat with host queens and defending workers is the enlarged femora of the front legs. The only reference to this feature is found in the original description of *Vespa arborea* Smith (= *V. austriaca*) (cited in Robson 1898) in which he stated that the legs of this species were "stouter and longer" than in *V. rufa*. The robust front legs are not only an advantage during colony invasion, but also are likely an adaptation for the frequent mauling and grabbing of host workers which occurs during early occupation of the colony (Reed 1982).

The sting is greatly curved in vespine inquilines presumably to facilitate penetration between the vulnerable intersegmental membranes of defending colony members. The sharp downward bend of the seventh sternum, likely an accommodation for the recurved sting, was also noted by Bischoff (1931). The abrupt curve at the distal tip of the stylet in the inquilines, as well as in *V. squamosa*, would appear to impede the thrusting of the two lancets. However, the distal end may be curved to hook a sclerite and thus enlarge the intersegmental membrane for further penetration by both the stylet and lancets.

There is no obvious glandular degeneration in *V. austriaca*, but a hypertrophy of one exocrine gland exists. Evidently this enlargement of the Dufour's gland has some role in vespine social parasitism, but unfortunately the function in any vespine is still unknown (Landolt and Akre 1979). Several different functions, such as sting lubrication, have been ascribed to the gland (Spradbery 1973, Maschwitz and Kloft 1971). The secretion is not considered toxic, although Barr-Nea et al. (1976) found some lethality to honey bees. Jeanne (1977) suggested that in *D. arctica* this gland may produce an allomone that has some pacifying effect upon the host queen and or workers. However, the mode of usurpation in *D. arctica* differs from that in *V. austriaca*, suggesting a different function for the gland in the latter. *D. arctica* usually passively invades queen nests and coexists with the queen prior to the emergence of the host workers (Evans 1975, Greene et al. 1978, Jeanne 1977), while

V. austriaca forcibly invades a host colony after worker emergence and does not coexist with the host queen (Reed 1982). Thus, the secretion of the Dufour's gland does not appear to act as a pacifying agent in *V. austriaca* parasitism, and may function as an alarm or dispersing chemical (Reed 1982). The possibility of differing functions of this gland is indicated by the condition of the gland in the two species prior to usurpation. In freshly dissected, preusurpation *D. arctica* parasites the gland was clearly empty, whereas in preusurpation *V. austriaca* females the gland was filled with a clear oil substance. A similar relationship between an enlarged Dufour's gland and social parasitism is found among the slave-making ants of the subfamily Formicinae (Parry and Morgan 1979, Regnier and Wilson 1971) and the dulotic ant *Harpagoxenus canadensis* M. R. Smith (Buschinger and Alloway 1978). In some of these slave-makers the gland discharges a chemical that disperses the defending host workers and attracts other slave-making workers (Regnier and Wilson 1971).

In conclusion, *V. austriaca* possesses morphological features significantly different from the host species. Some, such as the powerful mandibles and front legs, and large curved sting, function as important offensive weapons during colony invasion. Other characteristics, such as the large gastral retractor muscles that enable the parasite to tightly hold the sclerites together, serve as an important defense against stinging host workers. The function of the large Dufour's gland in vespine inquilines remains obscure; however, it probably plays a key role in usurpation and control of the host colony.

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LEPTOTHORAX FABERI N. SP., AN APPARENTLY
PARASITIC ANT FROM JASPER NATIONAL PARK,
CANADA (HYMENOPTERA: FORMICIDAE)*

BY ALFRED BUSCHINGER

Fachbereich Biologie, Institut für Zoologie, der Technischen
Hochschule, D 6100 Darmstadt, Schnittspahnstr. 3 (FRG)

1. Introduction

The myrmicine tribe Leptothoracini comprises an astoundingly rich variety of socially parasitic genera and species. Guest ants (*Formicoxenus*, *Leptothorax provancheri*), as well as slave-making genera (*Harpagoxenus*, *Chalepoxenus*, *Epimyрма*) and inquiline (*Doronomyrmex*) have been described (Buschinger, 1981); however, we may suspect that only a minor fraction of the existing species is already known to science. New species can be found nearly everywhere when populations of independent species are closely examined.

In August, 1979, I collected leptothoracine ants in several localities of Jasper National Park, Alberta, Canada. The main object was to find additional material of *Doronomyrmex pocahontas*, originally described from this locality (Buschinger, 1979). On August 19, when inspecting rotten sticks in the coniferous forest along Mt. Edith Cavill Road near Jasper, I found a colony of a *Leptothorax* species belonging to the "*L. muscorum*" group sensu lato. Among the nearly black ants I saw a dealate female which was considerably smaller than the ordinary queens, and more brownish in color. Its general appearance was that of a *Leptothorax kutteri* queen, an inquiline of *L. acervorum* in Europe (Buschinger, 1965).

*Manuscript received by the editor June 30, 1982

The colony was kept alive for four subsequent brood periods in artificially shortened annual cycles (Buschinger et al., 1975), and produced (besides alates and workers of the black "*muscorum*") a total of 56 males, 5 females and 1 worker of the small species. From a second colony that was established with one of the young females, I got an additional 4 males, 2 females, and one worker. This new, apparently parasitic species will now be described.

2. Description of *Leptothorax faberi* n. sp.

Figs. 1-5

Holotype female: total length 3.45 mm, head length 0.67 (excluding mandibles), head width 0.59 (behind eyes), scape length 0.49, greatest diameter of eye 0.16, thorax length 0.98, thorax width 0.58, length of petiole in lateral view 0.27, width of petiole 0.22, length of postpetiole 0.20, width of postpetiole 0.32, length of forewing 2.89, hind wing 1.90, length of hind femur 0.58, hind tibia 0.46. The end of the gaster is somewhat curved down so that its length (1.3mm) cannot be determined with precision.

Paratype females (selected measures of two females): total length 3.2/3.47 mm, head length 0.68/0.79 mm, thorax length 0.97/1.18 mm, thorax width 0.50/0.66 mm.

Habitus in general similar to the queens of the genus *Leptothorax*, subgenus *Leptothorax* sensu Smith (1950) (= *Mychothorax* Ruzsky). Mandibles with 5 or 6 teeth of normal size; one or two tiny teeth may be present between the normal ones in the middle of the masticatory border. Maxillary palps 5-segmented, labial palps 3-segmented. Antennae 11-jointed with a 3-jointed club. Anterior border of clypeus with a feeble notch (fig. 1a). Three ocelli present. Thorax (fig. 1b) as in *Leptothorax muscorum*. Epinotal spines of moderate size, acute; epinotal spine index (Buschinger, 1966) between 1.5 and 1.8. Wings as in *L. muscorum* (fig. 2). Petiole (fig. 1b) not pedunculated; viewed from above, the outline is nearly quadrate, with a slight convexity of the sides. In lateral view the anterior face is slightly concave, the posterior face distinctly so. The summit is flat, descending backward and forming a right angle with the anterior face, and an obtuse angle with the posterior one. A conspicuous ventral spine forms the anterior end of a ventral, concave, triangular field, the sharp, ventrolateral edges of which diverge towards the postpetiole.

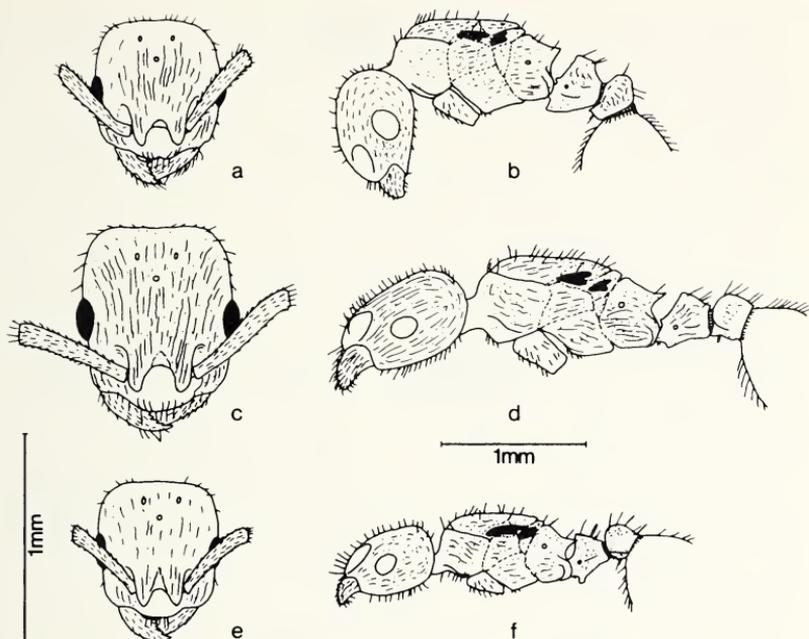


Fig. 1. Head in front view, and head, thorax, and petioles in lateral view of females of *Leptothorax*. a, b, *L. faberi* n. sp.; c, d, its host species, "*L. muscorum*", large black form; e, f, "*L. muscorum*", small brown form, for comparison.

Postpetiole (fig. 1b) from above about 1.4 times broader than the petiole, kidney-shaped with a slight anterior concavity. In lateral view, the anterior face is slightly convex, nearly perpendicular. Summit rounded, posterior face slightly concave, descending towards the gaster.

The seemingly distinct ventral spine is formed by a sickle-shaped, transverse protuberance with a sharp anterior edge.

Head, thorax, petiole, and postpetiole mostly coarse and rugulose, gaster smooth and shining. Body sparsely covered with erect, short and stiff hairs; legs and antennal scapes with abundant, appressed hairs; funiculus with dense, suberect hairs. Maximal length of hairs in head, thorax and gaster 0.06-0.08 mm.

Coloration: yellowish-brown with head, dorsal parts of thorax, petiole, postpetiole and gaster somewhat darker brown. Legs uniformly brown, antennae brown with a blackish-brown club.

One alate female was dissected. She had 6 ovarioles, a comparatively large poison gland, a Dufour's gland of ordinary size for most independent *Leptothorax* species, and an empty receptacle also of ordinary size and shape.

Allotype male: total length 3.44 mm, head length 0.63 (excluding mandibles), head width 0.65 (behind eyes), scape length 0.26, greatest diameter of eye 0.28, thorax length 1.21, width 0.70, length of petiole 0.32, width 0.25, length of postpetiole 0.24, width 0.29, length of forewing 3.09, hind wing 2.04, length of hind femur 0.79, hind tibia 0.55, length of gaster ca. 1.05 mm. Paratype males (selected measures of two males): total length 3.46/3.58 mm, head length 0.60/0.65 mm, thorax length 1.22/1.28 mm, thorax width 0.67/0.70 mm. Habitus in general like that of other males of the subgenus *Leptothorax*. Mandibles without teeth, masticatory border rounded or straight. Maxillary palps 5-segmented, labial palps 3-segmented. Antennae 12-jointed, without club. Clypeus prominent, vaulted, its anterior border straight. Eyes and the ocelli as large as usual for the subgenus *Leptothorax*.

Thorax with Mayrian furrows. Epinotum without distinct spines, but their place marked by two low ridges (fig. 3).

Petiole not pedunculated, with nearly straight anterior and posterior faces of the rounded node. A small ventral spine is present, with two diverging ventrolateral edges, as in the female. Postpetiole similar to that of the female, except that the anterior face is less steep and more convex, and the ventral spine or transverse edge is smaller (fig. 3).

Male genitalia: see fig. 3.

Head, sides of pronotum and of petiole coarse, dorsal and extended lateral parts of thorax, node of petiole, postpetiole and gaster smooth and shining. Body moderately covered with tapering, curved hairs of variable length, in the thorax reaching 0.10 mm, on the petiolar node 0.14 mm. Head and particularly the mandibles with abundant, long, tapering hairs. Antennae and legs with abundant, appressed or suberect hairs.

Coloration: whole body black or blackish-brown with the scutellum, the metanotum, sometimes the pronotum, the mandibles and legs somewhat lighter brown. In most males the scutellum differs so markedly in coloration from the surrounding parts of the thorax that this was the most valuable character for identifying the new species' males when they were still alive in the nest.

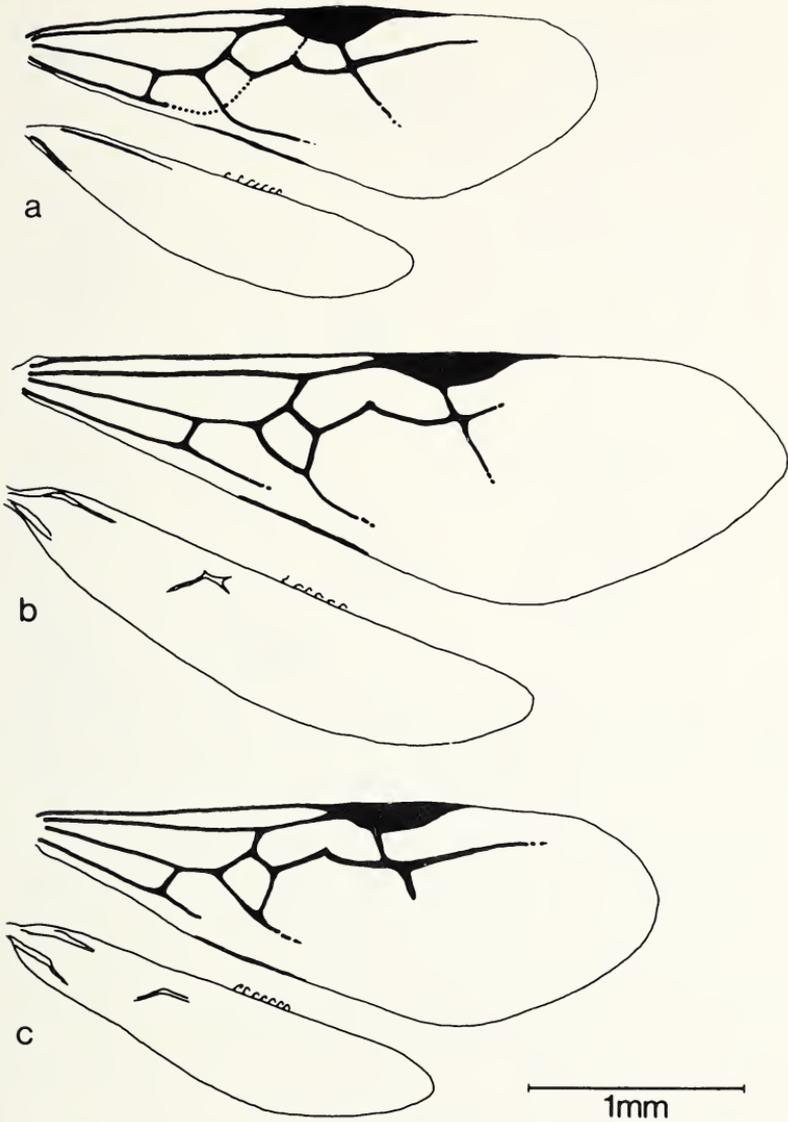


Fig. 2. Wings of females of *Leptothorax*. a, *L. faberi* n.sp.; b, "*L. muscorum*", large black form; c, "*L. muscorum*", small brown form. The dotted lines in the *L. faberi* fore wing (a) indicate veins that are present in the left, and absent in the right wing of the same specimen. Wing venation is variable in all species of this group.

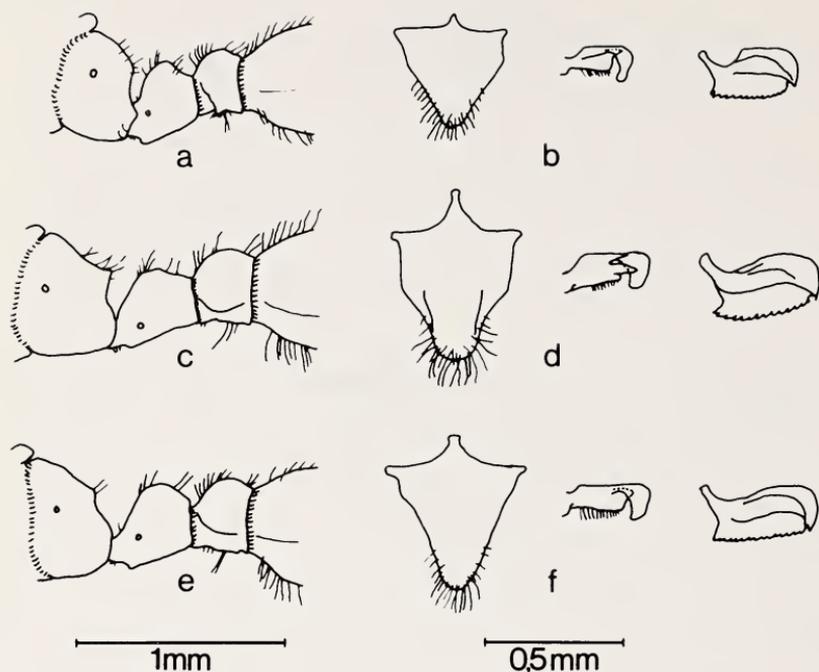


Fig. 3. Epinotum and petioles of males, and male genitalia (subgenital plate, volsella with lacinia, and sagitta) of *Leptothorax*. a,b, *L. faberi* n.sp.; c,d, its host species, "*L. muscorum*", large black form; e,f, "*L. muscorum*", small brown form. The shapes of the sagitta and volsella with lacinia vary considerably in all 3 species.

Allotype worker: total length 3.02 mm, head length 0.66 (excluding mandibles), head width 0.58, scape length 0.46, greatest diameter of eye 0.16, thorax length 0.91, width 0.43, length of petiole 0.24, width 0.20, length of postpetiole 0.17, width 0.30, length of hind femur 0.51, hind tibia 0.42, length of gaster approximately 1.05 mm.

Habitus similar to an ordinary worker of *L. muscorum*, but somewhat more stout and clumsy (fig. 4). Mandibles with 6-7 teeth, palps with 5 and 3 joints, as in the female. Eyes of moderate size, ocelli absent, anterior border of clypeus with a notch as in the female. Thorax with a deep meso-epinotal suture, and the promesonotal suture clearly visible. Pronotum comparatively wide. Epinotal spines as in the female, epinotal spine index 1.6. Petiole and postpetiole as in the female, as well as the appendages. Head and whole body coarse and rugulose except for the gaster, which is

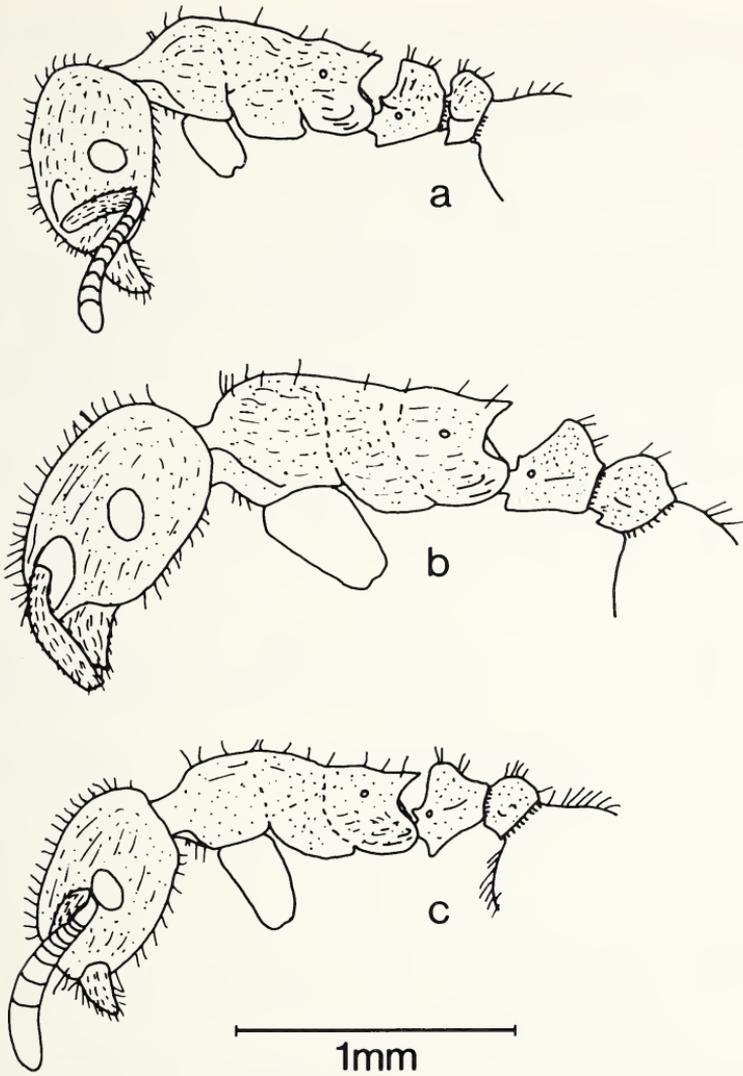


Fig. 4. Head, thorax, and petioles of workers in lateral view. a, *L. faberi* n.sp.; b, its host species, "*L. muscorum*", large black form; c, "*L. muscorum*", small brown form, for comparison.

smooth and shining. Pilosity as in the female. Coloration yellowish-brown with the head, the antennal club and the gastral tergites darker brown.

The karyotype (fig. 5) was determined from 8 male pupae, following the method of Imai et al. (1977). In 68 metaphase plates a haploid number of 15 chromosomes was found, 13 of which are metacentric or submetacentric and two are subtelocentric. The second-largest chromosome exhibits a very characteristic banding. In 7 metaphase plates one additional, subtelocentric chromosome was found; this, however, may be an artefact. The host species, on the contrary, has a haploid chromosome number of 17 as does the second, smaller "*L. muscorum*" from Jasper Park, and as occurs in European *L. muscorum*.

Type locality: Jasper National Park, Alberta, Canada, a few meters above the road from 93A to Mt. Edith Cavill parking lot, in about 1500 m elevation. Numerous nests of the host species and also of a smaller kind of "*L. muscorum*" were found inhabiting the rotten sticks and logs lying on the ground of a rather open coniferous forest.

Derivatio nominis: The ant is dedicated to my late friend, Dr. Walther Faber, from Vienna, Austria, whom I admired for his excellent studies in social parasitic ants.

Differential diagnosis: The new species closely resembles the European inquiline ant *Leptothorax kutteri*, particularly with respect to size, coloration, and the ventral spines in petiole and postpetiole. It differs from that species through the lack of erect hairs in the antennal scapes and the tibiae. Also, the characteristic sculpture of the head of *L. kutteri* females is absent in *L. faberi*. The remarkable light coloration of the male's scutellum and metanotum is, as far as I know, unique among leptothoracines belonging to the subgenus *Leptothorax* and their social parasites.

The host species (fig. 1) and *L. faberi* are easily distinguished by the latter's smaller size and lighter coloration (female). They also differ with respect to the karyotypes. *L. faberi* could only be confused with the second, smaller *Leptothorax "muscorum"* form in Jasper Park (fig. 1), which is the host species of *Doronomyrmex pocahontas*. However, this species differs in the shape of petiole and postpetiole from *L. faberi*, and it has a karyotype which is identical to that of the large, black *L. "muscorum"*, host species of *L. faberi*.

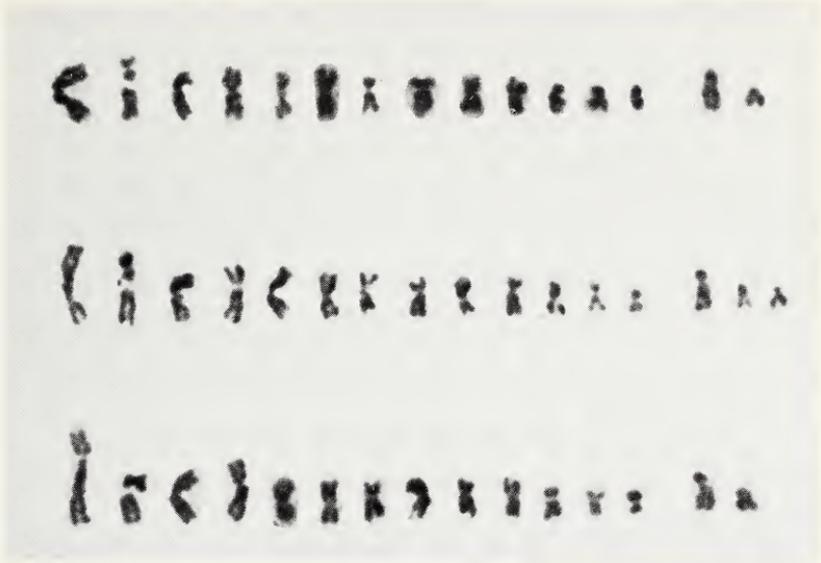


Fig. 5. Karyotype of *Leptothorax faberi* n.sp. The normal karyotype has $n = 15$ chromosomes, but 2 of 18 individuals had $n = 16$ in 2 out of 25 and 5 out of 18 metaphase plates respectively (center line).

3. Biological observations

All observations were made under laboratory conditions, and, due to the restricted material, they must be fragmentary. However, a few interesting facts could be recorded, particularly with respect to reproductive behavior. Sexualls of *L. faberi* were observed to leave the nest and to become sexually active in the morning, about 3 to 4 hours after the morning rise in temperature in our artificial 15/25°C temperature rhythm. Copulation was seen twice, the behavior being identical to that of *Leptothorax kutteri*, *Doronomyrmex pacis* and other social parasites of this group (Buschinger, 1971, 1974, 1975). A distinct sexual-calling behavior, resembling that of *L. kutteri*, was not seen, but poison gland secretion seems to serve as sexual pheromone as in the species mentioned above. The poison gland of one female was squeezed onto a small piece of filter paper, and the paper then put into a nest with *L. faberi* males. The males suddenly became excited, and a few began to mount the host species workers.

Mounting attempts of males on *L. faberi* females could also be released by gently squeezing a female within a swarming cage with males flying and crawling around.

One mated and dealate female was placed into a nest of the host species; however, it had to be removed quickly because it was seriously attacked by the workers. This same female then was put together with two workers from the mother colony, and with a few larvae from another host species colony, into an artificial nest. The *faberi* queen became fertile, and after a hibernation I increased her host worker stock using 25 worker pupae of *Leptothorax acervorum*. I used *L. acervorum* pupae because the normal host species colonies did not produce sufficient worker pupae: *L. acervorum* is an ideal "replacement host species" for several parasitic species. Thus, we succeeded in breeding *Formicoxenus nitidulus*, guest ant of *Formica*, with *L. acervorum* (Buschinger, 1976). After a second hibernation the original host species workers were dead, and the colony produced 1 *L. faberi* male. Further *acervorum* worker pupae were added, and in the third artificial brood period a total of 4 *faberi* males, 2 females, and 1 worker was produced. During this period the *faberi* queen died.

The second laboratory-mated *faberi* queen was placed into the mother colony, where it was accepted, apparently became fertile, and survived for two artificial annual cycles alongside its mother queen. Both died at the end of the third laboratory brood period of this colony.

The host species of *L. faberi* is a comparatively large, nearly black form which is related to *L. muscorum* Nyl., but it differs markedly from this European species. I cannot identify this form yet. A second, smaller species with more brownish coloration occurs sympatrically with the black form in Jasper Park. This smaller "*L. muscorum*" is the host species of *Doronomyrmex pocahontas* (Buschinger, 1979). It looks more similar to *L. muscorum* from Europe than to North American specimens, but it seems also to represent a distinct species. Besides the morphological differences of size and coloration, the two Canadian "*muscorum*" also differ markedly with respect to their sexual behavior. The "small brown" species' females exhibit a characteristic sexual calling behavior (Locksterzeln) similar to European *L. muscorum* Nyl. and most social parasites of this group. I was able to breed this species over several generations in the laboratory. The "large black" species on

the contrary, seems to make a mating flight. As with European *L. acervorum*, I could never induce mating in any kind of flight cage in the laboratory.

4 Discussion

The biology of *Leptothorax faberi* deserves to be discussed with respect to several features.

First of all, I am fairly convinced that this species represents an obligatorily parasitic ant. It seems unreasonable to assume that the one queen originally found should have run into the "*muscorum*" nest by chance during collecting, that it would have been accepted there, and that it could reproduce within the foreign nest. The very low number of only two workers produced in two colonies is another datum in favor of the opinion that *L. faberi* is a parasitic ant.

Finally, the presence of a postpetiolar ventral spine also supports this hypothesis, since most parasitic species among the Leptothoracini have it.

The production of host species sexuals within the parasitized colony even in its third laboratory brood period indicates that a host species queen must have been present. This was not checked by dissection, but several dealate host species females were living in the nest when it was collected. Thus, *L. faberi* seems to live as an inquiline ant alongside the fertile host colony queen(s), as do *Doronomyrmex pacis*, *Leptothorax goesswaldi*, *L. kutteri*, and others. Inquilines, however, are usually workerless. In *Doronomyrmex pacis* and *Leptothorax kutteri*, the worker caste is completely lacking in the vast majority of all the colonies we ever collected or kept in the laboratory, this being several dozen of *D. pacis* and about 100 of *L. kutteri*. However, a total of 2 or 3 workers of both species have been produced in laboratory culture, and one *L. kutteri* worker was found in a field colony (Brückner, in litt.). At present, it is impossible to decide whether the two *L. faberi* workers represent such rare exceptions, or whether the species usually will produce some more workers.

I also doubt that the exceptionally high ratio of males/females in the offspring of *L. faberi* represents the natural condition. Additional material must be collected in the field to clarify these problems.

With respect to systematic relationships, the new species clearly supports "Emery's rule," under which socially parasitic ants are always closely related to their respective host species group. No characters linking *L. faberi* with European *Doronomyrmex pacis* or *Leptothorax kutteri* could be found. The new species shares a characteristic structure in the petiole with the host species and with *Doronomyrmex pocahontas*. The Canadian species have two distinct small teeth at the base of the anterior face of the petiole just above its articulation with the epinotum (fig. 1). These teeth are lacking in their European relatives.

The holotype female, 2 allotype males and 1 worker, and voucher specimens of the host species are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (no. 32758).

5. Summary

Male, female and worker of an apparently parasitic ant, *Leptothorax faberi* n. sp., are described. The new ant species was found in a queenright colony of *Leptothorax muscorum* (sensu lato) in Jasper National Park, Canada. It differs from the host species in its smaller size, in the shape of the petioles (figs. 1, 3, 4), in sculpture and coloration. The karyotype with a haploid number of 15 chromosomes (fig. 5) is also different from that of the host species, which has $n = 17$ chromosomes. Very few workers have been raised in two laboratory colonies. Thus, *L. faberi* seems to represent an inquiline species.

6. Acknowledgments

I am grateful to my student, Karl Fischer, who assisted me during the collecting trip, and who also carried out the karyotype studies. I also thank the Jasper Park authorities for having tolerated our collecting activities. I am indebted to R. H. Crozier for critically reading the English text.

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REDESCRIPTION OF THE TYPE SPECIES OF
MYOPSOCUS, *M. UNDUOSUS* (HAGEN), AND
RESULTING NOMENCLATORIAL CHANGES IN GENERA
AND SPECIES OF MYOPSOCIDAE (PSOCOPTERA)*

BY EDWARD L. MOCKFORD,
Department of Biological Sciences
Illinois State University,
Normal, Illinois 61761

The assignment of species to the major genera in the Family Myopsocidae has been hampered by lack of detailed morphological information about the types of these genera. The genera involved are *Myopsocus* Hagen, *Lichenomima* Enderlein, *Phlotodes* Enderlein, and *Rhaptoneura* Enderlein.

Enderlein's (1910) genera were based entirely on wing venational characters. Some of these have later proven to be variable and of questionable value (Badonnel 1967). Roesler (1944) synonymized *Phlotodes* and *Rhaptoneura* at the generic level but maintained them as subgenera. Badonnel (1955) stated that genitalic characters justify the maintenance of *Rhaptoneura* and *Phlotodes* as genera but did not show what characters were involved. Smithers (1964) assigned all species which might fall in the genera *Myopsocus*, *Lichenomima*, *Phlotodes*, and *Rhaptoneura* to *Myopsocus* until the types could be studied. Badonnel (1967) following Enderlein (1910) and Roesler (1944) assigned to *Myopsocus* all species with Rs and M joined by a crossvein in the hindwing, thus synonymizing *Lichenomima* with *Myopsocus*, and assigned all species in which Rs and M in the hindwing are fused for a distance to *Phlotodes*, thus synonymizing *Rhaptoneura* with *Phlotodes*.

The present paper reports diagnostic features of the type of *Myopsocus unduosus* (Hagen), the type species of *Myopsocus* (Enderlein 1910). Genus *Myopsocus* is re-diagnosed on the basis of this examination, and an augmented diagnosis of *Lichenomima* is included. Generic synonymies are revised, and the species now assigned to *Myopsocus* and *Lichenomima* are listed.

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Myopsocus unduosus (Hagen)

Psocus unduosus Hagen 1859:201.

Myopsocus unduosus (Hagen) Hagen 1866:210.

Type material and its examination.—Types consist of two males, originally pointed, in the Museum of Comparative Zoology, Cambridge, Massachusetts. Each bears a type label with MCZ number 10118 and the label "Ceylon, coll. Nietner." I first examined these types in January 1970, ascertained that both are males of the same species, and selected one as lectotype. I then soaked the lectotype off the point, placed it in 80% ethanol, mounted the right wings on a slide in euparal, and cleared and figured the external genitalia. Early in 1982, I borrowed the wing slide and made figures from it.

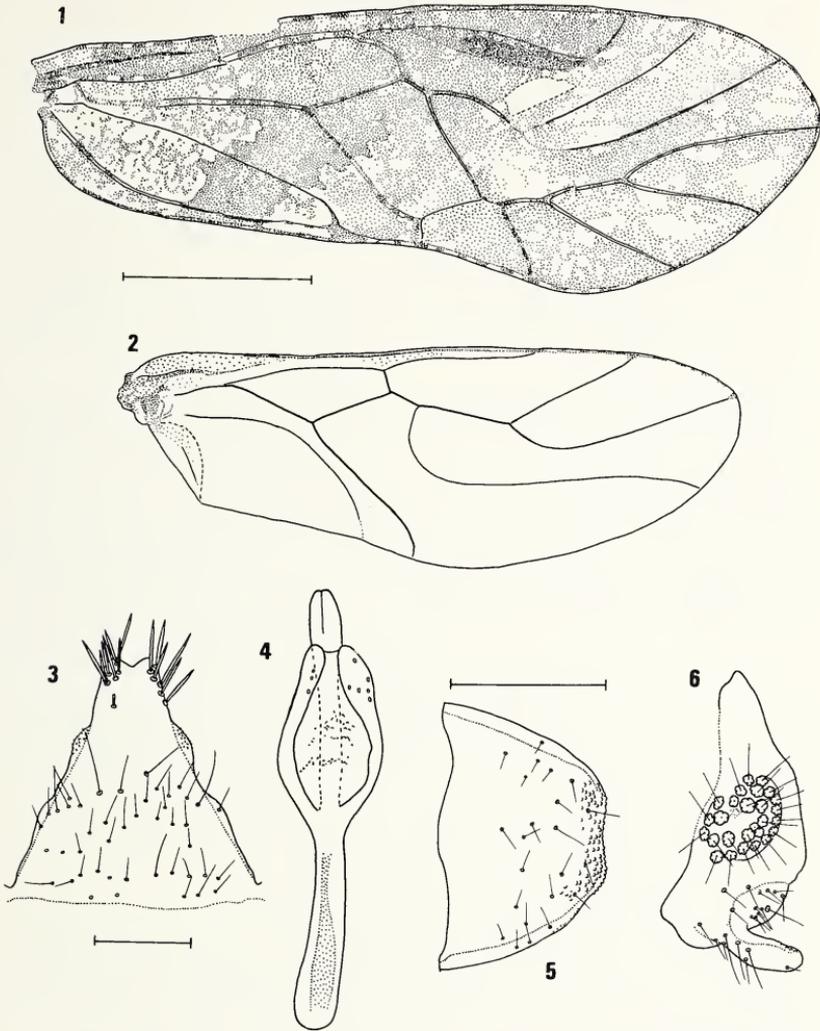
Measurements (mm).—Forewing length = 3.94; hindwing length = 3.22; posterior tibial length = 1.72; least distance between compound eyes = 0.27; transverse diameter of compound eye = 0.42.

Color characters.—Forewing (Fig. 1) with fairly distinct, mottled crossband in basal half of wing; a distinct stigmasaum darkly marked in middle; entire margin and most of veins with alternating dark and light marking. Hindwing (Fig. 2) unmarked except for brown clouding at base and along anterior margin and alternating dark and light marking along margin from distal end of R_1 to distal end of R_{4+5} . All femora dark brown with a narrow yellowish-white preapical ring.

Structural characters.—Forewing (Fig. 1) with relatively long Rs-M fusion, short M-Cu₁ fusion. Hindwing with Rs-M fusion slightly longer than segment of Rs before it. Hypandrium (Fig. 3) elongate, tapering distally, with slightly bulging, shagreened area on each side at about distal two-thirds of length; distal end on each side with field of heavy setae, each seta tapering toward end and base. Phallosome (Fig. 4) elongate, slender; median style separate from lateral arms at about two-thirds distance from base to tips of arms and extending beyond tips of arms. Epiproct (Fig. 5) semicircular except truncated distally, the distal end beset with minute tubercles. Paraproct (Fig. 6) bearing bluntly rounded distal process; sense cushion with 28 trichobothria, all with basal florets.

DIAGNOSTIC FEATURES AND SYNONYMY OF *MYOPSOCUS* HAGEN

Various authors have noted the constancy within and among species of the two character states Rs and M joined by a crossvein



Figs. 1-6. *Myopsocus unduosus* (Hagen) male lectotype. Fig. 1. Forewing; scale = 1.0 mm. Fig. 2. Hindwing; scale of Fig. 1. Fig. 3. Hypandrium; scale = 0.2 mm. Fig. 4. Phallosome (dorsal view); scale of Fig. 3. Fig. 5. Epiproct; scale = 0.2 mm. Fig. 6. Right paraproct; scale of Fig. 5.

versus fused for a distance in the hindwing of the Myopsocid genera under consideration. Enderlein (1910:68) stated about *M. unduosus*: "im Hinterflügel ist der Radialramus und die Media durch eine Querader mit einander verbunden." Obviously, the statement is not correct. Rs and M are fused for a distance in the hindwing; however, following Enderlein's erroneous statement, Roesler (1944) and Badonnel (1967) mis-assigned these two character states. Thus *Lichenomima* (Rs and M joined by a crossvein) was synonymized under *Myopsocus* and *Rhaptoneura* (Rs and M fused for a distance) was synonymized under *Phlotodes*. On the basis of examination of the type, it is evident that *Myopsocus* has as synonyms *Phlotodes* and *Rhaptoneura*. *Lichenomima* is probably tenable as a distinct genus.

Characters correlating with the fusion of Rs and M for a distance in the hindwing are the following: 1) phallosome generally with a median style (known exceptions: *M. aldabrensis* (New), *M. minor* (New and Thornton), *M. pallidus* (Smithers), *M. speciosus* (Smithers), *M. splendidus* (Badonnel)); 2) female subgenital plate terminating in a process tapered distally and with two large setae at the tip plus smaller setae in some species.

ASSIGNMENT OF SPECIES TO *MYOPSOCUS*

Given the above definition and synonymies, *Myopsocus* includes the following species, grouped according to their nomenclatural history:

1) Species originally placed in *Psocus* and subsequently transferred to *Myopsocus*:

australis Brauer 1865, Australia, Melanesia

unduosus Hagen 1859, Sri Lanka

2) Species originally assigned to *Myopsocus*, all subsequently transferred, in effect, to *Phlotodes*, or *Rhaptoneura*, or both in sequence:

chunius Thornton, Lee, & Chui 1972, Micronesia

eatoni McLachlan 1880, Europe, North Africa

furcatus Smithers 1964, Australia

griseipennis McLachlan 1866, Australia

hickmani Smithers 1964, Tasmania

incomptus Smithers 1964, Australia

**kolbei* Enderlein 1903 (type of *Phlotodes*), New Guinea

novaezealandiae Kolbe 1883, New Zealand
palauensis Thornton, Lee, & Chui 1972, Micronesia
punctatus Thornton, Lee, & Chui 1972, Micronesia

3) Species originally assigned to *Phlotodes*:

aenulus Badonnel 1967, Madagascar
aldabrensis New 1977, Aldabra
alticola Thornton 1981, Fiji
ambiguus Badonnel 1967, Madagascar
amicus Thornton 1981a, Tonga
angolensis Badonnel 1955, Angola, Madagascar
anomalus Smithers & Thornton 1979, Melanesia
antillanus Mockford 1974, Cuba, Hispaniola, Florida
ascoides Thornton 1981, Fiji
bellus Smithers & Thornton 1974, New Caledonia
bipunctatus Thornton 1981, Fiji
bomasus Smithers & Thornton 1974, New Guinea
brunneigenus Smithers & Thornton 1979, Melanesia
clarki Turner 1975, Jamaica
congolensis Badonnel 1949, Zaire
corticoides Smithers 1964a, Madagascar
cubanus Mockford 1974, Cuba
dentatus Smithers & Thornton 1974, New Guinea
fenestratus Smithers & Thornton 1974, New Guinea
graptus Thornton 1981, Fiji, Tonga
gregarius Smithers & Thornton 1979, Melanesia
gressitti Smithers & Thornton 1974, New Guinea
hoskinsi Smithers & Thornton 1979, Melanesia
inocellatus Smithers & Thornton 1974, New Guinea
lichenosus Enderlein 1931, Seychelles, Madagascar
lineatus Smithers & Thornton 1979, Melanesia
lyriferus Smithers 1964a, Madagascar
maculatus Smithers & Thornton 1974, New Guinea, Melanesia
marginatus Smithers & Thornton 1974, New Guinea
megops Smithers & Thornton 1979, Melanesia
minor New & Thornton 1975, Brazil
minutus Mockford 1974, Cuba, Mexico
mjöbergi Karny 1925, Sarawak, Borneo
napuka Thornton 1981, Fiji
obscurus Badonnel 1967, Madagascar

- peltatus* Smithers & Thornton 1974, New Guinea
pennyi New 1979, Brazil
personatus Badonnel 1967, Madagascar
pilipes Smithers & Thornton 1974, New Guinea
placidulus Smithers 1975, Australia
platyvalvulus Smithers & Thornton 1979, Melanesia
preclarus Smithers & Thornton 1974, New Guinea
punctatoides Thornton 1981, Fiji, Tonga
quadrisetosus Smithers & Thornton 1974, New Caledonia
rastafari Turner 1975, Jamaica
reptus Thornton 1981, Fiji
rimosus Smithers & Thornton 1974, New Guinea
samoanus Karny 1932, Samoa
scabiosus Smithers & Thornton 1974, New Guinea
splendidus Badonnel 1967, Madagascar
thecatus New & Thornton 1975a, Malay Peninsula
toxeres Smithers & Thornton 1974, New Guinea
venustus Smithers & Thornton 1974, New Guinea
vilazi Smithers & Thornton 1974, New Caledonia
zimmermani Thornton 1981, Fiji
- 4) Species originally assigned to *Rhaptoneura*:
- africanus* Badonnel 1955, Angola
ciliiferus Smithers 1964a, Madagascar
cryptus Smithers 1957, Natal
**dispar* Enderlein 1910 (type of *Rhaptoneura*), Paraguay
magnificus Smithers 1957, South & East Africa
muscosus Enderlein 1931, Seychelles
pallidus Smithers 1964a, Madagascar
setosus Smithers 1964a, Madagascar
speciosus Smithers 1957a, Madagascar
- 5) Species *incertae sedis*, originally assigned to *Myopsocus* and best left there until they are re-examined:
- bakeri* Banks 1916, Philippines, Guam
cinereus Navás 1932, Argentina
enderleini Banks 1913, Philippines
fraternus McLachlan 1866, Assam (originally assigned to *Psocus*)
pluviosus Navás 1934, India
taurus Banks 1941, Santo Domingo

RELATIONSHIPS OF *MYOPSOCUS UNDUOSUS* (HAGEN)

Badonnel (1967) constructed a classification of the species from Madagascar, and Smithers and Thornton (1974) augmented it to include many of the Old World species. *M. unduosus*, being known only from the male, and presenting such unique male characters as the phallosome with its basal half a simple rod, and the hypandrium with two distal fields of heavy setae, does not seem to fit into any of the groups that have been proposed. Smithers and Thornton (1974) noted that numerous other species could not be placed in their classification due to paucity of information.

AUGMENTED DIAGNOSIS OF *LICHENOMIMA* ENDERLEIN

Species assigned to *Lichenomima* (assigned to *Myopsocus* by most authors since Badonnel 1967) have veins Rs and M joined by a crossvein in the hindwing. Correlated with this character are absence of a median style of the phallosome (possible exception: *L. ariasi* New) and female subgenital plate distally with a transverse sclerite, more or less separate from the main plate, and never terminating in a single process tapering posteriorly.

Species assignable to *Lichenomima* appear to be those listed by Smithers (1967) plus the following:

ampla Smithers & Thornton 1974 (from *Myopsocus*), New Guinea

ariasi New 1979 (from *Myopsocus*), Brazil

capeneri Smithers 1973 (from *Myopsocus*), South Africa

chelata Thornton & Woo 1973 (from *Myopsocus*), Galapagos Islands

clypeofasciata Mockford 1974 (from *Myopsocus*), Cuba

coloradensis Banks 1907 (from *Myopsocus*), Colorado

elongata Thornton 1960 (from *Myopsocus*), Hong Kong

machadoi Badonnel 1977 (from *Myopsocus*), Angola

medialis Thornton 1981 (from *Myopsocus*), Fiji

posterior Navás 1927 (from *Psocus*), Costa Rica

pulchella New & Thornton 1975 (from *Myopsocus*), Brazil

sanguensis New 1973 (from *Myopsocus*), Nepal

varia Navás 1927 (from *Amphigerontia*), Costa Rica

Note.—*Myopsocus medialis* Thornton (1981), assignable to *Lichenomima* on the basis of hindwing venation, appears to be so different in several other features as to merit a distinct genus.

SUMMARY

Examination of the type of *Myopsocus unduosus* (Hagen), the type species of *Myopsocus*, allows the genera *Phlotodes* Enderlein and *Rhaptoneura* Enderlein to be synonymized with *Myopsocus*. The species now assigned to *Myopsocus* are listed according to their nomenclatural history. Species assigned to *Myopsocus* by most recent authors are re-assigned to *Lichenomima* Enderlein.

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PARSIVOLTINISM IN THREE SPECIES OF *OSMIA* BEES*

BY P. F. TORCHIO AND V. J. TEPEDINO
Bee Biology & Systematics Laboratory,
Agricultural Research Service, USDA,
Utah State University, UMC 53,
Logan, Utah 84322

Individuals of most insect species follow a relatively inflexible tempo of immature development and adult emergence that includes a single period of diapause in one generation per year at a specific stage in the life cycle. A few species depart from this pattern in that a small proportion of individuals of an age cohort require an additional year or more to complete development to the adult stage (Waldbauer 1978, Beck 1980). Among bees, for example, there are brief reports of delayed emergence for several species (Davidson 1896, MacSwain 1958, Krombein 1967, Torchio 1975, Parker 1980, Rust 1980) but none of these studies provides quantitative evidence to demonstrate that delayed emergence is an integral part of the life cycle.

In this study we supply quantitative evidence to document patterns of delayed emergence in three species of megachilid bees (*Osmia montana* Cresson, *O. californica* Cresson, *O. iridis* Cockerell and Titus). Individuals of these species complete development in either one or two years, i.e., the emergence pattern of each age cohort is bimodal. Waldbauer (1978) used the term "type c" to describe bimodal and polymodal emergence patterns in which the peaks of emergence of an age cohort occur in different years. Here we introduce the more descriptive term, "parsivoltine", to refer to this phenomenon. "Parsi" is adapted from the Latin *pars* for part or partial; -voltine, from the Italian *volta* for time or cycle is used in its usual entomological sense, as generations (cycles) per year.

Our study addresses the following questions: 1) Does the proportion of one- and two-year individuals in a cohort differ between the two years of study and/or between the two sampling sites? 2) Is there an association between sex and time required to complete development? 3) How are one- and two-year forms distributed

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between and within individual nests? 4) Are inter-individual differences in the time required to complete development due to environmental factors or to a genetic polymorphism, or both?

The three *Osmia* species are restricted to the western U.S. where they are sympatric and at least partially synchronic (late spring-early summer). Each nests gregariously in pre-existing holes, usually in wood. The biologies of *O. montana* and *O. californica* are summarized by Rust (1974); the biology of *O. iridis* is currently under study (Torchio, unpub.). Briefly, nests of each species are composed of a linear series of cells. Each cell is provided with pollen, nectar and an egg; cells are separated by partitions constructed of macerated leaf material (*O. montana*, *O. iridis*) or mud mixed with macerated leaf material (*O. californica*), and nests are plugged with one or more partitions. *Osmia montana* and *O. californica* are oligoleges of the Compositae; *O. iridis* is restricted to a non-composite host plant.

METHODS

Nests of these *Osmia* species were obtained from trap blocks placed at two field locations (Torchio 1976). Trap blocks of sugar pine contained 49 drilled holes to accommodate paper soda straws measuring 14.5 cm long and 7 mm inside diameter. One hundred nest blocks were placed at each of two study sites during both study years (1979-1980).

The Faust trapping site was located 42 km south of Logan, Cache Co., Utah at 1800 m elevation. This location is on a hillside with a SW exposure and is covered by large stands of mature aspen (*Populus tremuloides* Michx.) trees surrounded by open, grassland meadows. The Mendon site is located 24 km west of Logan at 1500 m elevation on a hillside having a SE exposure. Solid stands of maple (*Acer glabrum* Torr.) or aspen trees surrounded by open meadows were characteristic of the area.

During both study years, nest blocks were attached individually to standing trees during mid-May prior to *Osmia* flight and returned to the laboratory in early July where they remained at room illumination and temperature. All nests were dissected in early September; individual cocoons were opened to determine sex ratios of adults (one-year forms) and position of larvae (two-year forms) in nests. Larvae of two-year forms were weighed on an electrobalance (0.1

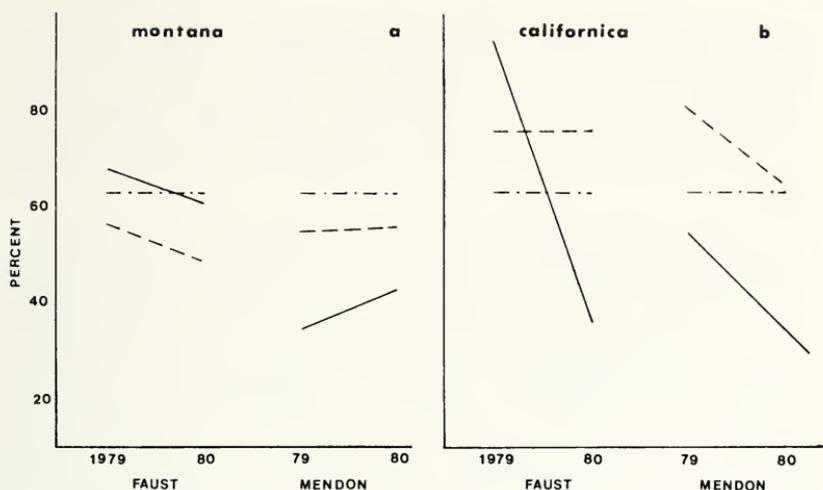


Figure 1. Percent of total offspring of *O. montana* (a) and *O. californica* (b) that were one-year forms (solid lines), and males (dashed line) at two northern Utah sites over two years. Dotted and dashed line represents the expected sex ratio as percent males.

mg) and all individuals were then inserted into clear, #000 gelatin capsules. Capsules were then placed in a constant 4 degrees C temperature cabinet on September 30 of each study year and transferred to a 26 degrees C temperature cabinet on June 1 of the subsequent year. A photoperiod of OL:24D was maintained throughout these treatments. Capsules containing two-year forms (now adults) were removed from the temperature cabinet on August 30 and reweighed.

RESULTS

Osmia montana

Almost 1100 nests were available for examination from the four site-years of sampling (Table 1). Nest utilization was higher in 1979 than in 1980 at both sites, and higher at Faust than at Mendon in both years.

There were differences between sites and years in the proportion of offspring that were one-year forms (Fig. 1a). At Faust a significantly higher proportion of one-year forms was produced in 1979

than in 1980 ($X^2 = 19.1$, $P < 0.001$) whereas at Mendon a significantly higher proportion of one-year cells were produced in 1980 than in 1979 ($X^2 = 6.3$, $P < 0.025$). However, the Faust site yielded a significantly greater proportion of one-year cells than did Mendon during both years (1979, $X^2 = 214.1$, $P \ll 0.001$; 1980, $X^2 = 47.4$, $P < 0.001$).

An association between sex and the number of years required to complete development was found (Table 1). For all site-years, there were significantly more males than females among one-year forms, and fewer than expected males among two-year forms (Faust 1979, $X^2 = 9.8$, $P < 0.005$; 1980, $X^2 = 22.6$, $P < 0.001$; Mendon 1979, $X^2 = 13.9$, $P < 0.001$; 1980 $X^2 = 8.8$, $P < 0.005$). Thus the sex ratio ($\delta/\text{♀}$) of one-year forms was always higher than that of two-year forms. However, the sex ratio of one- or two-year forms (taken separately) was not always the same from year to year or from site to site. At Faust the proportion of both one- and two-year males decreased in 1980 (Table 1; one-year forms, $X^2 = 7.4$, $P < 0.01$; two-year forms, $X^2 = 11.9$, $P < 0.01$) and, as a consequence, the combined sex ratio of offspring declined significantly from 1.3 (1979) to 0.96 (1980) ($X^2 = 21.4$, $P < 0.001$). Conversely, no such changes occurred at Mendon ($P > 0.75$ all comparisons).

The incidence of one- and two-year forms appears to be controlled by a genetic polymorphism rather than by the action of environmental variables upon individual offspring. If environmental cues such as photoperiod, thermoperiod, oxygen levels, etc. act either indirectly on the mother or directly on the progeny to determine the developmental fate of offspring, then a consistent pattern of distribution of one- and two-year forms in mixed nests (those containing both one- and two-year forms) should be evident. To examine this possibility we classified mixed nests as follows: 1) one-year forms in inner cells; two-year forms in outer cells; 2) a reversal of 1; 3) a double switch, i.e., nests having one-year forms positioned as bottom and top cells with a two-year form between; or, two-year forms sandwiching a one-year form. Only mixed nests that could be categorized with surety were counted; thus, nest totals in Table 2 are fewer than totals listed in Table 1 because some nests were not counted. Such a categorization of nests assumes that all nestmates are siblings. In general this is a valid assumption; supercedure of the nest of one female by another female is an infrequent occurrence.

Table 1. Number of live one- and two-year male and female offspring of *Osmia montana* reared from two sites in two years. Offspring are grouped by nest type, i.e., 1-yr nests contained only 1-yr offspring etc. SR = sex ratio. Number of dead cells shown in parenthesis next to total live cells.

Site, year and nest type	No. nests		No. 1-yr.		No. 2-yr.		SR	No. cells
	♂	♀	♂	♀	♂	♀		
Faust 1979								
1-yr	236	554	421	—	—	—	—	975
2-yr	132	—	—	163	158	1.0	—	321
mixed	189	272	159	179	165	1.1	—	775
totals	557	826	580	342	323	1.1	—	2071(561)
totals both forms ♂ 1168, ♀ 903, SR 1.29								
Faust 1980								
1-yr	136	327	366	—	—	—	—	693
2-yr	61	—	—	156	160	1.0	—	316
mixed	146	301	182	158	269	0.6	—	910
totals	343	628	548	314	429	0.7	—	1919(244)
totals both forms ♂ 942, ♀ 977, SR 0.96								
Mendon 1979								
1-yr	15	30	20	—	—	—	—	50
2-yr	83	—	—	120	111	1.1	—	231
mixed	75	114	58	81	95	0.9	—	348
totals	173	144	78	201	206	1.0	—	629(247)
totals both forms ♂ 345, ♀ 284, SR 1.21								
Mendon 1980								
1-yr	12	30	35	—	—	—	—	65
2-yr	12	—	—	55	47	1.2	—	102
mixed	38	86	30	64	74	0.9	—	254
totals	62	116	65	119	121	1.0	—	421(163)
totals both forms ♂ 235, ♀ 186, SR 1.26								

Table 2. Transitions within mixed nests between one- and two-year forms for *Osmia montana* and *californica*. Transition from inner one-year forms to outer two year forms = 1-2 yr and similarly for 2-1 yr. Double switch signifies the transitions 1-2-1 yr or 2-1-2 yr.

		<i>Osmia montana</i>			<i>Osmia californica</i>		
		1-2 yr	2-1 yr	Double switch	1-2 yr	2-1 yr	Double switch
Faust	1979	22	16	47	0	1	1
	1980	6	31	63	5	4	52
Totals		28	47	110	5	5	53
Mendon	1979	11	17	32	5	21	12
	1980	3	12	17	3	9	22
Totals		14	29	49	8	30	34

For example, in a study of marked *O. lignaria* only 5 of 111 nests (same type as used here) made in a greenhouse contained offspring produced by more than one female (Tepedino and Torchio 1982b).

Distribution of one- and two-year forms in mixed nests is summarized in Table 2. Nests with double switches were more numerous than those in the other two categories combined in all site years; transitions from two-year forms in inner cells to one-year forms in outer cells were about twice as common as the reverse situation. Thus, factors such as photo- and thermoperiods, which act on the maternal genotype to induce diapause in the offspring of other species of Hymenoptera (Parker and Tepedino 1982), do not seem to influence the determination of one- or two-year forms in *O. montana*.

The interspersion of one- and two-year forms in mixed nests creates the potential for fratricide. Observations of trap-nests both in field and laboratory demonstrated that one-year forms destroy any two-year larval siblings positioned above them in the nest when they emerge (Torchio, unpub.). We therefore examined the data for mixed nests to determine the number of surviving and "doomed" two-year offspring by sex. The category doomed was assigned to any two-year form with a one-year form between it and the inner limit of the nest. All two-year forms without one-year forms positioned below them were classified as surviving. Our estimates of the percent doomed two-year offspring should be regarded with cau-

tion. Although all three species nest in pre-existing holes in dead wood, in natural situations it may sometimes be possible for emergent one-year adults to gain egress without destroying their two-year siblings. For example, if the nest is in a rotting log emergent forms may be able to chew around nestmates. Thus, the estimates given here should be regarded as maximums.

The results of these comparisons (Table 3) demonstrate that a large portion of two-year forms was doomed in each site-year (range 40.5–61.3%). This mortality would be in addition to any losses due to enemies or developmental arrest. It is also interesting to note that in each site-year a significantly lower proportion of two-year females than males would be destroyed by their siblings (X^2 tests, $P \ll 0.001$ all cases). This is because *O. montana*, like most bees that construct nests in pre-existing holes (including *O. californica*, *O. iridis*), deposit female eggs in cells in the lower reaches of the nest and males in outer cells (Krombein 1967). Thus, the probability that a two-year male larva will be destroyed by an emerging sibling adult is greater than for a two-year female.

Table 3. "Doomed" offspring by sex from mixed nests of *Osmia montana* and *O. californica*.

Species, Site, Year	Males		Females		Totals	
	N	% Doomed	N	% Doomed	N	% Doomed
<i>O. montana</i>						
Faust 1979	179	84.9	165	35.8	344	61.3
1980	158	69.6	269	23.4	427	40.5
Totals	337	77.7	434	28.1	771	49.8
Mendon 1979	81	81.5	95	35.8	176	56.8
1980	64	64.1	74	24.3	138	42.8
Totals	145	73.8	169	30.8	314	50.6
<i>O. californica</i>						
Faust 1979	5	40.0	2	50.0	7	42.9
1980	207	69.1	69	18.8	276	56.5
Totals	212	68.4	71	19.7	283	56.2
Mendon 1979	79	46.8	40	17.5	119	37.0
1980	49	75.5	47	19.1	96	47.9
Totals	128	57.8	87	17.8	215	41.9

Osmia californica

Almost 500 nests were recovered in the four-site years of sampling (Table 4). Nest utilization was unchanged at Mendon during both years, but a substantial increase was recorded at Faust from 1979 to 1980.

The proportion of one-year cells declined significantly at both sites from 1979 to 1980 (Fig. 1b, Table 4; Faust $X^2 = 221.5$, $P \ll 0.001$; Mendon $X^2 = 30.0$, $P < 0.001$). In agreement with results for *O. montana*, the proportion of one-year forms produced at Faust was significantly higher than that produced at Mendon during both years (1979, $X^2 = 92.5$, $P \ll 0.001$; 1980, $X^2 = 5.7$, $P < 0.025$).

As with *O. montana*, there was an association between sex and number of years to complete development (Table 4). For all site-years (except Faust 1979 for which insufficient numbers of two-year forms were available for statistical tests) there was a higher proportion of males among one-year forms than among two-year forms when cells from mixed nests only were considered (Faust 1980, $X^2 = 4.3$, $P < 0.05$; Mendon 1979, $X^2 = 20.2$, $P < 0.001$; 1980, $X^2 = 10.2$, $P < 0.005$). When all cells were considered, the sex ratio of one-year forms was always higher than that of two-year forms; but only one of three comparisons was significant (Faust 1980, $X^2 = 2.4$, $P > 0.10$; Mendon 1979, $X^2 = 11.8$, $P > 0.001$; 1980, $X^2 = 2.0$, $P > 0.10$).

Between-year differences in the proportion of males and females among one- and two-year forms at each site were less evident than for *O. montana* (Table 4). At Mendon the combined sex ratio of offspring declined significantly from 4.2 (1979) to 1.8 (1980) ($X^2 = 30.0$, $P \ll 0.001$) but no such change was evident at Faust ($X^2 = 0.0$, $P > 0.90$). The decline in the sex ratio at Mendon was due to a significantly greater proportion of female progeny produced in 1980 for both one-year ($X^2 = 15.5$, $P < 0.001$) and two-year forms ($X^2 = 7.5$, $P > 0.01$). These results are the reverse of those found for *O. montana*.

The distribution of one- and two-year forms within mixed nests were similar to results obtained for *O. montana* (Tables 2, 4). Thus, nests having double switches were most numerous and transitions from one- (inner cells) to two-year forms (outer cells) were intermediate.

As with *O. montana*, a substantial proportion of two-year forms were "doomed" (range 37.0–56.5%, Table 3) because cells containing one-year forms were often constructed lower in the nest. The

proportion of "doomed" two-year females was also significantly lower than for that of two-year males (Faust 1980, $X^2 = 53.2$, $P < 0.001$; Mendon 1979, $X^2 = 9.8$, $P < 0.005$; 1980 $X^2 = 30.5$, $P < 0.001$).

Osmia iridis

Trap-nests were utilized by *O. iridis* only in 1979 (Table 5). Of the 83 nests recovered, 54 contained one-year forms exclusively; four nests contained two-year forms; and the remaining 25 nests were mixed. Although relatively few two-year individuals were produced (13.1%), the proportion of two-year females recovered was greater than that of one-year females (mixed nests, $X^2 = 16.1$, $P < 0.001$, total nests, $X^2 = 9.0$, $P < 0.005$, both sites combined).

Unlike other *Osmia* species studied, the predominant transition category of *O. iridis* in mixed nests was from the two-year form (inner cells) to the one-year form (outer cells) 16 of 25 nests). There were relatively few nests with either double switches (5) or with transitions from one-year (inner) to two-year (outer) forms (4).

The tabulation of "doomed" individuals in mixed nests demonstrated that two-year males were at greater risk than two-year females ($X^2 = 6.0$, $P < 0.025$).

Expected and observed sex ratio:

We calculated the expected equilibrium sex ratio ($\delta/\text{♀}$) for each species on the basis of male and female live weights (Table 6) as described previously for *O. lignaria propinqua* (Torchio and Tepedino 1980). Two interesting points emerged from this analysis. First, for each species, the expected sex ratio was the same regardless of whether larval or adult weights were used. Second, the expected sex ratios of these three species were very similar to each other and to *O. l. propinqua* (Torchio and Tepedino 1980). Apparently the optimal size ratio between females and males is the same for many *Osmia* species that nest in similar substrates.

When the expected and observed sex ratios were compared, consistent biases emerged: For *O. montana* the observed sex ratio was significantly biased towards females for all site-years ($P < 0.005$ or less, all tests). In contrast, observed sex ratios for both *O. californica* and *O. iridis* were generally biased towards males ($P < 0.001$ or less, all but *O. californica* Mendon 1980). In addition, there was

Table 5. Number of live one- and two-year male and female offspring of *Osmia iridis* reared from two sites in 1979. Offspring grouped as in Table 1. SR = sex ratio. Number of dead cells shown in parenthesis next to total live cells.

Site and nest type	No. nests	No. 1-yr.		No. 2-yr.		SR	No. cells
		♂	♀	♂	♀		
Faust							
1-yr	42	161	42	—	—	—	203
2-yr	1	—	—	1	0	—	1
mixed	17	36	4	16	14	1.1	70
totals	60	197	46	17	14	1.2	274(70)
totals both forms ♂♂ 214, ♀♀ 60, SR 3.57							
Mendon							
1-yr	12	41	14	—	—	—	55
2-yr	3	—	—	7	0	—	7
mixed	8	23	4	6	5	1.2	38
totals	23	64	18	13	5	2.6	100(36)
totals both forms ♂♂ 77, ♀♀ 23, SR 3.35							

Table 6. Mean fresh weights (mg) of adults and larvae of three species of *Osmia*. Weights for *O. montana* and *californica* are for two-year forms, those for *O. iridis* for one-year forms. N = sample size, ESR = expected sex ratio ($\delta/\text{♀}$).

	Adults		larvae		% wgt. loss	
	δ	♀	δ	♀	δ	♀
<i>montana</i>						
live wgt	71.9	125.3	93.1	161.7	23.0	22.6
± SD	16.1	16.9	19.2	20.3	3.0	2.1
N	21	34	21	34	21	34
ESR	1.74		1.74			
<i>californica</i>						
live wgt	73.3	121.2	94.1	156.6	22.0	22.8
± SD	14.5	19.7	18.6	21.8	4.3	3.5
N	23	16	23	16	23	16
ESR	1.65		1.66			
<i>iridis</i>						
live wgt	38.3	66.7				
± SD	4.9	9.5				
N	58	15				
ESR	1.74					

no consistent tendency for observed sex ratios to move towards the equilibrium sex ratio in 1980 for either *O. montana* or *O. californica* (Fig. 1).

DISCUSSION

The data presented above are noteworthy for several reasons. First, these three species provide the best documented examples of parsivoltine emergence patterns in bees. Indeed, among Hymenoptera, detailed examples of parsivoltinism are available only for diprionid sawflies (Prebble 1941, Griffiths 1959, Sullivan and Wallace 1967, Wallace and Sullivan 1974). Previous reports of such emergence patterns in bees have been based on small sample sizes (*Dianthidium pudicum consimile* (Ashmead) (Davidson 1896), *Melissodes robustior* Cockerell (MacSwain 1958), *Prochelostoma philadelphia* (Robertson) (Krombein 1967), *Perdita nuda* Cockerell, *Sphecodes* sp. (Torchio 1975), *Osmia marginipennis* Cresson (Parker 1980), and *Hoplitis biscutellae* (Cockerell) (Rust 1980)).

A second point of interest is that two-year forms of all three species undergo two periods of diapause (once as post-defaecating larvae during the first winter, and again as adults over the second winter) whereas one-year forms diapause only as adults. For most other insect species, diapause is stage specific and occurs only once in the life cycle (Beck 1980); there are a few reports of non-hymenopterous insect species that enter diapause in more than one stage (e.g., Harvey 1967, Lounibos and Bradshaw 1975). The physiological mechanisms which enable species to undergo two discrete periods of diapause are unknown (Chippendale 1977, Waldbauer 1978).

A third unusual result of this study is the relatively large proportion of individuals in each age cohort which were two-year forms (Fig. 1). When data for live offspring were combined for all site-years by species, 41% of all *O. montana*, 57% of all *O. californica* and 13% of all *O. iridis* required two years to complete development. In contrast, the percentage of individuals requiring prolonged periods to complete emergence in most other species with parsivoltine emergence patterns is low (Powell 1974, Waldbauer 1978, Shapiro 1979, Tauber and Tauber 1981).

A potential explanation for the high proportion of two-year forms among these species has been provided by Cohen (1966, 1968). In his treatment of optimal reproductive strategies, Cohen noted that when weather and/or resources exhibit large year to year fluctuations and, as a result, the year to year variance in reproductive success is also large, it would be adaptive for organisms to produce offspring types that differed in the time required to reach maturity. By this means, the effects of years unfavorable to reproduction would not fall upon all members of an age cohort (See also Powell 1974, Hedrick *et al.* 1976, Waldbauer 1978, Shapiro 1979, Real 1980, Tauber and Tauber 1981). Cohen (1966, 1968) also hypothesized that variance in reproductive success should be positively associated with the proportion of offspring that require an extra year (or more) to complete development; and that, as the viability of two-year forms decreased relative to one-year forms, the proportion of two-year forms in the population should also decrease. Thus, Cohen's theoretical results suggest that the high proportion of two-year forms in these *Osmia* species may be due to

substantial temporal heterogeneity in the environment and that viability of two-year forms is about the same as that of one-year forms. In addition, the data suggest that there may be differences among these species in the way a heterogeneous environment is experienced. The percentage of two-year forms appears to be higher for *O. montana* and *O. californica* than for *O. iridis* (Fig. 1), and this suggests that variance in reproductive success is lower for *O. iridis* than for the other species.

Although there are no data available to directly address these predictions, trap-nesting returns from northern Utah over the past 10 years (Torchio, unpub.) suggest that *O. montana* and *O. californica* populations are much more stable than are those of *O. iridis*. The latter species is only occasionally abundant and, more frequently, is totally absent from trap-nests. Conversely, trap-nest returns for *O. montana* and *O. californica* fluctuate within much narrower limits. Thus, the data available to us do not support Cohen's (1966, 1968) predictions.

Another characteristic expressed by these and other species that does not seem to conform to Cohen's (1966, 1968) predictions is the relative viability of one- and two-year forms. For example, Sullivan and Wallace (1967) reported that mortality increased and fecundity decreased with prolonged diapause in the sawfly, *Neodiprion sertifer* (Geoff.). Although we were unable to compare the mortality rate of one- and two-year forms because it was impossible to assign immature deaths in the first year to either category, it seems clear that mortality of two-year forms must be higher than that for one-year forms because some of the former will be destroyed when the latter exit the nests in the first year (Table 3). Thus Cohen's requirement that viability of one- and two-year forms be equal seems not to be satisfied. In this regard, the advantage of producing a greater proportion of two-year females than two-year males may simply be a mechanism to reduce mortality levels of two-year forms because females almost always occur in the inner cells of the nest where mortality due to emergence of one-year forms is minimal. Thus some degree of linkage between sex and developmental time in such a system would be selected for. Without linkage, sibling-effected mortality on two-year forms would be even higher.

Despite the apparent lack of agreement between the data and the predictions of Cohen (1966, 1968), the between year variation in

proportion of one- and two-year forms within sites for each species (Fig. 1) suggests that the relative fitness of these forms is determined by environmental conditions. What these conditions are and how they interact with the genotypes to maintain a balanced polymorphism (if indeed it is balanced) remains to be studied.

An interesting ramification of varying selective pressures upon one- and two-year forms is the indirect effect upon the sex ratio of the population. Elsewhere, we (Tepedino and Torchio 1982a) have suggested that data from a long-term field study of *O. lignaria propinqua* Cresson (a univoltine species) supports Fisher's (1958) theory of an equilibrium sex ratio. In the three species studied here, however, it appears that any approach toward equilibrium sex ratio values is dependent upon constraints imposed by selection for parsivoltinism. For example, since there is an association between the two-year form and the female sex, an increase in the relative fitness of two-year forms in any year could divert the population away from equilibrium and towards a female bias in subsequent years. The potential for such diversion should depend on the genetic system responsible for the polymorphism. However, the absence of any consistent tendency for population sex ratios of these species to move towards equilibrium (Fig. 1) suggests that this may be a real phenomenon.

SUMMARY

Offspring from nests constructed in wooden domiciles by three non-social species of *Osmia* bees at two sites in northern Utah displayed differences in the time required to complete development to the adult stage. Some members of each age cohort emerged in the following year, but a substantial proportion required two years to complete development. We propose the term "parsivoltine" to describe such emergence patterns.

There were differences in the proportion of one-year forms, both between years, within sites and between sites, within years for each species. The factors influencing these changes are unclear at present. The distribution of one-year and two-year individuals within nests suggests that environmental factors alone do not act on either the female parent or on her offspring to determine the developmental fate of the offspring. Many nests contained both one- and two-year

forms in unpatterned linear arrangements. All three species appear to be genetically polymorphic for the time necessary to complete development.

There was an association between sex and time required to complete development. Two-year forms were more frequently female than male and one-year forms were more frequently male than female. Female offspring are also typically placed in the innermost cells of the nest. In these linear nests, if a two-year form occurs between the nest exit and a one-year form, then the latter will frequently destroy the former to gain egress from the nest. Thus, this association between sex and developmental time may act to lower sib caused mortality.

In addition, the association between sex and developmental time may constrain an approach to the equilibrium sex ratio because of selection for a particular developmental form.

Although spatiotemporal heterogeneity of weather and/or resources has frequently been offered as an explanation for such developmental polymorphisms, it is by no means clear that this is the case for these species of *Osmia*. The high proportion of two-year forms, and the differences between developmental forms in mortality, and perhaps fecundity as well, do not fit the profile which is typically offered for parsivoltine species.

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A REVIEW OF THE GENUS *MALLADA*
IN THE UNITED STATES AND CANADA,
WITH A NEW SPECIES (NEUROPTERA: CHRYSOPIDAE)

BY PHILLIP A. ADAMS¹ AND J. ALLAN GARLAND²

Analysis of the Canadian chrysopid fauna (Garland, 1981) revealed an undescribed species of *Mallada* ranging into southern Ontario. Accordingly, a draft description and illustrations were transmitted to the senior author. As few of our species have been given modern redescrptions, it is appropriate to review the status of all four known members of this genus from the U.S. and Canada.

The taxonomic status of *Mallada* was discussed by Adams 1975, and a detailed treatment of genitalic morphology given by Principi 1977. The genus is characterized by: left mandible toothed, inner gradate crossvein of forewing ending in a branch of radial sector, not on pseudomedia (Fig. 20); pseudomedia not comprising any crossveins; micropoculae or cuticular glands present on male pronotum, microtholi absent, tignum and gonapsis present, arcessus normal; ectoprocts and hypoalva (eighth and ninth sternites) without unusual projections, larva trash-carrying and overwintering (Séméria, 1977).

Mallada is primarily an Old World genus, constituting a major part of the chrysopid fauna of Europe, Africa, India, Southeast Asia, and Australia. Although New 1980 does not subdivide the Australian "*Chrysopa*" into genera, or species groups, it is possible tentatively to assign species on data given; 15 of the 47 species of Chrysopinae fall into *Mallada*. Tjeder 1966 points out that 19 of the 39 African "chrysopas" (*Saurius* + *Glenochrysa* + *Chrysoperla* + *Brinckochrysa* + *Apertochrysa* + *Anisochrysa*) are assignable to *Anisochrysa* (i.e., *Mallada*), and places 22 additional Old World species in that taxon. Aspöck et al. 1980 list 15 European *Mallada* species (as *Anisochrysa*). In the New World, there are only 5 known species, *M. (Triadochrysa) triangularis* Adams 1978 from Mexico, and the other North American species discussed below.

¹Department of Biology, California State University, Fullerton, California 92634.

²Department of Entomology, Macdonald College of McGill University, Ste-Anne-de-Bellevue, Quebec H9X 1C0

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Mallada macleodi sp. nov.

DESCRIPTION. Head narrow, pale green, eyes large, antennae unmarked; genae with a shiny narrow black band from margin of eye, extending to anterior lateral edges of clypeus; labrum black posterolaterally, green medially (Fig. 3); palpi blackish throughout; frons raised anteriorly; face with scattered setae, some longer anteriorly on clypeus.

Thorax pale green, pronotum with two anterolateral brown patches; setae whitish. Legs green, pretarsal claws deeply excised.

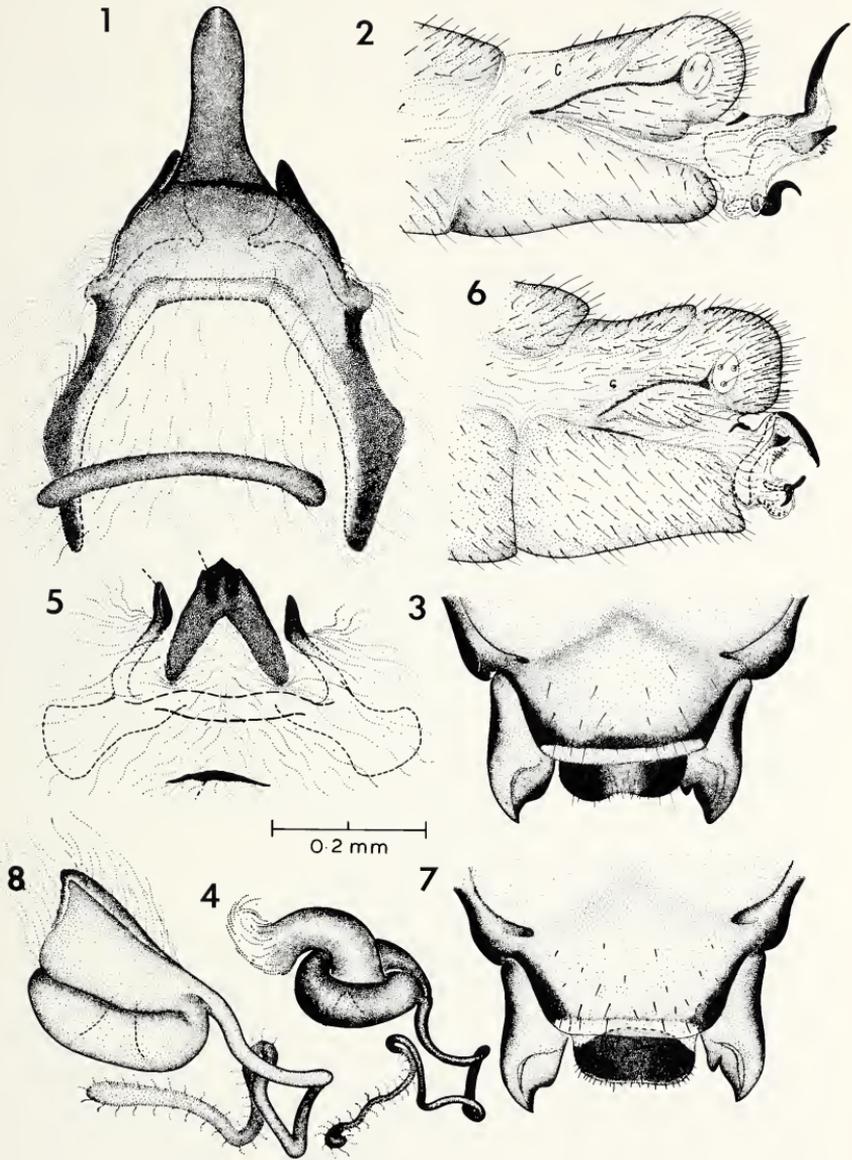
Abdomen green, setation normal, microtholi absent.

Male terminalia (Fig. 2). Sternites VIII+IX fused, elongate; dorsal apodeme long, prominent; ventral apodeme absent. Genitalia (Fig. 1) with broad transverse tignum; gonarcus expanded laterally, rectangular dorsally; entoprocessus prominent, expanded ventromedially; arcessus broadly continuous with dorsum of gonarcus, sclerotised proximally, produced caudad and slightly down-curved, apex bluntly pointed; gonosaccus rudimentary, with only a few small straight gonosetae positioned between the ventromedial expansions of the entoprocessus; gonapsis (Figs. 9, 10) three-pronged, with lateral wings narrow, the caudal process dorsoventrally expansive proximally and tapering as an acuminate downcurved hook, broad internal saccus terminates in a vertical lobe; gonocristae sparse and only minutely developed on hypovalva.

Female terminalia. Subgenitale membranous proximally, with many microthecae; apical lobe notched; transverse callus prominent, with an ental excavation but not a cavity. Spermatheca (Fig. 4) pillbox-shaped; vela tubular, conspicuously bent toward spermathecal bulb.

Wings. Pterostigmata prominently marked, brownish. Venation narrowly margined with brownish amber, especially in forewing, gradates of forewing dark, of hind wing amber. Many crossveins of forewing dark; costals all dark, male with 19 (22.7) 26, female with

Fig. 1-4, *Mallada macleodi*: 1, dorsal aspect of male genitalia (Ontario); 2, same, terminalia with structures everted; 3, labrum and mandibles, female, Ontario; 4, same as 3, spermatheca. Fig. 5-8, *Mallada perfectus*: 5, dorsal aspect of genitalia; British Columbia; 6, same as 5, male terminalia with structures everted; 7, labrum and mandibles, female, British Columbia; 8, same as 7, spermatheca. Scale is for genitalia and spermathecae.



21 (24.2) 26 (mean in parentheses). Inner gradate series of forewing normal for the genus, terminating on a branch of the radial sector (Fig. 20). Forewing length: male 10.0 (11.5) 12.5, $n=10$; female 12.0 (13.0) 13.7, $n=10$ (mm, mean in parentheses). TYPE MATERIAL. Holotype: TEXAS, Erath Co.: Stephenville, 20. iv.1981, ♂, C. W. Agnew (MCZ No. 32576).

Paratypes. ARIZONA. Santa Cruz Co.: 2 mi SW Patagonia, 30.VII.1948, F. Werner & W. Nutting, rich willow-cottonwood bottom, 4050 ft. (MCZ). Yavapai Co.: Granite Dells 4 mi. N. of Prescott, 28.vii. 1970, 1 ♂, L. Martin (LACMNH). KANSAS. Manhattan: VI, 1 ♂, R. C. Smith (CNC, det. Smith [as *Chrysopa cockerelli*]); VI 1 ♂; 17.VI.1920, 1 ♀; 19.VIII.1920, 1 ♀; 9.VII.1921, 1 ♂; 8.IX.1921, 1 ♀; 23.VI.1922, 1 ♂; 1.VIII.1922, 1 ♂; 6.VIII.1931, 2 ♂, 1 ♀; 11.VIII.1931, 1 ♂, (R. C. Smith, KSU). ONTARIO. Durham Co.: Kendal, 17.VII.1967, 1 ♀; 24.VII.1967, 1 ♀, J.C.D. Riotte & L. Kohalmi, ultra-violet light (ROM). Lambton Co.: Pinery Prov. Pk., Ausable River near riverside campground, 3.VII.1977, sweeping understory shrubs, 1 ♂, E. Oleksuk (ROM #770108). Renfrew Co.: White Lake, 4.VIII.1966, 1 ♀, P. D. Hebert, ultra-violet light (ROM, in fluid).

TEXAS. Chisos Mts., 9-10.VII, 1 ? [abdomen missing], 9-12. VII, 1 ♂, W. Nutting & F. Werner (MCZ Paratype No. 32576). Erath Co., Stephenville, 8.v.28.v.1981, 52 specimens, C. W. Agnew (MCZ, PAAC, CWA). Burnett Co.: Inks Lake St. Park, 4.iv.1981, 1 ♀, C. W. Agnew (CWA). Randall Co.: Palo Duro Canyon St. Park, 11.v.61, 50 specimens, L. Martin, R. H. Reid, W. A. Rees, R. J. Ford (LACMNH). MARYLAND. Howard Co.: 12.vii.1967, 1 ♂, 1 ♀, at white light, E. MacLeod [labelled as "*Chrysopa* sp. indet., det. E. G. MacLeod] (PAAC).

REMARKS. The specific epithet recognized Ellis G. MacLeod, who many years ago collected material of this species, pointed out its existence to the senior author, and generously presented material for study. This species is easily separable from *luctuosus* and *sierra* by its lack of black pronotal markings, but is easily confused with *perfectus*, which differs in having an entirely black labrum, usually fewer and paler costal crossveins, and more prominently brown-bordered venation. It is safest to verify identifications by genitalic dissection.

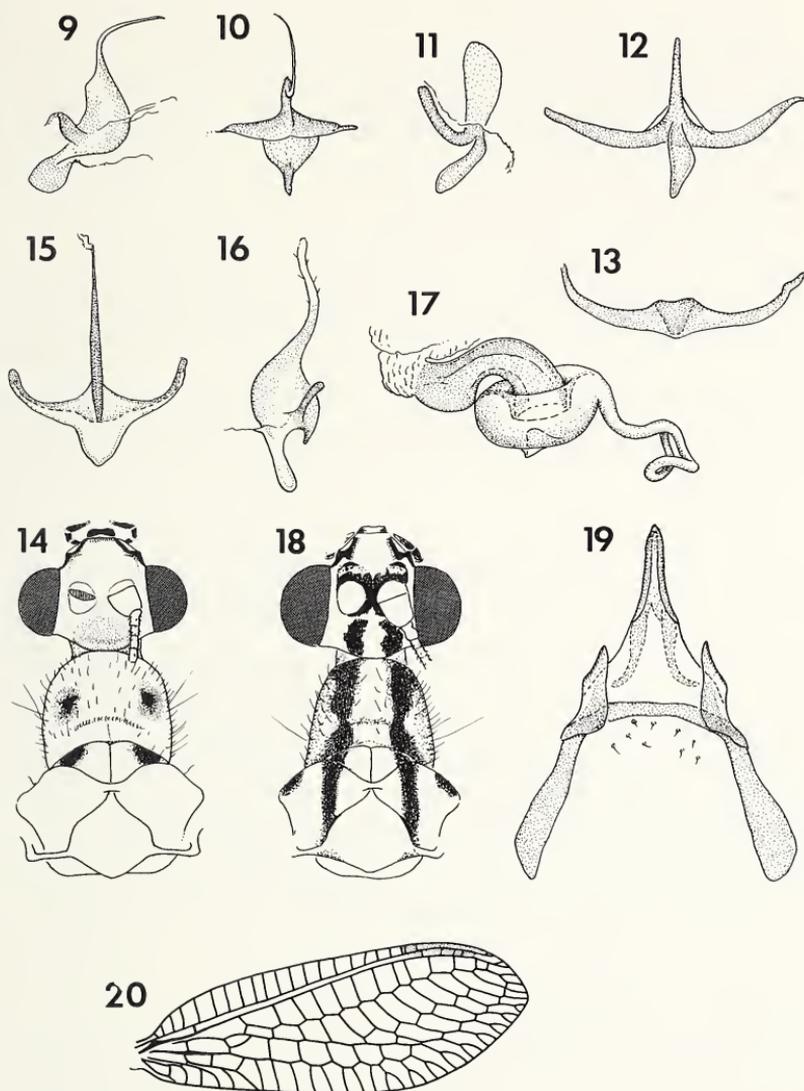


Fig. 9-10. *Mallada macleodi*: gonapsis, lateral and dorsal views, Texas. Fig. 11-12, *M. perfectus*: gonapsis, lateral and posteroventral views, Shasta Co., Calif. 13-14, *M. sierra*: gonapsis dorsal, head and thorax, dorsal; Fig. 15-19, *M. luctuosus*: 15-16, gonapsis, ventral and lateral views; 17, spermatheca; 18, head and thorax, dorsal; 19, gonapsis and arcessus, ventral. Fig. 20, *M. macleodi*, venation of male forewing, Ontario, showing inner gradate vein ending on a branch of radial sector (and an extra crossvein, in the last gradate cell, a not-uncommon condition).

The new species clearly was the insect which the late Dr. R. C. Smith studied from Manhattan, Kansas (Smith 1922, as *Chrysopa cockerelli*). His immatures were debris carriers and overwintered as larvae, confirming the generic assignment. Smith found adults in June (CNC), others in August in association with willows; he deserves credit for observing that the "black lines to mouth not connecting, though the labrum is light brown" (Smith *op. cit.*: 1367, including Fig. 163). Consequently, we have a fairly complete description of the immature stages of the new species, and it is the only Nearctic representative of *Mallada* to have been studied in such detail.

On present evidence, the new species occupies the central part of the continent, ranging into Canada in southern Ontario and coming into contact with the more western *M. perfectus* in Arizona and New Mexico.

Mallada perfectus (Banks 1895)

Chrysopa perfecta Banks 1895: 516–517. Holotype ♀ MCZ No. 11914, El Taste, Baja Calif.

Chrysopa cockerelli Banks 1903:154–155, **new synonymy**. Holotype ♀ MCZ No. 11375, East Las Vegas, N. M.

Chrysopa marginalis Banks 1906a:5 (not *C. marginalis* Navás 1905).

Chrysopa injusta Banks 1906b:98–99, **new synonymy**. Holotype ♀ MCZ No. 11374, Mts. nr Claremont, Calif. (Baker).

Mallada perfectus (Banks), Adams 1975:172.

DESCRIPTION. Genal stripe black, labrum (Fig. 7) wholly black, palpi black, antennae pale. Body light green with no middorsal stripe, pronotum with two cinnamon-brown patches. Wings with costal veinlets black at ends, pale in middle, ♂ costal veinlets: 16–(18.7)–21, N=10; ♀: 18–(20.3)–22, N=10 (mean in parentheses); transverse veins conspicuously brown-bordered.

Male terminalia. Apodeme of ninth tergite articulates on short apodeme of sternites 8+9 (Fig. 6), arcessus (Fig. 5) short, broad, with lateral subapical projections; gonapsis (Fig. 11–12) with spatulate emergent process, well-developed arms and simple internal bulb. Gonocristae small, but larger than in *M. macleodi*.

Female. Spermatheca with broad-based usually short erect vela.

DISTRIBUTION. Calif., Ore., Wash., British Columbia, Wyoming, Utah, Colo., Ariz., N.M., Baja Calif.

REMARKS. This species occurs throughout the Western United States, but is commonest in the Southwest. The short mediuncus and spatulate process of the gonapsis readily distinguish the males from those of *M. macleodi*, and the females are identifiable by the broad-based erect vela. Some Arizona specimens have the vela nearly as elongate as that of *macleodi*, but never curved.

Mallada sierra (Banks) **new combination**

Chrysopa sierra Banks 1924:431.

DESCRIPTION. This species is structurally and colorationally like *M. perfectus*, except for the following: pronotum with 2 black spots each surrounded by a patch of cinnamon brown (Fig. 14). Mesoprescutum with 2 black spots. Wings with black spot at base of costal area; forewing with black spot at intersection of 2A2 and 3A. Crossveins darker than in *perfectus*, and brown-bordering of veins less pronounced. Gonapsis (Fig. 13) with chisel-shaped reduced medial process and reduced bulb. Gonocristae less developed than in *perfectus*.

MATERIAL EXAMINED. Holotype ♀, Calif., [Los Angeles Co.], San Gabriel Mts., Sister Elsie Peak, 10-vi [F. Grinnell] MCZ No. 14858. Additional: CALIF., Shasta Co., 10 mi. N. Redding, Mountaingate, 1000 ft., 4-8.vi.1981, 7 ♀, R. B. Miller (PAAC), 8 mi. N. Redding, 800 ft., 30.v-6.vi.1981, 4 ♂, 3 ♀, R. B. Miller (PAAC). ARIZ. Santa Rita Mts., 24.vii.1927, R. H. Beamer (PAAC ex R. C. Smith). ORE. Jackson Co.: Green Springs, 27.viii.1962, J. S. Buckett, 1 ♀. WASH. Yakima Co.: Ft. Simcoe, 1.viii.1962, J.F.G. Clarke, 1 ♀, (USNM).

REMARKS. This species is readily distinguished by the pronotal and mesonotal markings, and in the male by the simplified structure of the gonapsis. There has been some question as to whether *sierra* is a distinct species or merely a colorational variety of *perfectus*. In Shasta County, where these two species are sympatric, *sierra* appears early in the season, and *perfectus* somewhat later, pointing to the possibility of some seasonal isolation; in 1981, *sierra* was relatively common while *perfectus* was scarce (R. B. Miller, pers. comm.) thus providing some indication of the independence of population fluctuations in these two taxa. The interaction of these two

species is at present under study by C. A. Tauber (pers. comm.), who reports that they interbreed readily in the laboratory. Despite this, because of the consistence of the colorational and male genital differences, plus slightly divergent seasonality, it seems preferable to regard *sierra* as distinct.

Mallada luctuosus (Banks)

Chrysopa luctuosa Banks 1911:343.

Mallada luctuosus (Banks) Adams 1975:172.

DESCRIPTION. Green, antennae pale, head and thorax marked with black and brown as in Fig. 18; brown stripes continue over metathorax and abdomen. Thorax with longitudinal pleural stripe. Forewings with bases of longitudinal veins, except costa and radius, dark, transverse veins dark; hind wings less prominently dark-veined. Abdominal sternites heavily dark-marked.

Genitalia. Arcessus (Fig. 19) elongate. Gonapsis (Fig. 15, 16) with emergent process thin, ribbonlike apically with seta-like projections; anterior pocket wide-based. Spermatheca with tubular arcuate vela inserted in doughnut shaped body, ventral impression small.

MATERIAL EXAMINED. Holotype ♂, N.M., Ft. Wingate, 26.vi, MCZ No. 11383. Additional: ARIZONA. Madera Can., Santa Rita Mts., 16.viii.1949, P. Adams (PAAC); Cochise Co.: Huachuca Mts., Sunnyside, 14.vii.58, L. Martin (PAAC); Chiricahua Mts., S.W. Research Station, 5 mi. W. Portal, 5400 ft., 1.viii.1966, R. E. Dietz (PAAC), 28.vi.1960, J. M. Linsley (U. Calif. Davis); Globe, Pinals, 18.vii.1948, W. Nutting, F. Werner (MCZ). COLORADO. Mesa Verde Nat. Park, Campground, 12.vii.1959, J. & C. Northern (LACMNH). NEBRASKA. Meadville, 10.vi.31, B. Patterson (FMNH, Chicago).

REMARKS. This species is immediately recognizable among *Mallada* species by the dark longitudinal veins and conspicuous black and brown body markings. It is interesting to note that the forms of the arcessus, gonapsis, and spermatheca are more similar to those of *macleodi* than are those of *perfectus*, despite the extreme colorational differences.

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D. K. McE. Kevan encouraged one of us (J.A.G.) to study the Canadian chrysopid fauna, which led to discovery of the Ontario specimens and preparation of the draft manuscript and species description, including privately financed travel to Ottawa and Boston. Material for study was loaned by H. D. Blocker, Kansas State University (KSU); Mary Hathaway, and K. Jepson, Museum of Comparative Zoology, Harvard University (MCZ); J. E. H. Martin, Biosystematics Research Institute, Agriculture Canada, Ottawa (CNC); C. W. Agnew, Texas Agricultural Experiment Station; G. B. Wiggins and B. D. Marshall, Royal Ontario Museum (ROM), C. L. Hogue, Los Angeles County Museum of Natural History (LACMNH). R. B. Miller collected critical material of *M. sierra* and *perfectus*.

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POLYGyny AND POLYDomy IN THREE NORTH
AMERICAN SPECIES OF THE ANT GENUS
LEPTOTHORAX MAYR (HYMENOPTERA: FORMICIDAE)¹

BY

THOMAS M. ALLOWAY,² ALFRED BUSCHINGER,³ MARY TALBOT,⁴
ROBIN Stuart,² AND CYNTHIA THOMAS²

GENERAL INTRODUCTION

This paper deals with certain behavioral and ecological factors which may be relevant to the evolution and maintenance of social parasitism in ants. We will argue that some of the same factors which might predispose one species to evolve into a social parasite might make resistance to parasitism difficult for a closely related species.

After their mating flight, the queens of most nonparasitic ant species found new colonies alone. A queen of such a species finds a suitable nesting place, excavates a small cavity, and seals herself inside. She then lays a clutch of eggs and feeds her first larvae a special "baby food" derived metabolically from the degeneration of her wing muscles and fat body. These larvae mature to become female workers which forage for food, enlarge the nest, feed the queen, and rear subsequent broods of workers and reproductives. Mature ant colonies usually occupy only one nest (monodomy). However, the number of queens in typical mature colonies varies. Colonies of some species never contain more than one functional queen (monogyny), while colonies of other species often have multiple queens (polygyny) (Buschinger 1974).

However, the queens of all known obligatory slave-making, inquiline, and temporary-parasite species found colonies non-inde-

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2. Erindale College, University of Toronto, Mississauga, Ontario, CANADA L5L 1C6.

3. Fachbereich Biologie, Institut für Zoologie, Technische Hochschule, 61 Darmstadt, Schnittspahnstr. 3, Federal Republic of Germany.

4. The Lindenwood Colleges, Saint Charles Missouri, U.S.A. 63301.

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pendently. The parasite queen finds a colony of her host species, enters it, and somehow usurps the role of a host-species queen. The host-species workers then raise the parasite queen's brood.

Species of temporary parasites possess a completely functional worker caste. At first, the temporary-parasite workers and the host-species workers exist alongside one another. However, when the host-species workers die, they are not replaced; and a pure colony of the temporary-parasite species develops. The workers of slave-making parasites are highly specialized for fighting and raiding the nests of host-species colonies; and as a consequence of their raids during which they capture host-species worker pupae and larvae, a force of host-species workers (or "slaves") is maintained. Inquiline parasites either have no worker caste at all; or, if one is present, the workers seem to play no role in maintaining the colony. In some cases, a continuing supply of host-species workers is maintained by the host-species queen's coexisting with the inquiline queen (Buschinger, 1970; Wilson, 1971).

This paper presents data concerning several aspects of the behavioral biology of three North American species of the ant genus *Leptothorax* Mayr: *L. ambiguus* Emery, *L. curvispinosus* Mayr, and *L. longispinosus* Roger. These species interested us because they are hosts to three closely related parasite species. All three species are enslaved by the obligatory slave-makers *L. duloticus* Wesson and *Harpagoxenus americanus* (Emery); and *L. curvispinosus* is the host of the workerless inquiline species *L. minutissimus* M. R. Smith (Alloway, 1979; Creighton, 1950). Thus, studies of the behavior and ecology of these three nonparasitic species may elucidate the ethological and ecological circumstances under which social parasitism evolves and is maintained.

NUMBER OF QUEENS AND THE SEX OF BROODS IN NESTS

Headley (1943) and Talbot (1957) reported that the number of queens in nests of *L. curvispinosus* and *L. longispinosus* is quite variable. Some nests contain several dealate queens, some contain one, and some contain none at all. Observations indicated that the number of queens in nests of *L. ambiguus* is also variable (Alloway, unpublished data). In addition, we found that many queenless nests of all three species contained broods which either included worker and queen pupae at the time of collection or matured into worker and queen (as well as male) pupae.

These observations raised a number of hypotheses. Nests containing more than one dealate queen suggested that some colonies of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* are polygynous. The production of female pupae in queenless nests raised at least three possibilities which are not mutually exclusive. First, a queenless nest might be part of a polydomous colony with the female pupae being the progeny of one or more queens located in another nest at the time of collection. Second, these species might possess numerous ergatomorphic reproductives, individuals which resemble workers morphologically but which have a spermatheca, can be inseminated, and are capable of laying fertilized female eggs (Buschinger 1975, 1978). Third, a queenless nest might be the remnant of a colony whose queen had died.

MATERIALS AND METHODS

Over a two-year period, nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* were collected during late March, April, May and early June; and weekly collection of *L. ambiguus* and *L. longispinosus* were obtained throughout June, July, and August of one summer. We recorded the number of queens present in every nest. In nests containing pupae at the time of collection, the kind of pupae present (queen, worker, and/or male) was also noted. Finally, nests of all three species were collected during the early spring of one year and cultured in the laboratory to determine the sex and caste of the pupae which matured from larvae present in the nests at the time of collection.

Results

Table 1 contains data regarding the proportions of nests collected during the springs of two years which contained 0, 1, or more than 1 queen. About 1/5 of the nests contained more than one dealate queen; about 1/3 contained no queen; and the remainder contained 1 queen. Tables 2, 3, and 4 reveal that the proportion of queenless nests was similar across years and throughout the season.

Table 2 presents the numbers and proportions of nests of all three species collected in the spring and containing pupae of various kinds. Table 3 presents similar data for nests of *L. ambiguus* and *L. longispinosus* collected throughout the summer. These tables reveal that many freshly collected queenless nests contained female (worker and queen) pupae. Table 4 presents data concerning the broods

Table 1. Number and Percent of Nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* Containing 0, 1, or More Than 1 Queen

Number of Queens	<i>L. ambiguus</i>	<i>L. curvispinosus</i>	<i>L. longispinosus</i>	Total
0	453 (29.7%)	177 (36.3%)	237 (37.0%)	867 (32.7%)
1	765 (50.3%)	228 (46.7%)	311 (48.6%)	1304 (49.2%)
More than 1	304 (20.1%)	83 (17.0%)	92 (14.4%)	479 (18.1%)
Total	1522 (100.0%)	488 (100.0%)	640 (100.0%)	2650 (100.0%)

which matured from queenless and queenright nests of the three species collected in the early spring and then cultured in the laboratory. Once again, many queenless nests produced female pupae.

Discussion

First, we want to stress that variability in the number of queens in nests of *L. curvispinosus* and *L. longispinosus*, first noted by Headley (1943) and Talbot (1957), is not a local or transitory phenomenon and note that the number of queens in nests of *L. ambiguus* is also quite variable. However, of far greater importance is the large proportion of queenless nests of all three species which produce female (as well as male) pupae. This fact raised questions about the possible existence of ergatomorphic reproductives and polydomy.

POLYGYNY AND WORKER FERTILITY

To demonstrate that a species of ant is facultatively polygynous, one must show that two or more fertile inseminated females can coexist in nests. Headley (1943) and Talbot (1957) reported the occurrence of multiple queens in some nests of *L. curvispinosus* and *L. longispinosus*. However, these authors did not determine whether more than one queen was inseminated and egg-laying. Wilson (1974a, b) observed several multiple-queen nests of *L. curvispinosus* and reported that all the queens laid eggs. However, as we shall show, uninseminated queens and workers sometimes lay eggs. Thus, the question of the occurrence of polygyny involving fertile inseminated queens remained open. In addition, the production of female pupae in many queenless nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* suggested, as one possibility, the hypothesis that these species might possess frequent ergatomorphic female reproductives.

Table 2. Number and Percent of Queenright and Queenless Nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* Containing Pupae and/or Alate Reproductives of Various Types at the Time of Collection (1977-78)

Species	Queenright Nests			Total
	♀ and/or ♀ Only	♀ and/or ♀ and ♂	♂ Only	
<i>L. ambiguus</i>	180 (83.3%)	31 (14.4%)	5 (2.3%)	216 (100.0%)
<i>L. curvispinosus</i>	23 (53.5%)	19 (44.2%)	1 (2.3%)	43 (100.0%)
<i>L. longispinosus</i>	76 (66.1%)	33 (28.7%)	6 (5.2%)	115 (100.0%)
Total	279 (74.6%)	83 (22.2%)	12 (3.2%)	374 (100.0%)

Species	Queenless Nests			Total
	♀ and/or ♀ Only	♀ and/or ♀ and ♂	♂ Only	
<i>L. ambiguus</i>	90 (80.4%)	16 (14.3%)	6 (5.4%)	112 (100.0%)
<i>L. curvispinosus</i>	19 (59.4%)	9 (28.1%)	4 (12.5%)	32 (100.0%)
<i>L. longispinosus</i>	35 (50.0%)	24 (34.3%)	11 (15.7%)	70 (100.0%)
Total	144 (67.3%)	49 (22.9%)	21 (9.8%)	214 (100.0%)

Materials and Methods

To determine whether polygyny involving inseminated queens occurs in these species, we dissected all the queens present in samples of nests containing more than one dealate queen. To determine whether ergatomorphic female reproductives occur frequently, we dissected all the "workers" from five queenless nests of each species which had produced female broods when cultured in the laboratory.

For each queen or worker dissected, we noted the following characteristics:

- a. the number of ovarioles.
- b. the length of the ovaries. In young virgin queens, the ovaries are thin and about 3/4 the length of the queen's gaster. When a queen becomes fertile, her ovaries grow until they eventually become as long as her entire body. In old fertile queens, the folded and coiled ovarioles enlarge until they almost completely fill the gaster.
- c. the presence or absence of any growing oocytes in the ovarioles. The ovarioles of sterile individuals contain no oocytes; and in hibernating fertile queens, the oocytes are transparent. As yolk is

deposited in growing oocytes, they become opaque; and ripe eggs are white.

- d. the presence or absence of corpora lutea in the bases of the ovarioles. These yellowish residues of nutritional cells remain in the ovaries when eggs have been laid.
- e. the presence or absence of a full or empty spermatheca. Individuals with no spermatheca or an empty spermatheca are incapable of laying fertilized eggs which develop into workers or queens. An empty spermatheca appears as a small, transparent bladder on the common oviduct. When full of sperm, the spermatheca is white and superficially resembles a ripe egg in size and coloration.

Results:

Our dissections enabled us to distinguish several physiologically different kinds of queens. To simplify the presentation of data, we

Table 3. Number of Queenright and Queenless Nests of *L. ambiguus* and *L. longispinosus* Collected during June, July, and August and the Composition of their Broods

<i>L. ambiguus</i>						
	Queenless nests			Queenright nests		
	Type of Brood			Type of Brood		
	♂ only	♀ and ♀	♀, ♀, and ♂	♂ only	♀ and ♀	♀, ♀, and ♂
June	0	5	0	0	28	0
July	0	11	17	1	37	71
August	2	9	8	2	32	77

<i>L. longispinosus</i>						
	Queenless nests			Queenright nests		
	Type of Brood			Type of Brood		
	♂ only	♀ and ♀	♀, ♀, and ♂	♂ only	♀ and ♀	♀, ♀, and ♂
June	0	0	1	0	2	1
July	0	0	4	0	1	12
August	0	0	1	0	0	3

will employ a set of terms developed by Buschinger (1968) to describe these individuals. These terms are defined as follows:

A-queen: An inseminated, fully fertile queen. The ovaries are as long, or nearly as long, as the whole body. The ovarioles contain many developing oocytes; and conspicuous corpora lutea are present. The spermatheca is full of sperm. Such queens are normally more than a year old.

b-queen: An inseminated young queen. At the time of our study (in mid-summer), the ovaries were about half their eventual length and contained developing oocytes. Sometimes a small corpus luteum was visible in the base of one or two ovarioles. The spermatheca was full. We believe that these females had mated the previous summer and were in the process of becoming fully fertile. After mating, newly inseminated queens have very short ovarioles with no developing oocytes. If a nest, before the mating season, contains one or more A-queens and one or more b-queens with growing oocytes, we conclude that that nest represents all or part of a colony which adopted one or more newly mated queens the previous summer.

Table 4. Number and Percent of Queenright and Queenless Nests of *L. ambiguus*, *L. curvispinosus* and *L. longispinosus* Collected in the Spring of 1979 which Produced Broods of Various Compositions when Cultured in the Laboratory

<i>Queenright Nests</i>				
<i>Species</i>	♀ and/or ♀ only	♀ and/or ♀ and ♂	♂ only	Total
<i>L. ambiguus</i>	68 (47.5%)	60 (42.0%)	15 (10.5%)	143 (100.0%)
<i>L. curvispinosus</i>	95 (65.5%)	49 (33.8%)	1 (0.7%)	145 (100.0%)
<i>L. longispinosus</i>	42 (56.0%)	22 (29.3%)	11 (14.7%)	75 (100.0%)
Total	205 (56.5%)	131 (36.1%)	27 (7.4%)	363 (100.0%)
<i>Queenless Nests</i>				
<i>Species</i>	♀ and/or ♀ only	♀ and/or ♀ and ♂	♂ only	Total
<i>L. ambiguus</i>	37 (52.1%)	24 (33.8%)	10 (14.1%)	71 (100.0%)
<i>L. curvispinosus</i>	35 (43.2%)	38 (46.9%)	8 (9.9%)	81 (100.0%)
<i>L. longispinosus</i>	12 (38.7%)	12 (38.7%)	7 (22.6%)	31 (100.0%)
Total	84 (45.9%)	74 (40.4%)	25 (13.7%)	183 (100.0%)

c-queen: An uninseminated, old, sterile female. The ovaries are short and contain no oocytes. The spermatheca, if present, is empty; but it may not be present. The wing muscles are degenerate and have been replaced by fat body. (The term d-queen would denote a young dealate female which had not been inseminated. The reproductive organs resemble those of c-queens, but the wing muscles have not yet degenerated. We found no d-queens, probably because we performed our dissections before the sexual brood had eclosed.)

C-queen: An uninseminated, egg-laying female with ovarioles like those of an A-queen. Sometimes there is no spermatheca. In this paper, we report the occurrence of significant numbers of individuals of this type for the first time in Leptothoracine ants. However, they occur rather frequently in colonies of *Formica polyctena* Foerster (Ehrhardt 1970) and *Monomorium pharaonis* (L.) (Petersen & Buschinger 1971). The origin of these females in nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* is unclear. They may be old individuals which were once inseminated but whose supply of sperm has been exhausted. However, the existence of egg-layers with no spermatheca indicates that insemination is not a necessary prerequisite for fertility. Recently U. Winter (personal communication) found that *Harpagoxenus sublaevis* males often transmit very little or no sperm during their first copulation. Thus, a queen which had mated only once with such a male might become fertile after receiving only the secretions of the males' accessory glands. Perhaps a similar mechanism accounts for the existence of C-queens in these species of *Leptothorax*.

The results of the dissections of queens of each species and of workers will be presented separately.

1. *Leptothorax ambiguus*

A total of 88 dealate females from 30 multiple-queen colonies was dissected. Only about 1/2 the multiple-queen nests contained more than one A-queen and were thus "truly polygynous" (see Table 5). Three of these truly polygynous nests also contained one or two b-queens and were thus in the process of developing polygyny to a higher degree.

Table 5. Number and Type of Dealate Females in Multiple-Queen Colonies of *Leptothorax ambiguus*

Colony No.	n Dealate					Remarks
	♀♀	A-♀♀	b-♀♀	c-♀♀	C-♀♀	
1	2	2	-	-	-	
2	2	2	-	-	-	
3	2	2	-	-	-	
4	2	2	-	-	-	
5	2	2	-	-	-	
6	2	2	-	-	-	Colonies No. 1-15 are truly polygynous
7	2	2	-	-	-	
8	2	2	-	-	-	
9	4	2	2	-	-	
10	3	2	-	-	1	
11	3	3	-	-	-	
12	3	2	1	-	-	
13	3	2	1	-	-	
14	5	4	-	-	1	
15	13	2	-	3	8	
16	2	1	1	-	-	
17	2	1	1	-	-	
18	2	1	1	-	-	Colonies No. 16-23 are becoming polygynous
19	2	1	1	-	-	
20	3	1	2	-	-	
21	3	1	1	-	1	
22	3	1	1	-	1	
23	2	-	2	-	-	
24	2	1	-	-	1+	Colony fragment?
25	2	-	1	-	1+	+C-♀ without spermatheca
26	2	1	-	-	1	
27	2	1	-	-	1	
28	3	-	1	-	2	
29	2	-	-	2	-	Colony fragment?
30	6	-	-	2	4	
Total	88	43	16	7	22	

Another 7 nests (No. 16-23 in Table 5) were in the process of becoming polygynous. They contained 1 A-queen and 1 or 2 b-queens. One nest (No. 23) contained 2 b-queens only and was thus also becoming polygynous, although it lacked an A-queen. A number of nests contained one or more C-queens. Most of these

individuals were living with A-queens. Two C-queens without a spermatheca were found in this sample (in nests No. 24 and 25).

2. *Leptothorax curvispinosus*

A total of 64 dealate queens from a sample of 23 multiple-queen nests was dissected. As was the case for *L. ambiguus*, we found all four categories of dealate females in *L. curvispinosus* (see Table 6). However, approximately 3/4 of the *curvispinosus* nests (74%) contained multiple A-queens, as compared to only about 1/2 of the *ambiguus* nests. In addition, all 7 of the multiple-queen *curvispinosus* nests which had only 1 A-queen contained one or more b-queens and were thus becoming polygynous. The total number of C-queens was much lower in *curvispinosus* than in *ambiguus*. However, we found 3 C-queens with no spermatheca; and 2 of these were fully fertile.

3. *Leptothorax longispinosus*

A total of 79 queens from a sample of 26 multiple-queen nests was dissected. The proportion of nests containing more than one A-queen was 65%; and all but one of the other nests contained either one or more b-queens living with an A-queen or more than one b-queen without an A-queen (see Table 7). The only exception was nest No. 23 which contained 7 C-queens living with a single A-queen. One of these C-queens had no spermatheca.

4. The number of ovarioles in queens

Table 8 shows that queens of *L. ambiguus* usually have 6 ovarioles (both ovaries combined). Six is the usual number of ovarioles for most European species of the subgenus *Leptothorax* sensu stricto (=Myrafant M. R. Smith 1950) and for species of the subgenus *Mychothorax* (=Leptothorax sensu M. R. Smith) (Buschinger, unpublished data). However, *L. curvispinosus* queens most commonly have 8 ovarioles; and *L. longispinosus* queens most commonly have 7. Moreover, the number of ovarioles in *L. longispinosus* queens is very variable; and the distribution of ovarioles in single specimens of this species can be quite asymmetrical. One queen with 10 ovarioles had 6 on the left side and 4 on the right; another with 11 ovarioles had 4 on the left and 7 on the right. There was no evidence that the number of ovarioles is correlated with a queen's function in a nest. The number of ovarioles often varied considerable among

Table 6. Numbers and Type of Dealate Females in Multiple-Queen Colonies of *Leptothorax curvispinosus*

Colony No.	n Dealate ♀♀	A-♀♀	b-♀♀	c-♀♀	C-♀♀	Remarks
1	2	2	-	-	-	
2	2	2	-	-	-	
3	2	2	-	-	-	
4	2	2	-	-	-	
5	2	2	-	-	-	
6	2	2	-	-	-	Colony No.
7	2	2	-	-	-	1-16 truly
8	2	2	-	-	-	polygynous
9	2	2	-	-	-	
10	3	3	-	-	-	
11	3	3	-	-	-	
12	3	3	-	-	-	
13	4	4	-	-	-	
14	4	2	2	-	-	
15	4	3	1	-	-	
16	4	3	-	-	1 ⁺	+C-♀ without spermatheca
17	2	1	1	-	-	Colony No.
18	2	1	1	-	-	17-23
19	4	1	3	-	-	becoming polygynous
20	3	1	1	1 ⁺	-	+c-♀ without spermatheca
21	3	1	1	-	1	+C-♀ without spermatheca
22	3	1	1	-	1	
23	4	1	3	-	-	
Total	64	46	14	1	3	

queens in single nests, especially in *L. longispinosus*. Moreover, b- and C-queens on average had no fewer ovarioles than A-queens.

5. Workers

All the queenless nests whose workers were dissected contained one or more egg-laying individuals (see Table 9). However, none of the fertile workers possessed a spermatheca. Thus, we presume that all their offspring are males. Workers invariably had only two ovarioles (one per ovary); and these were never as long and never contained as many corpora lutea as the ovarioles of egg-laying A- and C-queens. Thus, the number of eggs produced by a fertile worker is probably much less than that produced by a queen.

Table 7. Numbers and Type of Dealate Females in Multiple-Queen Colonies of *Leptothorax longispinosus*

Colony No.	n dealate ♀♀	n dealate			Remarks
		A-♀♀	b-♀♀	C-♀♀	
1	2	2	-	-	
2	2	2	-	-	
3	2	2	-	-	
4	2	2	-	-	
5	2	2	-	-	
6	2	2	-	-	
7	2	2	-	-	
8	2	2	-	-	Colonies No. 1-17 truly polygynous
9	2	2	-	-	
10	2	2	-	-	
11	3	3	-	-	
12	3	3	-	-	
13	4	4	-	-	
14	4	4	-	-	
15	6	6	-	-	
16	3	2	1	-	
17	3	2	1	-	
18	2	1	1	-	Colonies No. 18-22 and No. 24-26 becoming polygynous
19	2	1	1	-	
20	3	1	2	-	
21	3	1	2	-	
22	4	1	3	-	
23	8	1	-	7 ⁺	+1C-♀ without spermatheca
24	2	-	2	-	
25	4	-	4	-	
26	5	-	5	-	
Total	79	50	22	7	

Table 8. Ovariole Numbers in Queens of *Leptothorax ambiguus*, *L. curvispinosus*, and *L. longispinosus*

n. ovarioles	4	5	6	7	8	9	10	11	n♀♀	
<i>L. ambiguus</i>	1	1	<u>82</u>	4	-	-	-	-	88	$\bar{x} = 5.99$ $s = 0.39$
<i>L. curvispinosus</i>	-	-	-	11	<u>44</u>	6	-	-	61	$\bar{x} = 7.92$ $s = 0.53$
<i>L. longispinosus</i>	1	4	19	<u>32</u>	18	1	2	2	79	$\bar{x} = 7.05$ $s = 1.22$

Discussion:

These data establish two important points. First, polygyny involving multiple inseminated queens occurs in some nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus*; and polygynous nests imply the existence of polygynous colonies. Polygyny in these three members of the subgenus *Leptothorax* sensu stricto as well as in *L. schaumii* and *L. flavicornis* (Buschinger, unpublished observations) is somewhat surprising in that the majority of European members of the subgenus are strictly monogynous (Buschinger 1967). The form of polygyny exhibited by *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* is also interesting in that the frequent joint presence of A- and b-queens indicates that colonies of these species can adopt young conspecific queens. We will argue below that this tendency to adopt queens is important for understanding the evolutionary origins of parasitic colony foundation.

Second, although our dissections of workers in queenless colonies which produced female pupae revealed that some workers lay eggs, our failure to find any workers with a spermatheca indicates that ergatomorphic reproductive females of the kind seen in the slave-maker *Harpagoxenus sublaevis* are at least not common in *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus*.

Polydomy

This latter finding suggested two possibilities which are not mutually exclusive:

- a. Some queenless nests of these species which produce broods containing female pupae may be parts of polydomous colonies. In such cases, the female pupae would be the progeny of queens located in other nests at the time of collection.
- b. Some queenless nests may represent declining colonies with no queen. The female pupae are the offspring of a dead queen.

Materials and Methods

We collected groups of acorn nests which were very close together in nature and brought the nests back to the laboratory where the ants were established in artificial nests. We then arranged the artificial nests in arenas to duplicate the spatial arrangement of the natural nests and observed the ensuing behavioral interactions. As controls, we tested the effect of placing nests from different parts of

Table 9. Numbers and Percent of Sterile and Fertile Workers in Queenless Nests of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus*

<i>L. ambiguus</i>			
Nest No.	Sterile Workers	Fertile Workers	Total
1	7 (64%)	4 (36%)	11
2	9 (60%)	6 (40%)	15
3	12 (71%)	5 (29%)	17
4	12 (86%)	2 (14%)	14
5	24 (80%)	6 (20%)	30
<i>L. curvispinosus</i>			
Nest No.	Sterile Workers	Fertile Workers	Total
1	13 (93%)	1 (7%)	14
2	18 (72%)	7 (18%)	25
3	17 (81%)	4 (19%)	21
4	16 (70%)	7 (30%)	23
5	15 (71%)	6 (29%)	21
<i>L. longispinosus</i>			
Nest No.	Sterile Workers	Fertile Workers	Total
1	12 (67%)	6 (33%)	18
2	5 (56%)	4 (44%)	9
3	5 (21%)	19 (79%)	24
4	17 (74%)	6 (26%)	23
5	7 (50%)	7 (50%)	14

the same collection site much closer together than they had been found and of placing nests from different sites together.

Two kinds of arenas were employed. One type consisted of a 1 m² area on a table top. The other was a square plexiglass enclosure having an area of 2025 cm² surrounded by plexiglass walls 6 cm high. The ants were confined to the arenas by a thick barrier of petroleum jelly. Colonies were fed an artificial ant diet (Bhatkar & Whitcomb 1970) three times a week; water was continuously available. The experimental room was kept on a 15-h light and 9-h dark photoperiod at a temperature of 22°C ± 1°C.

Results

A total of 28 experiments involving 96 nests of *L. ambiguus* and 5 experiments involving 11 nests of *L. longispinosus* were performed.

Certain pertinent facts about each experiment are contained in Table 10.

The most frequent result for nests which had been close together in nature was so-called "fusion". After a day or two, the ants from the different nests peacefully moved into one of the artificial nests and remained there indefinitely. We are not sure why fusion occurred so frequently in the laboratory. One factor may have been that our artificial nests are somewhat larger than the average acorn. In any case, these peaceful mergers suggest that the ants from adjacent nests were members of the same colony and are thus compatible with the polydomy hypothesis.

Other experiments (e.g. *L. ambiguus* experiments 9, 10, and 23 and *L. longispinosus* experiment 5) supported the polydomy hypothesis more dramatically. The ants continued to occupy more than one nest among which they maintained a more or less continual exchange of workers, brood, and queens. Thus, over a period of several days, a nest was sometimes polygynous, sometimes monogynous, and sometimes queenless. In other experiments, (e.g. *L. ambiguus* experiments 12, 13, 14, 15, 16, 22, 24), it appeared that we observed interactions between two polydomous colonies or between a polydomous and a monodomous colony. For example, in experiments 15 and 16, we had examples of four nests which had been found in two close pairs separated by a somewhat greater distance. The ants from each pair of nests quickly fused, but there was prolonged fighting among the ants from the different pairs of nests.

The results of the control experiments also supported the polydomy hypothesis. Ants from nests not found close together in nature did not usually coexist peacefully. When nests from different parts of the same collection site or from different sites were placed near one another, the result was usually widespread and protracted fighting. However, we observed two exceptions to this rule. In *L. ambiguus* experiment 19, 3 nests which had been an average of 96 cm apart in nature were placed together in a 2025-cm² arena. There was no fighting; and after 12 days, the ants from two queenright nests which had been 118 cm apart in nature peacefully moved into one nest. Even more surprising was the fusion of ants in two queenright nests from different collection sites which we observed in *L. ambiguus* experiment 18. We cannot explain these anomalous results, although we speculate that these species have a limited

Table 10. Results of Polydomy Study
Experiments with *L. ambiguus*

Experiment Number	Type of Experiment	Number of Nests	Mean Distance (cm)	Result
1	Natural distance	3	29	Fusion
2	Natural distance	4	26	Fusion
3	Natural distance	2	7	Fusion
4	Closer than normal	2	277 in nature	Fighting
5	Different sites	3	—	Fighting
6	Different sites	3	—	Fighting
7	Different sites	3	—	Fighting
8	Closer than normal	3	466 in nature	Fighting
9	Natural distance	8	34	Partial fusion much exchange of workers, broods, and queens
10	Natural distance	8	36	Partial fusion much exchange of workers, broods, and queens
11	Natural distance	2	14	Fusion
12	Natural distance	3	32	2 closest fuse, other coexists peacefully
13	Natural distance	5	14	Four merge and attack fifth nest
14	Natural distance	4	20	3 from tight cluster merge, attack, and destroy the fourth

15	Natural distance	4	49	Two pairs of nests. Ants from both pairs merge; then the 2 united nests fight
16	Natural distances	4	45	Same as 15
17	Natural distance	2	6	Fusion
18	Different sites	2	—	No fighting, fusion after 23 days.
19	Closer than nature	3	96	Two merge after 12 days, third remains unchanged. No fighting.
20	Natural distance	2	25	Fusion
21	Natural distance	3	10	Partial fusion much exchange of workers, brood and queens.
22	Natural distance	3	14	Two merge, attack, and destroy the third; then they partially occupy the "enemy" nest.
23	Natural distance	4	23	Frequent exchange of workers, brood, and queens. No fusion.
24	Natural distance	3	39	A close pair of nests and one farther away. The pair merge, attack and destroy the third.
25	Natural distance	—	15	Fighting among all 3 nests. No fusion.
26	Natural distance	3	14	No fighting, but no exchange of workers, brood or queens.
27	Natural distance	2	46	No fighting, but no exchange of workers, brood, or queens.
28	Natural distance	2	58	A little fighting at first. No exchange of workers, brood, or queens.

Table 10. Results of Polydomy Study
Experiments with *L. ambiguus*

Experiment Number	Type of Experiment	Number of Nests	Mean Distance (cm)	Result
1	Natural distance	3	29	Fusion
2	Natural distance	4	26	Fusion
3	Natural distance	2	7	Fusion
4	Closer than normal	2	277 in nature	Fighting
5	Different sites	3	—	Fighting
6	Different sites	3	—	Fighting
7	Different sites	3	—	Fighting
8	Closer than normal	3	466 in nature	Fighting
9	Natural distance	8	34	Partial fusion much exchange of workers, broods, and queens
10	Natural distance	8	36	Partial fusion much exchange of workers, broods, and queens
11	Natural distance	2	14	Fusion
12	Natural distance	3	32	2 closest fuse, other coexists peacefully
13	Natural distance	5	14	Four merge and attack fifth nest
14	Natural distance	4	20	3 from tight cluster merge, attack, and destroy the fourth
15	Natural distance	4	49	Two pairs of nests. Ants from both pairs merge; then the 2 united nests fight
16	Natural distances	4	45	Same as 15
17	Natural distance	2	6	Fusion
18	Different sites	2	—	No fighting. fusion after 23 days
19	Closer than nature	3	96	Two merge after 12 days, third remains unchanged. No fighting.
20	Natural distance	2	25	Fusion
21	Natural distance	3	10	Partial fusion much exchange of workers, brood and queens.
22	Natural distance	3	14	Two merge, attack, and destroy the third; then they partially occupy the "enemy" nest.
23	Natural distance	4	23	Frequent exchange of workers, brood, and queens. No fusion.
24	Natural distance	3	39	A close pair of nests and one farther away. The pair merge, attack and destroy the third
25	Natural distance	—	15	Fighting among all 3 nests. No fusion.
26	Natural distance	3	14	No fighting, but no exchange of workers, brood or queens.
27	Natural distance	2	46	No fighting, but no exchange of workers, brood, or queens.
28	Natural distance	2	58	A little fighting at first. No exchange of workers, brood, or queens.

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Table 10 (Continued)
Experiments with *L. longispinosus*

Experiment Number	Type of Experiment	Number of Nests	Mean Distance (cm)	Result
1	Natural plus one from another site	3 from outside plus one	14 among three from same site	Ants from same-site nests fuse, then attack and destroy the outsider. Colony then partly occupies the "enemy" nest with much exchange of workers, brood, and queens.
2	Closer than normal plus a nest from another site introduced after 3 days.	2	55 in nature for ants from same site	Fighting until ants from one nest kill off ants from the other. Nest from other site also eliminated.
3	Natural distance	2	40	Fusion followed by later re-occupation of both nests with much exchange of workers, brood, and queens.
4	Natural distance	2	5	Fusion
5	Natural distance	2	5	Eventual fusion after 9 days of much exchange of workers, brood, and queens.

number of possible "colony odors". Ants from colonies with different odors fight, but ants from colonies with sufficiently similar odors do not fight and may merge (for a discussion, see Holldobler and Wilson, 1977).

Finally, although some data indicate that polydomy occurs in *L. ambiguus* and *L. longispinosus*, other data indicate that monodomy also occurs. As already noted, many apparently polydomous colonies became monodomous in the laboratory. Similar fusions may occur in nature. In addition, several experiments suggested interactions either between a polydomous and a monodomous colony or between two or more monodomous colonies. There were several instances in which the ants from two or more nests merged and then attacked the ants from another single nest. These results suggest that the ants which merged had comprised a polydomous colony and that the ants which were attacked belonged to another colony. Finally, the results of *L. ambiguus* experiments 25 and 26 suggested interactions among three monodomous colonies; and those of experiments 27 and 28 suggested interactions between two monodomous colonies.

Discussion

The evolutionary significance of polydomy and the question of what proportion of the queenless nests producing broods containing female pupae can be accounted for by polydomy will be discussed below. Here we simply note that some of the queenless nests of *L. ambiguus* and *L. longispinosus* which produce broods containing female pupae are almost surely parts of larger polydomous colonies in which there happened to be no queen at the time of collection. In the absence of data, it would be premature to conclude that polydomy occurs in *L. curvispinosus*. However, queenless nests are common in *L. curvispinosus*; and this fact and the many other similarities between *L. curvispinosus* on the one hand and *L. ambiguus* and *L. longispinosus* on the other suggest that *L. curvispinosus* is also facultatively polydomous.

Colony Foundation

One sign of an incipient ant colony is a nest containing one or more queens, an immature brood, and no workers. Such apparently incipient colonies of *L. ambiguus*, *L. curvispinosus*, and *L. longi-*

spinosus are not easy to find. Under oak and hickory trees where there have been abundant nut falls, most inhabited nests are occupied by more mature colonies. However, over several years, we discovered several apparently incipient colonies of *L. ambiguus* and *L. longispinosus*.

Materials and Methods

We searched for incipient colonies of *L. ambiguus* and *L. longispinosus* in late summer and early autumn. An incipient colony was defined as a nest containing one or more dealate queens with a brood, but no workers.

Results

A total of 15 apparently incipient nests was found, 8 of *L. ambiguus* and 7 of *L. longispinosus*. Table 11 lists the number of queens and the type of brood present when the nests were collected.

We tried to culture incipient colonies in the laboratory. However, perhaps because the artificial nests lacked a source of moisture, we had little success. Although the queens (perhaps unnaturally) foraged for food and water, their broods gradually languished and died. Only *L. ambiguus* nest 7 and *L. longispinosus* nest 5 produced workers in the laboratory.

Table 11 shows that the number of queens in apparently incipient nests of *L. ambiguus* ranged from 2 to 10; and the number of queens in apparently incipient nests of *L. longispinosus* ranged from 1 to 15. These data indicate that queens of *L. longispinosus* found new colonies on a facultatively polygynous basis. So far we have failed to find an instance of apparently monogynous colony foundation in *L. ambiguus*. However, it would be premature to conclude that polygynous colony foundation in *L. ambiguus* is obligatory.

Since we were mainly interested in the behavior of colony-founding queens, we did not dissect the foundresses to determine their reproductive status. However, the presence of male pupae in *L. ambiguus* nests 4 and 8 suggests that one or more of the queens may have become fertile without insemination.

Multiple colony foundresses showed no hostility toward one another. To the contrary, apparently "cooperative" acts were common. All brood was kept in a single pile and seemed to be tended jointly. Mutual grooming was frequent; and queens often regurgitated to one another upon returning from foraging trips. Some groups of queens "took turns" foraging.

Table 11. Apparently Incipient Colonies of *L. ambiguus* and *L. longispinosus*

Incipient Colonies of <i>L. ambiguus</i>		
Colony No.	Number of ♀♀	Brood When Collected
1	5	eggs and larvae
2	3	eggs and larvae
3	2	eggs, larvae, pupae
4	10	eggs, larvae, pupae
5	2	larvae
6	2	eggs and larvae
7	4	eggs and larvae
8	4	eggs, larvae and pupae

Incipient Colonies of <i>L. longispinosus</i>		
Colony No.	Number of ♀♀	Brood When Collected
1	1	Nil
2	1	eggs, larvae, pupae
3	1	Nil
4	5	eggs and larvae
5	2	larvae
6	1	larvae
7	1	eggs, larvae, pupae

Discussion

These data indicate that colonies of *L. longispinosus* can be founded either by a single queen (haplometrosis) or by more than one queen (pleometrosis) and that colonies of *L. ambiguus* can be founded pleometrotically. These preliminary findings indicate that the colony-foundation behavior of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* deserves more thorough investigation. Among the questions remaining to be answered are the following:

- a. Can pleometrosis in these species lead directly and smoothly to polygynous mature colonies; or is there an obligatory period of monogyny between a colony's pleometrotic beginnings and the later adoption of supernumerary queens (Holldobler & Wilson 1977)?
- b. How closely related are multiple colony foundresses? Are they always sisters? If so, how do they get together to found a new colony?
- c. Is foraging for food and water a laboratory artifact; or do colony-founding queens of these species normally forage?

Finally, although we have no direct evidence, we suppose that many colonies of these species must originate when a queenright portion of a polydomous colony becomes permanently separated from the other parts, a process known as "budding". Incipient nests containing only queens and an immature brood seem too rare to account for all colony foundation in these species.

GENERAL DISCUSSION

We can now reconstruct the colony life histories of these species in some detail. New colonies of *L. longispinosus* can be established either by a single newly mated young queen (haplometrosis) or by two or more such individuals (pleometrosis). New colonies of *L. ambiguus* are established pleometrotically; and it seems likely that further research will establish that colonies of this species and of *L. curvispinosus* can be founded either pleometrotically or haplometrotically. Young colonies of these species probably occupy only one nest (monodomy). However, as they grow, some colonies of *L. ambiguus* and *L. longispinosus* come to occupy two or more nests (polydomy) among which there can be an exchange of workers, brood, and queens. Mature colonies of all three species containing one or more fully fertile inseminated queens also sometimes adopt additional conspecific queens. Finally, we hypothesize that new colonies can be formed as a result of the break-up of polydomous colonies into two or more autonomous units (budding).

When considering these facts, one immediately notes a large amount of behavioral variability. Although we do not yet know whether any individual queen is potentially capable of doing more than one thing, young queens as a class can either join an established colony, found a new colony alone, or found a new colony in the company of one or more other queens. Colony life cycles and demographics are also variable. A colony can apparently have one or more queens at almost any stage of its development and can occupy one or more than one nest when mature enough to produce reproductives. Such behavioral variability is unusual, and its adaptive significance is obscure. Thus, the behavioral ecology of these three species offers many opportunities for empirical and theoretical analysis.

Two problems are particularly salient. First, we have demonstrated that some queenless nests are parts of polydomous colonies;

and we presume that others are remnants of declining colonies. However, we can neither distinguish the two kinds of nests nor determine their relative frequencies. Reference to the proportion of nests producing all-male broods is not helpful because, in some species of Leptothoracine ants, female larvae can hibernate twice before pupating (Buschinger et al. 1975). Thus, a queenless colony might continue to produce female pupae for one or two years. Further work is needed to devise a simple means of distinguishing declining colonies from the queenless nests of polydomous colonies.

Second, we would like to know how frequently these species employ the various modes of colony foundation which we have observed and postulated. Altogether, we report observations of 872 nonincipient nests of *L. ambiguus*, 342 nonincipient nests of *L. longispinosus*, and of 8 and 7 apparently incipient nests of these two species. If one assumed that the frequency of apparently incipient nests represented the frequency of incipient colonies in the population, one would have to conclude that the average lifespan of a colony is unreasonably long. Thus, we were led to propose budding as a frequent means of colony foundation. This proposal needs verification.

However, it was the degree to which *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* are subject to social parasitism which initially aroused our interest; and several of the behavioral processes which we have described suggest means by which social parasitism might either evolve or be maintained. Colonies of all three species sometimes adopt newly mated conspecific queens, and colonies of *L. ambiguus* and *L. longispinosus* are sometimes founded pleometrotically. Since both these forms of polygyny require the peaceful coexistence of queens and of workers which are the offspring of different queens, both forms of polygyny are factors which might render these species susceptible to social parasitism. To be accepted by a host-species colony, a parasite queen must somehow convince the host workers and perhaps the host queen or queens that she is a legitimate potential colony member. Since the queens and workers of these species naturally accept supernumerary queens, the parasite female's task is probably simplified.

Moreover, the tendency to seek adoption by existing colonies and the tendency to join pleometrotic foundress associations may represent preadaptive traits from which parasitic modes of colony founda-

tion might have evolved in such a group of closely related species. The queens of slave-making, temporary, and inquiline parasites found new colonies by securing adoption in a host-species colony (Buschinger 1970; Wilson 1971). Although the colony-foundation behavior of such social parasites often involves an element of violence which is probably lacking from the processes by which colonies of *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* adopt additional conspecific queens or additional foundresses join associations (Wesson 1939; Alloway, personal observations), the tendencies to join conspecific colonies or foundress associations could form a basis from which more elaborate parasitic colony-foundation might evolve.

Finally, the kind of polydomy seen in *L. ambiguus*, and *L. longispinosus* also embodies factors which may be both preadaptive for the evolution of socially parasitic behavior and significant in rendering a species subject to social parasitism. Polydomy in these species can involve a more or less continuous exchange of workers, brood, and queens among a colony's multiple nests. Such commerce requires a worker caste which is adept in carrying brood and adults in a fashion which might be preadaptive for slave-raiding (Buschinger 1970). In this context it is noteworthy that Wilson (1975) and Alloway (1980) have shown that *L. ambiguus*, *L. curvispinosus*, and *L. longispinosus* sometimes behave like facultative slave-makers.

Polydomy also requires workers in one nest to accept and tend a brood from another nest even though it may carry a somewhat unfamiliar "nest odor". Yet, any tendency to care for unfamiliar brood might render a species vulnerable to social parasitism. The more ready host-species workers are to accept unfamiliar brood, the less exactly a parasite's brood need mimic that of the host.

SUMMARY

New colonies of *L. longispinosus* can be founded by a single young queen; and colonies of *L. ambiguus* and *L. longispinosus* can be founded by groups of two or more young queens. Mature colonies of these two species and of *L. curvispinosus* can become polygynous or enhance the degree of their pre-existing polygyny by adopting young conspecific queens. Some colonies of *L. ambiguus* and *L. longispinosus* occupy more than one nest and exchange

workers, queens, and brood among nests (polydomy). Other colonies have only one nest (monodomy). The significance of these findings for understanding the evolutionary origin and maintenance of social parasitism is discussed.

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A NEW COLONIAL *ANELOSIMUS* SPIDER FROM
SURINAME (ARANEAE: THERIDIIDAE)

BY HERBERT W. LEVI¹ AND DEBORAH R. R. SMITH²

Until recently, only a few colonial spiders were known. The recent increase in field work in the tropics revealed a number of new colonial species (Buskirk, 1981). Some of these colonial spiders belong to the theridiid genera *Anelosimus* and *Achaearanea*. The genus *Anelosimus* in America was revised by Levi, 1956, and the knowledge updated in 1963 and 1972, with new species described in 1967 and 1979. Those *Anelosimus* species known to be colonial are: *A. studiosus*, *A. eximius*, *A. rupununi* and *A. lorenzo*. Another species has now been found in Suriname. While reexamining some of the related species in preparation for this description, it was found that the synonymy of *A. jabaquara* Levi 1956 with *A. dubiosus* (Keyserling, 1891) in Levi (1963) was in error. While *A. jabaquara* was illustrated in 1956, *A. dubiosus* is here illustrated for the first time since its description in 1891 (Fig. 4).

***Anelosimus saramacca* new species**

Figures 1-3

Type. Male holotype from Voltzberg-Raleighvallen Nature Reserve, Saramacca Province, Suriname [lat. 04° 40' N, long. 56° 10' W], Feb. 1982 (D. Smith Trail), with 1♂, 5♀ paratypes in the Museum of Comparative Zoology; 1♂, 2♀ paratypes in the Cornell University collection kept at the American Museum of Natural History; 2♀ paratypes in the British Museum, Natural History.

Description. Female. Carapace orange, lighter on sides. Sternum orange with some black pigment. Legs yellow-white with distal part of articles darker. Dorsum of abdomen with some black and white pigment, sides orange-white. Venter of abdomen with some black and white pigment, black patch anteriorly and behind genital groove, and black patch in front of spinnerets. Eyes subequal in size.

¹Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.

²Field of Neurobiology and Behavior, Department of Entomology, Cornell University, Ithaca, NY 14853

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Anterior median eyes their diameter apart, 0.3 diameters from laterals. Posterior median eyes slightly more than their diameter apart, their diameter from laterals. Total length, 3.2 mm. Carapace, 1.3 mm long, 0.9 mm wide. First femur, 1.7 mm; patella and tibia, 1.7 mm; metatarsus, 1.3 mm; tarsus, 0.8 mm. Second patella and tibia, 1.4 mm; third, 1.1 mm; fourth, 1.5 mm.

Male. Carapace, sternum orange. Legs yellow-white. Abdomen orange to black. Eyes subequal in size, spacing as in female. Total length, 2.3 mm. Carapace, 0.9 mm long, 0.6 mm wide. First femur, 1.2 mm; patella and tibia, 1.3 mm; metatarsus, 0.8 mm; tarsus, 0.6 mm. Second patella and tibia, 1.0 mm; third, 0.8 mm; fourth, 1.0 mm.

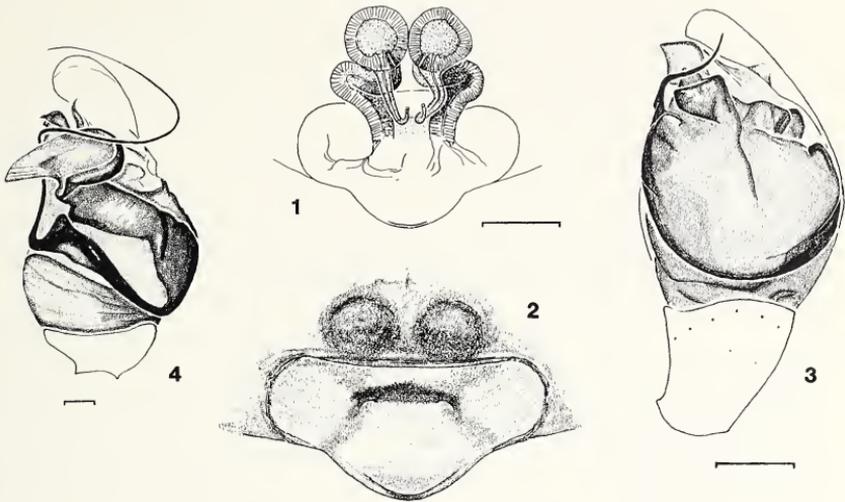
Diagnosis. Unlike *A. jabaquara* and *A. dubiosus*, *Anelosimus saramacca* has a short terminal embolus (Fig. 3). The female has an epigynum with a subtriangular depression enclosing a transverse mark; the openings appear posteriorly at the ends of the mark (Figs. 1, 2).

Natural History. A single colony of *A. saramacca* was found in an area of swampy lowland rainforest, approximately midway between Voltz Berg and Van Stockum Berg. The web was similar to that of *Anelosimus eximius*, but much smaller. It was located in a small sapling, about 30 cm above the ground. The web consisted of a nearly circular hammock or sheet of silk about 80 cm in diameter, and a pyramid shaped barrier web about 1 m tall. In the center of the hammock were retreats consisting of green leaves, some of which were curled.

The colony contained at least 1000 individuals, including males, females and immatures. There were many more adult females than adult males. Large numbers of females with egg cases were found in the leaf retreats. A quick inspection revealed at least 140 females with egg cases.

The egg cases closely resemble those of *A. eximius* and *A. studiosus*—they are pale brown, nearly spherical, and 1.5 mm in diameter. Several egg cases were collected, but many later proved to be empty or hatched out. Six egg cases containing eggs or embryos had a clutch size of 15.2 ± 1.8 eggs.

Like *A. eximius*, *A. saramacca* shows cooperative behavior. Several adults and immatures were seen feeding together on large prey items, and the web appears to be a product of cooperative effort.



Figs. 1-3. *Anelosimus saramacca* new species. 1, 2. Epigynum. 1. Dorsal, cleared. 2. Ventral. 3. Left male palpus.

Fig. 4. *Anelosimus dubiosus* (Keyserling). Left male palpus. Scale lines, 0.1 mm.

Anelosimus dubiosus (Keyserling)

Figure 4

Theridium dubiosum Keyserling, 1891, 3: 187, pl. 6, fig. 133. ♂. Male holotype from N. Freiburg (Nova Friburgo, Est. Rio de Janeiro), Brazil in the British Museum, Natural History, reexamined.

Description. Carapace, legs orange. Abdomen white with a dorsal gray band. Total length, 3.4 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 2.2 mm; patella and tibia, 2.5 mm; metatarsus, 1.5 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 1.3 mm; fourth, 1.8 mm.

Note. *Anelosimus jabaquara* Levi, 1956 is not a synonym of this species as thought in 1963. *Anelosimus dubiosus* differs by having a much longer filamentous embolus (Fig. 4) than *A. jabaquara* (Levi, 1956, fig. 18) and *A. saramacca* (Fig. 3).

ACKNOWLEDGMENTS

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expedition was defrayed in part by the Explorers Club, Sigma Xi, the Grace Griswold Memorial Fund, the Cornell Insect Collection, and members of the Cornell Department of Entomology (Dr. William L. Brown, Penelope Kukuk and Maurice Tauber). We also wish to thank the staff of STINASU, the Suriname Nature Conservancy, for their help and cooperation. The senior author thanks the National Science Foundation for grant no. 81-20492 for research and publication support, and Paul Hillyard for the loan of a specimen from the British Museum (Natural History).

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BIOLOGY AND SYSTEMATICS OF THE
BEE GENUS *CRAWFORDAPIS*
(COLLETIDAE, DIPHAGLOSSINAE)

BY GARD W. OTIS¹, RONALD J. MCGINLEY², LYN GARLING³,
AND LUIS MALARET³

Crawfordapis luctuosa (Smith) is a robust, dusky-haired bee, presently known from only a few localities in Mexico and Central America. Individuals can be as long as 24 mm and superficially resemble the more familiar diphaglossine bees of the genera *Ptiloglossa* and *Caupolicana* to which they are related. All three genera are placed in the Caupolicanini which is characterized by the complete pre-pisternal groove and very elongate first flagellar segment. While *Crawfordapis* is currently considered to be monotypic, Michener (1966) raised the possibility that the material from the more northern localities (Mexico and Guatemala) may represent a distinct species. Much more material from different localities is needed before that problem can be considered.

The purpose of this paper is to present biological observations made on *Crawfordapis* by three of us in Costa Rica (L.G., L.M., G.O.). In addition, the larva of *Crawfordapis* is described and the systematic interrelationships of diphaglossine genera are reviewed (R.M.).

BIOLOGY

Description of the Site

Two nesting aggregations of *Crawfordapis luctuosa* were observed approximately 5 km east of Monteverde, Province of Puntarenas, Costa Rica (10°18'N, 84°47'W) on trails at 1540 m elevation. The surrounding vegetation is best described as elfin forest, with some characteristic plant species being *Lycopodium cernuum*, *Senecio megaphyllus*, *Clibadium* sp., *Gunnera* sp. and *Myrica phanerodouta*

¹Environmental Biology Dept., University of Guelph, ON N1G 2W1, Canada.

²Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

Present address: Dept. of Entomology, N.H.B. 105, Smithsonian Inst., Washington, D.C. 20560.

³Dept. of Zoology, University of Florida, Gainesville, FL 32611

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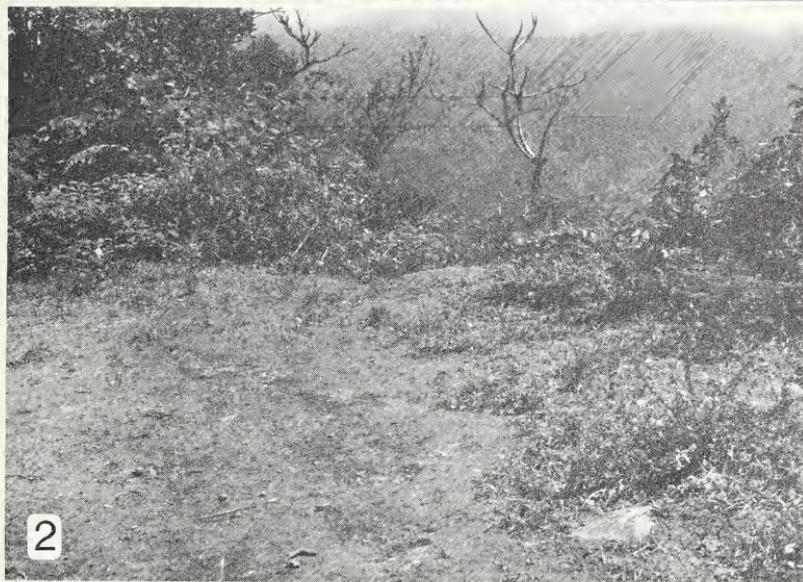
(details in Lawton and Dryer, 1980). Frequent rains deposit approximately 3000 mm of precipitation annually on this area. Heavy mists augment this precipitation. Mean annual temperature is about 16°C (max = 27°C, min = 10°C) and during prolonged rainstorms, the temperature can remain at 15–16°C for 3–4 days. The wind generally blows 15 to 20 km/hr, but ranges from nearly calm to winds in excess of 100 km/hr during rainstorms (R. Lawton, pers. comm.).

Nesting aggregation No. 1 was directly on the Continental Divide, on a narrow ridge known as "La Ventana". The aggregation was first noticed in August 1975 and was still active but reduced in size to only 5 nests in February 1981. W. Guindon (pers. comm.) indicated the site was active as early as 1966. Bees apparently maintained nests in this area throughout the year (R. Lawton, pers. comm.). Nests were built in the lee of a slope which partially protected them from mist and rain (Fig. 1). In July 1977, there were 97 nests with tumuli in the approximately 18 m aggregation. The majority of the nests were within an elliptical area of about 8 m. Of the nests 29 were completely exposed in the trail, 50 were on nearly level ground and partially obscured by grasses and other herbs, and 18 were on the face of the sheltering embankment.

Nesting aggregation No. 2, located at the head of the valley on the road to Penas Bancas, was exposed to high winds and unprotected from rain (Fig. 2). In February 1978, the aggregation consisted of not more than 100–150 nests, but had enlarged to at least four hundred active nests by August 1978. Nests were found both on the edge of the road and down the adjacent steep, bare slope. By the last visit to the site in February 1981, the number of active nests had declined to 230. The adjacent slope had become covered with dense vegetation and lacked nests.

Description of the Nest

Entrances to active nests had tumuli approximately 7.5 cm in diameter and 4–7 cm in height (Fig. 3). The frequent rains obliterated tumuli of all nests except those in which bees were actively digging. Nest entrances consistently measured 1.0 cm in diameter. In each of three nests excavated in horizontal ground, the tunnel began nearly vertically for 7–14 cm and then continued downward at an angle of approximately 75°. In the diagrammed nest (Fig. 4)



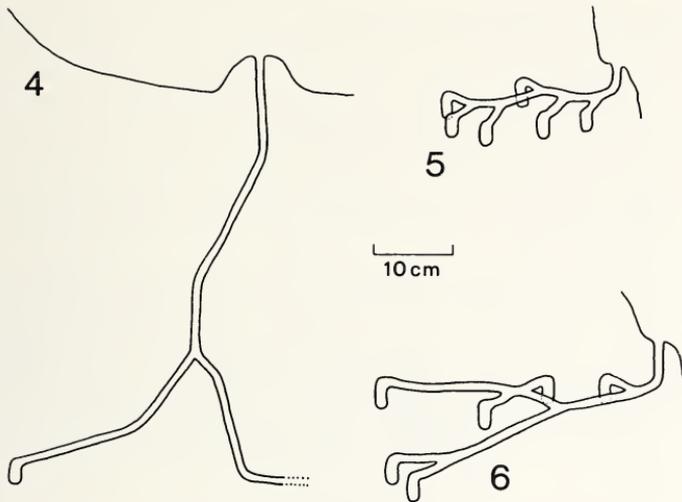
Figures 1-2. *Crawfordapis luctuosa* nesting sites. Fig. 1. Nest aggregation No. 1. Most nests were on level ground, either exposed or partially obscured by grasses. A smaller number of nests were in the nearly vertical embankment which sheltered the site from wind and mist. Fig. 2. Nest aggregation No. 2.



Figure 3. Nest tumulus. Nests in which bees were actively digging were readily discerned by the presence of a dirt mound around the nest entrance.

the tunnel changed directions again at a depth of 24 cm, continued downward at a 75° angle another 8 cm, and diverged into two tunnels. One of these angled toward the embankment at an angle of 50° from vertical for another 12 cm, then at a depth of 41 cm continued slightly below horizontal for another 18 cm. A single, terminal cell was found at the end of that tunnel. The other tunnel continued downward another 16 cm from the branching point before becoming nearly horizontal at a depth of 47 cm. This tunnel could not be followed because the soil was too soft.

Two additional nests were excavated on the nearly vertical embankment at aggregation No. 1. These nests differed from those in level ground in having very short (3–5 cm) vertical portions of the tunnel before becoming nearly horizontal. Nest B (Fig. 5) had a single horizontal tunnel that extended 22 cm into the embankment. Along the slight downward slope of this main tunnel were 6 nearly horizontal lateral tunnels 4–8 cm long. The two closest to the exterior contained pupae and the tunnels had been filled with soil. The next three contained larvae, and the distal cell was empty. Nest C



Figures 4-6. Diagrammatic representation of three *C. luctuosa* nests. Fig. 4. Nest at base of the embankment. Figs. 5-6. Nests excavated in the embankment.

(Fig. 6) had one cell (contents unrecorded) only 4 cm from the vertical entrance tunnel. Another 8 cm further down, the main tunnel diverged into two. One tunnel continued to slope downward and contained two terminal cells with pupae. The other tunnel sloped slightly upward and had two lateral cells with larvae and an empty terminal cell which was 34 cm from the face of the embankment.

Each completed cell was lined with a shiny, cellophane-like membrane which is characteristic of Colletidae. It was not possible to lift the cell and contents out of the soil as described for *Ptiloglossa guinnae* Roberts (Roberts, 1971). Cell contents were soupy; fermentation odors were not recorded. Cocoons were tough, nearly transparent membranes 17 mm in diameter by 35 mm in length.

General Activity Pattern

Females of *Crawfordapis luctuosa* were active aboveground primarily between the hours of 0930 and 1400 hr, with few bees leaving the nests after 1300 hr on observation days February 19 and 20, 1978 (Fig. 7). A similar activity pattern was recorded on July 16, 1977. This sharply contrasts with the crepuscular activity pattern of *Ptiloglossa guinnae* which occurs in similar habitats (Roberts, 1971). In some instances, bees were seen returning to the nests in the morning before any bees left the nesting aggregation. It is possible

that these bees had spent the night away from their nests as occurs with *Bombus* species at high elevations (O. R. Taylor, pers. comm.). Before leaving the nest for the first time in the morning, females often remained just below the nest entrance for a few moments and then upon exiting, hovered nearby for a short time before flying off. Temperatures within the nest entrance remained at 12°C throughout the day on February 20 when ambient temperature was between 10–11°C.

Males remained outside the nests at all times. During the activity period of the females, the males flew over the nesting aggregation and nearby at heights of 1–3 m. They rapidly approached any flying object, including female *C. luctuosa*, swallows, a hummingbird, a ctenuchid moth and a dragonfly. Males often seized females returning to the nests but it was not ascertained whether copulations occurred.

Nest Visitation Behavior

On February 19 and 20, 1978, 46 nests within a 2.16 m subarea of aggregation No. 2 were mapped and numbered. Sixteen female bees were captured while leaving nests. Each bee and her corresponding nest of origin were given an identifying color combination. The bees were marked by paint spots on the thorax, while their nests of origin were indicated by a wooden chip about 1 cm in length placed near the entrance. All observed departures from and arrivals to mapped nests were recorded by noting time, markings (or lack thereof) of bees and nest number or color. A nest "visit" was defined as the disappearance of the bee beneath the ground surface for any length of time.

Of the 46 nests mapped, 40 (80%) were entered at least once by a bee. The number of observed visits per nest made by marked or unmarked bees to the 16 color-coded nests ranged from 0–15 over the two days (Table 1).

Of the 16 marked bees, four were not observed again. The remaining 12 marked bees visited nests a total of 78 times. Four of the marked bees (BG, GO, YBY, OB) concentrated their visits on a single nest, while others entered up to 12 different nests over the two days (Table 2).

The duration of visits of both marked and unmarked bees varied widely from less than 1 minute to a maximum of 151 minutes. The

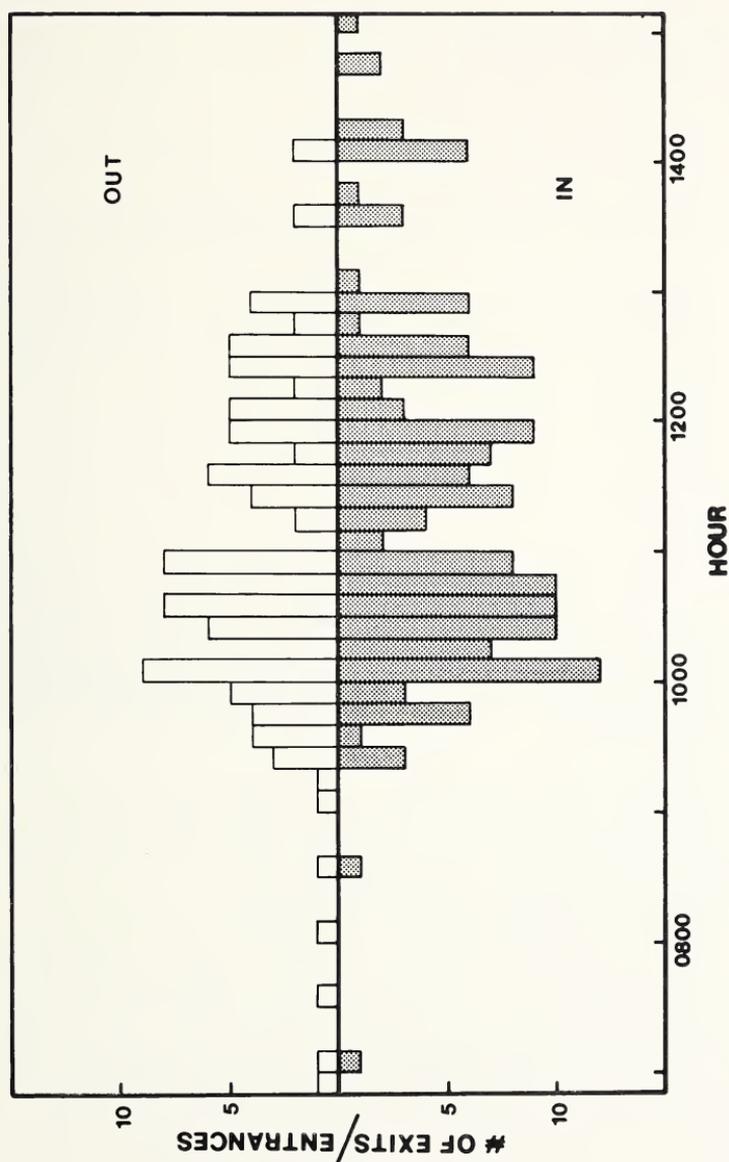


Figure 7. Number of bees exiting and entering nests in 10-minute intervals on February 19, 20, 1978.

Table 1. Number of visits by all bees to color-coded nests

	Nest Color-Code															
	YB	OY	YO	GO	BG	YBY	Y	OBO	O	OB	BY	YG	B	GB	OG	BOY
No. of visits	8	15	4	7	11	8	0	4	2	8	2	0	7	4	3	0

Table 2. Number of visits made by marked bees to particular nests.

Marked bee	Nest Categories												Total visits
	1°	2°	3°	4°	5°	6°	7°	8°	9°	10°	11°	12°	
YB	3	2	2	2	2	2	1*	1	1	1	1	1	19
OY	6*	4	2	1	1	1	1	1	1	1			19
YO	2*	2	2	1	1	1	1	1					11
GO	5	1	1	1	1								8
BG	5*												5
Y	1	1	1										3
YBY	3*												3
OB	3*												3
OBO	2												2
O	1	1											2
BY*,YG	Each visited one nest once.												

*Asterisked entries indicate that the visits were made to the nest from which the bee was originally captured.

visits of 1 minute or less were likely to have been exploratory rather than "working" visits. Of a total of 69 timed visits, 30 (43%) were in the "exploratory" category. The average duration of the remaining 39 "working" visits was 18.1 minutes ($S = 26.36$) (Fig. 8).

The duration of foraging trips of 4 of the marked bees was noted by timing of their absences from the nest area. Whether or not they returned with pollen was not noted. Absences ranged from 19–42 minutes, the average being 30.4 minutes ($n = 11$, $s = 13.79$). It seemed that bees returned from foraging trips in distinct pulses of several bees at a time. The foodplants are not known.

This preliminary data on the movements of marked bees to different nests generates several hypotheses for further testing.

- 1) Multiple nest entering is part of searching behavior for a female's own nest.

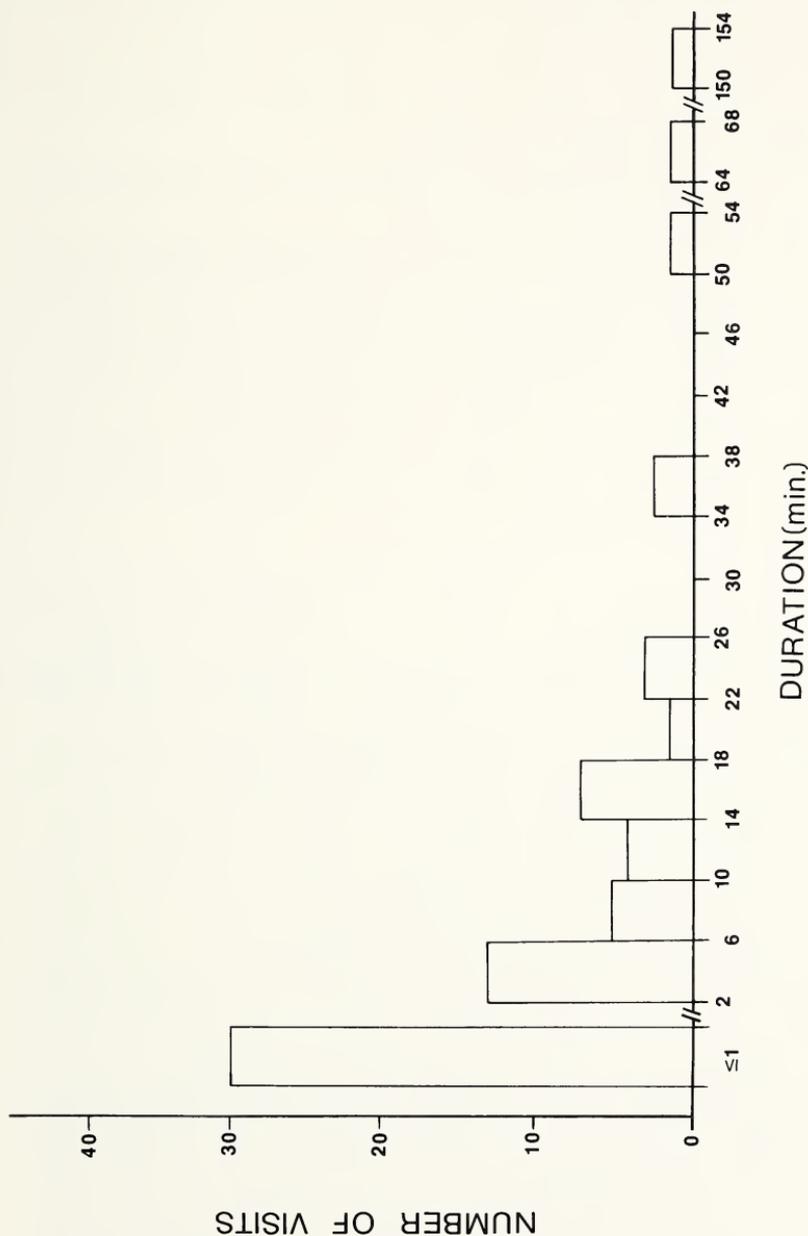


Figure 8. Number of visits by bees to nests as grouped in 4-minute intervals. The first category of visits of ≥ 1 minute may represent searching behavior and is set apart from the other categories.

- 2) Individuals are locating abandoned nests to provision rather than starting completely new ones.
- 3) Individuals are "stealing" provisions from nests of other individuals.
- 4) Individuals are usurping nests which other individuals are actively excavating or provisioning.
- 5) Several individuals are contributing to excavation, provisioning or oviposition within a single nest.

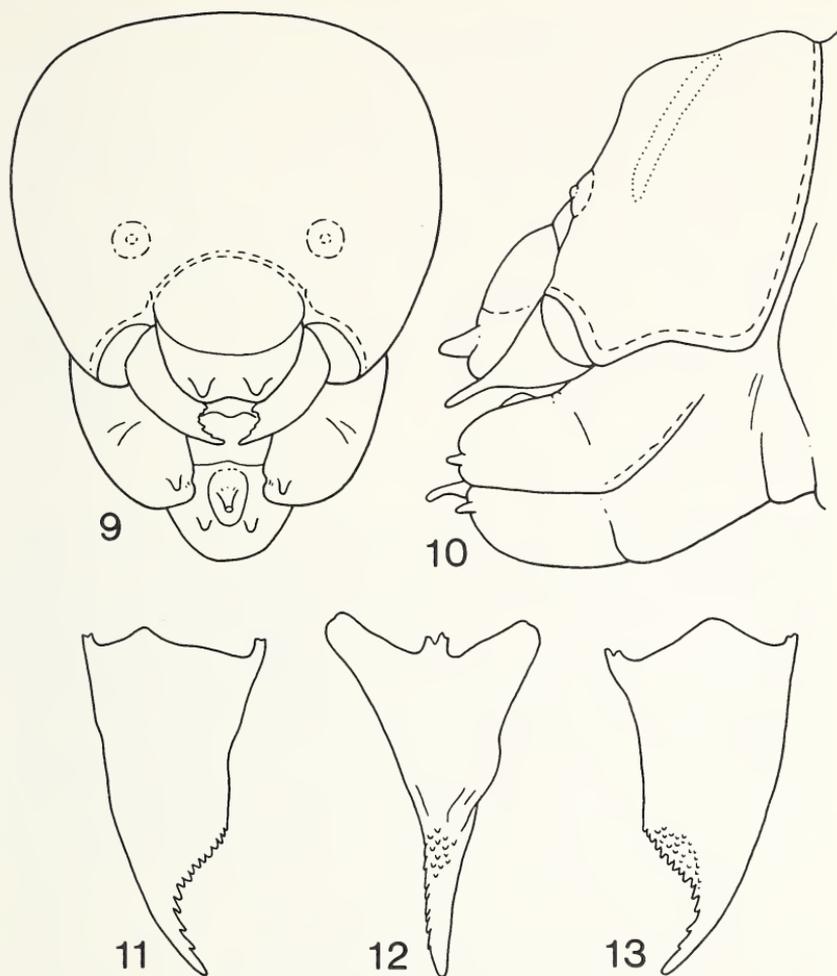
The latter hypothesis is particularly interesting since no species of the family Colletidae is known to be parasocial (Michener, 1974). It is plausible that females not only construct their own nests but also usurp partially constructed or provisioned nests of other females as has been reported in some other Hymenoptera that nest in aggregations (Brockmann and Dawkins, 1979; Brockmann *et al.*, 1979; Eickwort, 1975; Eickwort, 1981; Eickwort *et al.*, 1977). Further studies of *Crawfordapis luctuosa* are needed to better understand its social behavior and biology.

SYSTEMATICS

Description of Larva

The following description follows the format used for describing other colletid larvae (McGinley, 1981).

HEAD (Figs. 9–13): (2) Labrum nonspiculate; (3) epipharynx and (4) hypopharynx spiculate; (5) maxilla spiculate on inner surface. (7) Head size normal in comparison to body (head not relatively large as in Xeromelissinae); (8) head capsule somewhat elongate, slightly produced in lateral view; (10) frontal swellings above antennae absent; (10a) median frontal swelling above antennae absent (present only in *Ptiloglossa*). (14) Anterior tentorial pit low in position (high in all other known diploglossines); (15) posterior tentorial pit at junction of hypostomal ridge and posterior thickening of head capsule; (15a) tentorial development unknown (tentorium of specimen examined was incomplete, probably due to nearness of specimen to pupation). (16) Posterior thickening of head capsule moderately developed (17) straight medially, not curved forward; (19) median longitudinal thickening of head capsule absent; (20) hypostomal ridge well-developed; (25) epistomal ridge complete but thin, (26) arching dorsally to level of antennae. (27) Parietal bands distinct, broad and shallow. (28) Antennal prominence absent; (29)



Figures 9–13. Mature larva of *Crawfordapis luctuosa*. Figs. 9, 10. Head capsule, frontal and lateral view. Figs. 11–13. Right mandible, dorsal, adoral and ventral view.

antennal papilla a moderate-sized convexity, (31) bearing three sensilla. (32) Clypeus moderate in length; (34) labrum not projecting in lateral view; (35, 36, 37) labral tubercles very well-developed, narrowly rounded and strongly projecting (unlike those of other diphaglossines); (38) labral apex emarginate, (39) without sensilla-bearing swellings as in other diphaglossines. (41) Mandibles elon-

gate, (42) moderately slender in dorsal view, (43) broad basally in adoral view; (44) mandibular spiculation absent; (46) outer surface of mandible smooth, distinct tubercle and setae absent; (51) apical portion of mandible, in adoral view, attenuate; (52) cusp moderately well-defined; (53) cuspal projection absent; (54) cuspal region multi-dentate; (55, 55a) dorsal apical edge with distinct, moderately large teeth; (57) apical concavity weakly developed; (60, 60a) ventral apical edge smooth, teeth absent. (61) Labiomaxillary region produced; (62) labium and maxilla distinct, (63) subequal in length. (65) Inner apical surface of maxilla rounded, not produced mesiad; (66) unlike all other known bee larvae except those of *Ptiloglossa*, maxilla with a longitudinal groove on adoral surface; (67) cardo and stipes sclerotized; (69, 70) maxillary palpus moderately elongate and slender, (71) apically positioned on maxillary apex in lateral view; (72) galea absent. (73) Labium divided into prementum and postmentum; (75) palpus elongate and slightly decurved, (76) subequal to maxillary palpus in length. (77) Salivary lips well-developed; (78, 79, 80) salivary opening narrow, circular, at end of long spoutlike salivary lips, (83) which project from a well-defined platelike structure at apex of labium; (82) apical labial swellings absent. (84) Hypopharynx normal in size, (85) bilobed, (86) exceeded by labium and maxilla; (87) hypopharyngeal groove distinct, sclerotized laterally.

BODY (Fig. 14): (88) Integument spiculate, density of spicules greater on dorsum than on venter; (93) body moderate in length, (94) robust, (95) widest posteriorly in lateral view; (96) intersegmental lines moderately incised; (97) intrasegmental lines indistinct; (98) dorsal tubercles weakly developed, most prominent on abdominal segments 5-7; (103) lateral tubercles absent (present on one specimen from Panama); (104) ventrolateral tubercles absent; (106) abdominal segment 10 moderate in length, (107) rounded, (108) dorsal in attachment to segment 9; (109) venter of segment 10 slightly produced (very weakly so in specimen from Panama), (110) without conspicuous, darkly pigmented spiculation; (111) dorsal surface of segment 10 smooth, without lines or ridges; (113) anus apical. (114) Spiracles large, (115) not on elevations; (117) atrium very broad and shallow, (118) not produced above body surface; (119) atrial wall faintly ridged, (120) with four to five broken rings of spicules; (121) atrial rim absent; (122) peritreme wide; (123) primary tracheal collar absent; (126) subatrium apparently extremely

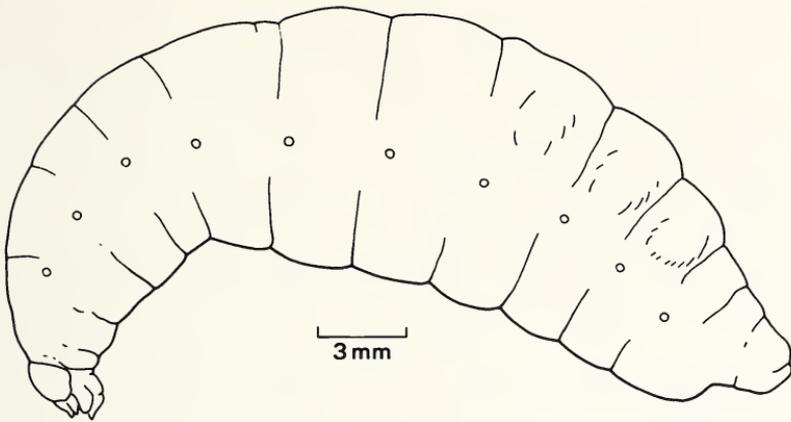


Figure 14. Mature larva of *Crawfordapis luctuosa*.

short. (The structure of diphaglossine larval spiracles remains poorly understood, especially with regard to the subatrium. The atrium is connected to the trachea by a long, nonringed tube. While this tube is characteristic of diphaglossines, its internal structure and homologies are not known.)

MATERIAL STUDIED: Two postdefecating larvae; 5 km east Monteverde, Puntarenas Province, Costa Rica; July 16, 1977 (G. W. Otis); specimens in the larval bee collection of the American Museum of Natural History. Two postdefecating larvae; Bouquete, Chiriqui Province, Panama; April 25, 1981 (R. W. Brooks); specimens in the personal collection of R. W. Brooks.

Analysis of Larval Characters

McGinley (1981) described the mature larvae of 30 colletid species including those of seven diphaglossines. Two cladograms for the diphaglossine genera appeared to be most strongly supported by larval characters. One of the cladograms, for reasons discussed in the above mentioned paper, appeared to be the preferable working hypothesis of diphaglossine phylogeny. This cladogram is presented in Figure 15, with *Crawfordapis* now included. The polarities of the characters listed in Table 3 were determined by out-group comparison, i.e., consideration of character state distributions in all other bee larvae as well as in nonapoid larvae, especially those of specoid wasps.

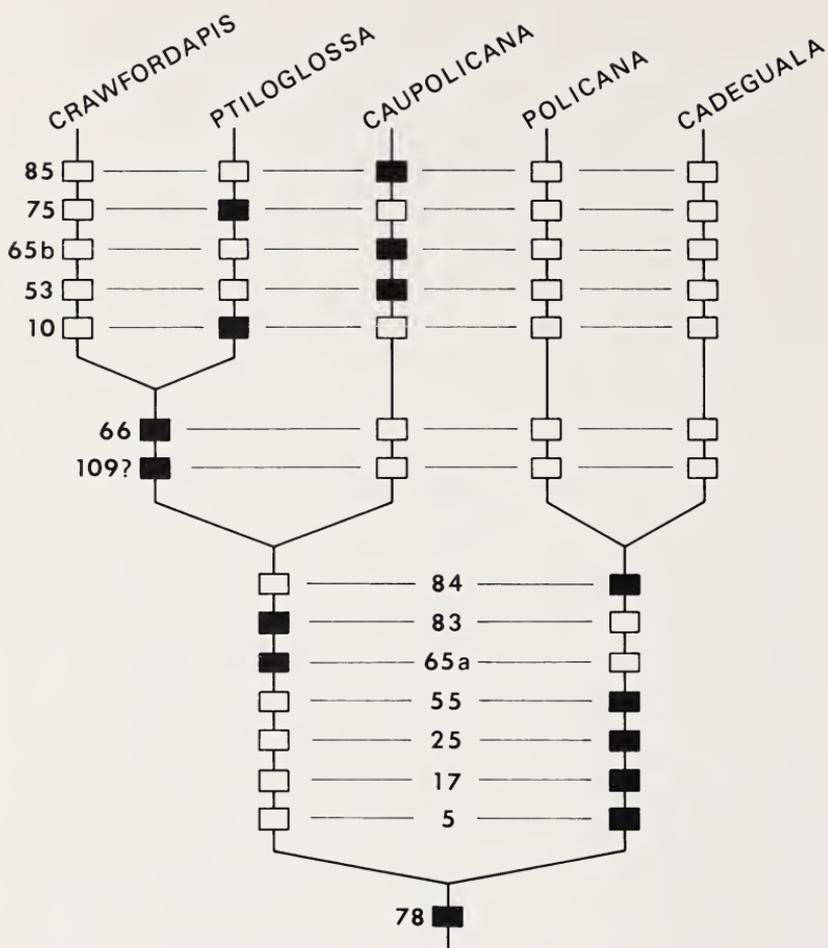


Figure 15. Cladogram of diphaglossine genera based on larval characters. Numbers refer to the characters listed in Table 3. Black rectangles represent presumed apomorphic characters; white rectangles represent plesiomorphic characters. Character 109 appears to be variable in *Crawfordapis*.

The larval cladogram corroborates the currently recognized diphaglossine classification based on adult characters (Michener, 1966). Recognition of the Caupolicanini (*Ptiloglossa*, *Crawfordapis*, *Caupolicana*) is supported by the presence of the unusual salivary plate (character 83, Fig. 9) and the rounded, nonprojecting inner maxillary surface (character 65).

Table 3. Larval Characters Used in Diphaglossine Cladogram

Plesiomorphic	Apomorphic
5. Maxilla spiculate	Nonspiculate
10. Median frontal swelling absent	Present
17. Median portion of posterior thickening of head capsule straight	Curved forward
25. Epistomal ridge complete	Incomplete
53. Cuspal region of mandible without distinct projection	Cuspal projection present
55. Teeth on dorsal apical edge of mandible distinct basally	Teeth fused basally, forming distinct platelike wedge
65. Inner apical surface of maxilla produced mesiad	a. Inner surface rounded b. Inner surface strongly produced forward
66. Inner surface of maxilla smooth	Inner surface of maxilla with longitudinal groove
75. Labial palpus moderately elongate, straight	Extremely elongate, decurved
78. Salivary lips transverse, not spoutlike	Elongate, spoutlike
83. Salivary plate absent	Present
84. Hypopharynx normal in size	Conspicuously narrow
85. Hypopharynx bilobed	Rounded
109. Venter of abdominal segment 10 not produced	Produced

The sister-group relationship of *Ptiloglossa* and *Crawfordapis* is strongly supported by the presence of a longitudinal groove on the inner maxillary surface (character 66). Weaker support for this relationship is indicated by character 109, the projection of the venter of abdominal segment 10 (this projection is conspicuous in some specimens of *Crawfordapis* but is only weakly developed in one specimen from Panama).

Adult Characters

In a study of adult diphaglossines, Michener (1966) discussed the similarities of *Crawfordapis* to *Ptiloglossa* and *Caupolicana*. Four characters found in *Crawfordapis* were said to be more or less *Caupolicana*-like: (4) outer hind tibial spur of male normal, articulated at base like inner spur; (6) lateral extremities of terga of male without areas of short, dense, erect hair; (7) sixth tergum of male with posterior margin not thickened or sulcate; (9) eighth sternum of male with apical process rather heavily pigmented, not down-curved. The similarity based on character 4 is definitely symplesiomorphic as the fusion of the hind tibial spur and the tibia is found only in *Ptiloglossa*. The other three characters appear to be plesiomorphic as well in that they represent the absence of some rather unusual features.

Similarities between adult *Crawfordapis* and *Ptiloglossa* appear to be apomorphic for diphaglossines: (1) clypeus strongly elevated above level of adjacent parts of face; (2) marginal cell prolonged basally as a narrow sinus to apex of stigma; (3) expanded second and third hind tarsal segments of female considerably expanded above. This evidence also supports the *Crawfordapis*-*Ptiloglossa* sister-group relationship indicated by larval characters, but must be considered tentative until a comprehensive cladistic analysis of adult colletids has been performed.

SUMMARY

Crawfordapis luctuosa, a large colletid bee, was studied at two nest aggregations in the mountains of Costa Rica. The aggregations were in exposed sites formed by landslides or clearing. Female bees slowly abandoned the aggregations as they became overgrown with vegetation. Several nests are described. In contrast to the crepuscular habits of the closely related genus *Ptiloglossa*, *Crawfordapis* was active primarily between 0930 and 1400 hrs. Some individually marked females showed a high degree of constancy in nest visitation, while others visited several nests in succession. The exact explanation of this behavior is not yet known. The previously unknown larvae of *Crawfordapis luctuosa* are described. Information from these larvae supports the placement of the genus in the

tribe Caupolicanini that was suggested from the systematic study of adults, and indicates that *Crawfordapis* may be the sister-group of *Ptiloglossa*.

ACKNOWLEDGMENTS

We wish to thank C. D. Michener and J. G. Rozen, Jr., for making helpful suggestions on the manuscript and R. W. Brooks for the loan of *Crawfordapis* larvae from Panama. The Tropical Science Center, San Jose, Costa Rica provided permission to study *Crawfordapis* within the Monteverde Cloud Forest Reserve. The Organization for Tropical Studies provided logistical support for a portion of the field work. Thanks are due also to the community of Monteverde for its friendly support of biologists and appreciation of their work.

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THE LIFE CYCLE OF
HETEROPODA VENATORIA (LINNAEUS)
(ARANEAE: HETEROPODIDAE)^{1,2}

BY

JOHN ROSS³, DAVID B. RICHMAN³, FADEL MANSOUR⁴,
ANNE TRAMBARULO³, AND W. H. WHITCOMB³

The giant crab spider, *Heteropoda venatoria* (L.), is known to occur throughout much of the tropics and subtropics of the world where it is valued as a predator of cockroaches (Guthrie and Tindall 1968, Hughes 1977, Edwards 1979). Its feeding habits, like those of most spiders, vary somewhat and it has also been known to eat scorpions and bats (Bhattacharya 1941), although it is questionable as to whether it normally attacks such prey. This spider is often found associated with human habitation, possibly due to the abundance of prey (Subrahmanyam 1944, Edwards 1979). Although biological notes on *H. venatoria* have been published by several workers (Lucas 1871, Minchin 1904, Bristowe 1924, Bonnet 1930, Ori 1974, 1977), the only life history work to date was published by Bonnet (1932) and Sekiguchi (1943, 1944a,b, 1945). Bonnet (1932) based his study on only 12 spiders (of which seven matured) and lacked data on the postembryonic stages. Sekiguchi (1943, 1944a,b, 1945) presented a more nearly complete study, but the papers are difficult to translate and they still lack some data, especially in regard to variation in the number of instars and carapace width. We have raised *H. venatoria* in the laboratory and present here our data on life cycle of this important beneficial arthropod.

MATERIALS AND METHODS

Spiders were obtained from avocado groves in south Florida, near Homestead, Dade County. Egg sacs taken from our laboratory

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³Dept. of Entomology and Nematology, Univ. of Florida, Gainesville, FL 32611.

⁴Agricultural Research Organization, Newe Ya'ar, P.O. Haifa, Israel.

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population of *H. venatoria* were used to obtain data for eggs, first and second postembryos and spiderling instars. Immature spiders, through 4th–5th instars, were housed in Tygon® flexible plastic tubing, an adaptation of methods developed by Peck and Whitcomb (1967). Two tubing sizes were employed, 13 mm and 24 mm diameter. The smaller bore tubing was cut to 10 cm lengths while the 24 mm tubing was cut into lengths of 20 cm to house spiders from 5th to 9th instars. Plastic foam culture-vial stoppers for 14–19 mm openings sealed the end of the tubing. Tube ends had only to be dipped into water weekly to maintain adequate moisture and humidity levels for the spiders. An open cell foam plug allowed for adequate ventilation while preventing the spider's escape from the tube. While these cages were not as large as would perhaps be ideal, they were easily maintained and stored in a relatively small area, and the spiders stayed healthy in them.

Moist cotton swabs were used to clean the tubes when clear vision into them was obscured by prey debris, spider wastes or mold. A rolled piece of 9 cm diameter filter paper was inserted into the 24 mm diameter tubes to further reduce cleaning frequency as the spiders tended to retreat onto the papers and defecate. Changing the filter paper at regular intervals maintained a high degree of sanitation.

Adult spiders were housed in 0.5 l clear plastic cups. A heated cork boring tool was used to fashion holes in lids in which were inserted open cell, plastic culture tube stoppers which allowed for ventilation. Paper can lids were inverted as bottoms to the plastic cup spider cages and these were lined with 9 cm filter paper to facilitate cleaning.

First instar *H. venatoria* were reared on adult vestigial-winged fruit flies, *Drosophila melanogaster* Meigen, for which the spiders showed a clear preference over an occasional cabbage looper larva, *Trichoplusia ni* (Hübner). Later instars were fed on adult native fruit flies (family Drosophilidae, genus unknown), which were larger than *D. melanogaster*, but the spiderlings showed greatest weight gain on mealworm larvae (*Tenebrio molitor* L.). Mealworms became the mainstay of the spiders' diet through the 10th and 11th instars, when the spiders were fed adult crickets, *Acheta domesticus* (L.), to extend feeding intervals. Houseflies, *Musca domestica* L., were introduced in the pupal stage during the middle instars and were fed on as the adult flies emerged.

Earlier instar spiders were maintained in a laboratory room and transferred during penultimate or adult stages to an environmental growth chamber. Temperatures in the room were stabilized at 27°C in the summer and 24°C in the winter, $\pm 2^\circ\text{C}$. The spiders were kept under fluorescent lights. The eggs, postembryos, and first instars used for later observations were all maintained in the environmental chamber, which was kept at a constant 26.7°C on a 13:11 L:D light period. Humidity was controlled within the chamber by a supersaturated NaCl solution bath in a 20 × 15 × 8 cm tray. The tray was partially filled with small pebble-sized rocks to increase the surface area available for moisture exchange. The humidity control method was adapted from a technique described by Winston and Bates (1960) and it stabilized humidity levels within the 60–70% range as monitored by a hygrothermograph.

Mating was observed in plastic gerbil cages, which were modified to prohibit escapes by gluing taffeta-like cloth between the upper and lower portions of the cage.

Carapace widths were measured at the widest points with an ocular micrometer and a binocular microscope.

RESULTS AND DISCUSSION

The courtship and mating of *H. venatoria* was described by Bonnet (1932) and Sekiguchi (1944b). Our observations generally agree with these published accounts except where noted in the following discussion. In the current study, males introduced to a cage with a female were observed to construct a sperm web approximately 2 hours prior to mating. After sperm induction male spiders groomed their pedipalps for 5–25 seconds. The males vibrated their bodies prior to mounting, as described in detail by Rovner (1980). After mounting, the male rubbed his first pair of legs on the female's abdomen before and sometimes during insertion of the pedipalps. Copulation occurred in bouts lasting from one to six hours over a period of 24 hours. The pedipalps were inserted alternately, for an average of 20.4 seconds for each insertion ($n = 70$, $SD = 6.8$ seconds). Bonnet (1932) reported that insertion lasted 6–7 seconds, not counting transfer time. Males were often cannibalized by the female after mating, which could account for the higher proportion of females to males found in the field.

Approximately 12–14 days after mating, a circular, flattened, creamy white egg sac was produced by the female. The size of the sac ranged from 1.27 to 2.54 cm in diameter, and was from 3.18 to 6.35 mm thick. A network of silk was deposited on the underside of a flat surface, such as a leaf or plastic housing container lid. The eggs (each ca. 1.5 mm dia.) were deposited on this base, and covered with another layer of silk. After the egg sac was sealed around the edges and removed from the foundation, the female carried it with her pedipalps underneath her body during the incubation period. The female usually did not eat during this time. Infertile egg sacs were sometimes dropped or eaten by the female. A large number of infertile egg sacs (54% of those produced in the laboratory) were constructed by the reared spiders. This might be expected due to the artificially imposed mating schedule. An average of 2.16 fertile egg sacs were produced per female, with five the highest number. An average of 163 eggs were laid in each fertile egg mass ($n = 13$ egg masses, $SD = 28.97$) constructed by the experimental spiders. Bonnet (1932) reported 207 spiderlings emerging from the one egg mass from a female he had raised after obtaining it as an immature spider on bananas shipped from Africa. Sekiguchi (1944a) obtained 188–436 eggs/mass. In field observations we have found as many as 400 spiderlings in one egg sac. This may indicate that a high degree of variability in egg mass size is common. No data were taken on the numbers in consecutive egg sacs.

Peck and Whitcomb (1970) included a discussion of the postembryonic stages and reviewed the terminology used in the literature to describe them. The definitions used in the present study follow theirs and are given below to avoid confusion. The first postembryo is defined as being that stage after the chorion of the egg had been shed from most of the embryo, but remained as a crumpled mass at the posterior end. The second postembryo is defined as being that stage after the vitelline membrane had been shed and the embryo was completely free, with legs able to move. After the first molt the spiderling was considered to be a first instar. This molt occurred inside the egg sac. Bonnet (1932) and Sekiguchi (1944a) considered the emerged spiderlings to be second instars.

Several egg sacs were removed from CO₂-anesthetized female spiders, opened, and placed in covered petri dishes for observation. The egg stage lasted from 8–14 days ($n = 6$ egg masses). Eclosion

required approximately 4 hours and began with assistance from a pair of brownish "egg teeth" positioned on the patellar region of each pedipalp. The chorion was split anteroventral to the leg region with swelling pulses (30–60 seconds between pulses and 2–3 pulses per set) to about 2/3 of the diameter of the embryo. The membranes were drawn towards the spinnerets by an alternating combination of abdominal contractions and withdrawal movements of the legs, similar to those observed in molting. The shed membrane remained attached to the spinnerets until it was discarded at the beginning of the second postembryonic stage along with the vitelline membrane surrounding the legs. The first postembryonic stage lasted from 1–2 days for four egg masses, but four other egg masses required 5–6 days to become second postembryos (total $n = 8$).

During the second postembryonic stage the specimens were relatively quiescent. Eye pigment began to appear about the fifth or sixth day of the second postembryonic stage, with markings around the carapace margin and on the abdomen becoming visible soon afterwards. Dark setae appeared shortly before the first molt occurred. The duration of the second postembryonic stage was 9–10 days ($n = 3$). The first instar spiderlings remained in the egg sac approximately one week before emerging. One female which mated on the 28th of March, 1980, produced an egg sac 12 days later. From this egg sac 277 first instar spiderlings emerged after 32 days. All of the longevity data came from this group of spiderlings.

The duration of each instar is summarized in Table 1. Males were more likely (as noted by Bonnet 1932) to have one or two fewer molts than females, but this was not an absolute rule. Sekiguchi (1945) recorded complete data for only one female *H. venatoria* and found a total of 11 instars. He, however, apparently included the second postembryo as the first instar. Of the adults in our study for which complete data are available, the males ($n = 3$) had 8–10 instars ($\bar{X} = 8.7$, $SD = 1.2$) which lasted 241.7 days ($SD = 56.2$) and the females ($n = 13$) had 9–12 instars ($\bar{X} = 10.6$, $SD = 1.0$) which lasted 315.6 days ($SD = 21.0$). The survival rate from first instar to adult in the laboratory was approximately 85%. Total length of life from egg to death for our laboratory reared specimens was for males ($n = 4$) 355–586 days ($\bar{X} = 464.5$ days, $SD = 112.0$) and for females ($n = 16$) 298–710 days ($\bar{X} = 580.3$ days, $SD = 128.6$). Rovner (per. com.) found that some females of *H. venatoria* can survive for three years as adults in the laboratory.

Table 1. Carapace width and duration of stadia in laboratory reared *Heteropoda venatoria* (L.).

Instar	Carapace width			Duration of stadium		
	(mm)	n	S.D.	(days)	n	S.D.
1st	1.37	10	0.06	11.80	44	1.56
2nd	1.69	32	0.08	14.68	40	1.33
3rd	2.20	27	0.13	26.32	37	5.28
4th	2.60	22	0.16	27.97	30	4.21
5th	3.10	41	0.26	28.52	31	5.67
6th	3.44	38	0.21	36.11	37	5.41
7th	3.79	39	0.16	36.42	33	6.60
8th	4.06	39	0.29	44.46	28	10.56
9th	4.53	43	0.57	40.69	26	16.63
10th	5.36	43	0.55	35.48	23	12.57
11th	6.67	33	0.71	28.11	9	6.57
12th	—	—	—	23.0	4	7.83

The mean carapace width for each instar (not separated by sex) is shown in Figure 1 to have a nearly linear relationship with the stadia, as might be expected. This and the large number of stadia seem to agree with a suggestion made by Hagstrum (1971) that large spiders have added stadia, rather than accelerated growth between successive molts. Sekiguchi (1945) shows similar data for the female of *H. venatoria* in Japan. The carapace widths for our spiders are summarized in Table 1.

The ratio of females to males for reared spiders was 2.4/1 (22 females/9 males). The sex ratio for adult specimens collected in Homestead, Dade Co., FL, on August 14-19, 1981 was 3.4/1 (71 females/21 males). The sex ratio in Homestead might be due to cannibalism of the males by females, as mentioned previously. Of the females collected, 18.3% were carrying egg sacs, and all instars were observed to be present in the field. Summer seemed to be the major period of egg production both in the laboratory and in the field.

This spider probably offers one of the best possibilities for the use of spiders in biological control as it is well adapted for living in close association with humans and is readily reared. As these spiders habitually feed on cockroaches, *H. venatoria* behavior and ecology may be an important key in the biological control of one of mankind's oldest pests.

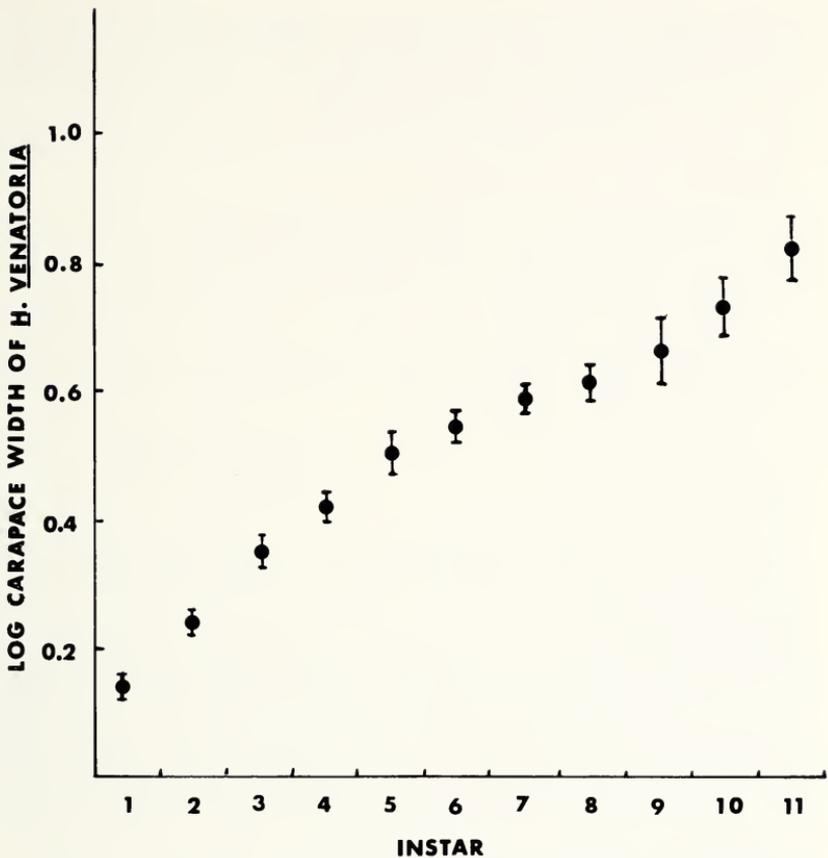


Figure 1. Relationship between logarithm of mean carapace width and stadia for laboratory-reared *Heteropoda venatoria* (L.). Standard deviations are shown for each point.

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We would like to thank Dr. Stratton H. Kerr and Dr. Martin H. Muma for suggestions regarding the manuscript, and Takuji Hayakawa and John Watts for help with the collection and rearing of the spiders. Mr. Hayakawa also provided valuable help in translating the papers published by Dr. Sekiguchi.

SUMMARY

The giant crab spider, *Heteropoda venatoria* (L.) was reared in the laboratory. These spiders reached adulthood after 8-10 instars

for the males and 9–12 instars for the females and took approximately one year to mature from the egg. The postembryonic stages were found to last approximately 2 weeks.

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DESCRIPTION OF A NEW SPECIES OF
KROMBEINIUS (HYMENOPTERA: PERILAMPIDAE)
FROM THE PHILIPPINES, AND THE PHYLOGENETIC
RELATIONSHIPS OF THE GENUS*

BY D. CHRISTOPHER DARLING
Department of Entomology,
Cornell University, Ithaca, N.Y. 14853

The genus *Krombeinius* (Hymenoptera: Perilampidae) was recently described (Bouček 1978) to include perilampids with an amalgam of the characters of *Euperilampus* Latreille and *Perilampus* Walker. The habitus suggests *Euperilampus*, and there are two synapomorphies to unite these two genera (Darling 1983): postspiracular sclerite reduced to a narrow triangle, less than one-half as wide as the adjacent pronotum; and pronotum massive, at least one-third the length of the mesoscutum. However, *Krombeinius* exhibits the wing venation, presence of a marginal rim on the scutellum, and large third metasomal tergite characteristic of *Perilampus*. I regard these as plesiomorphic similarities. The genus is characterized by the absence of the defining apomorphic characteristics of *Euperilampus*, i.e., by symplesiomorphy.

In this paper I present new information on the structure of the male genitalia and labrum of the type species of *Krombeinius*. These structures have proved to be of considerable value in defining genera in the Perilampidae (Darling 1983). From this analysis I suggest autapomorphies for defining *Krombeinius*. In addition, I describe a new species of *Krombeinius* from the Philippines, and discuss the affinities of the three included species.

Taxonomic studies of *Krombeinius* have been hampered by the scarcity of material. The type species, *K. eumenidarum*, was described by Bouček (1978) from a series of specimens (2 male, 2 female) reared from the larvae of an eumenine wasp in Sri Lanka. All specimens were prematurely killed and had to be liberated from the pupal cuticles, producing some abnormalities in the type material. Also included by Bouček (1978) in this genus was *Perilampus megalaspis* Cameron, known only from the type material (3 females)

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and an additional female, all from Sarawak, Malaysia. During my study of material in the U.S. National Museum of Natural History, Washington [USNM], I located an additional male specimen of *K. eumenidarum*. This specimen [India: Kerala Survey, 12.5 Pechiparai, 25–27 August 1974] was dissected and re-mounted and is the basis for the description of the labrum and male genitalia. In addition, the C. F. Baker Collection [USNM] contained a new species of *Krombeinius* from the Philippines, which I describe herein.

Abbreviations used in text: F1–7: funicular segments 1–7; MSC: length of mesoscutum along midline; OOL: length of ocular-ocellar line; PN: length of pronotum along midline; POL: length of posterior ocellar line; SC: length of scutellum along midline; T2–8: metasomal tergites 2–8.

Krombeinius

Krombeinius Bouček, 1978: 302, Figs. 1,2.

Type species: *Krombeinius eumenidarum* Bouček, 1978: 302, Fig. 1. [original designation].

Diagnosis:

Hymenoptera: Chalcidoidea: Perilampidae (sensu Graham, 1969). Species of *Krombeinius* can be distinguished from *Monacon* Waterston, *Burksilampus* Bouček, *Steffanolampus* Peck and *Perilampus* Latreille by the narrow postspiracular sclerite, less than one-half the width of the adjacent pronotal panel, and from *Euperilampus* by having the marginal vein longer than the postmarginal (Fig. 1).

All known species are moderately large, 3 to 5½ mm long, black without metallic reflections and are restricted to the Oriental region. There are three species currently placed in *Krombeinius*: *K. eumenidarum* Bouček, *K. megalaspis* (Cameron) and *K. saunion*, n.sp.

A revised key to the species of *Krombeinius* is not presented. The key of Bouček (1978) separates *K. eumenidarum* and *K. megalaspis*. An additional character to separate these two species is the inner orbits: costate in *K. eumenidarum* (Fig. 8), and smooth in *K. megalaspis* (Fig. 12). *K. saunion* is readily distinguished from these two species by the prominent spine at the apex of the scutellum (Fig. 1,15). The apex of the scutellum is truncate in the other two species (Figs. 7,11).

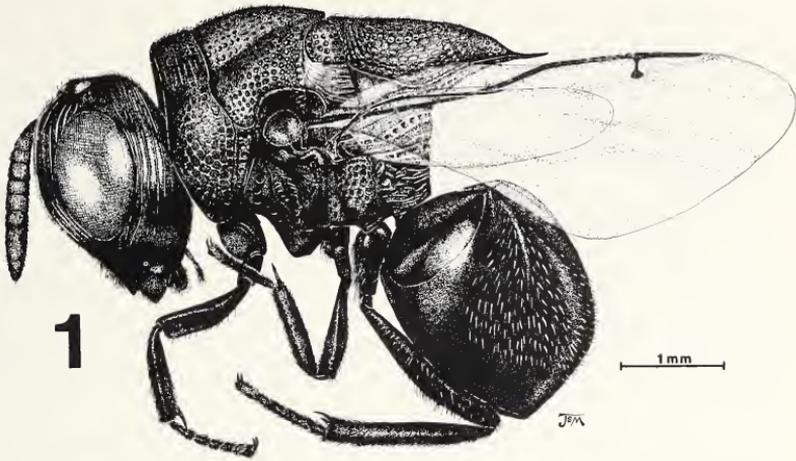
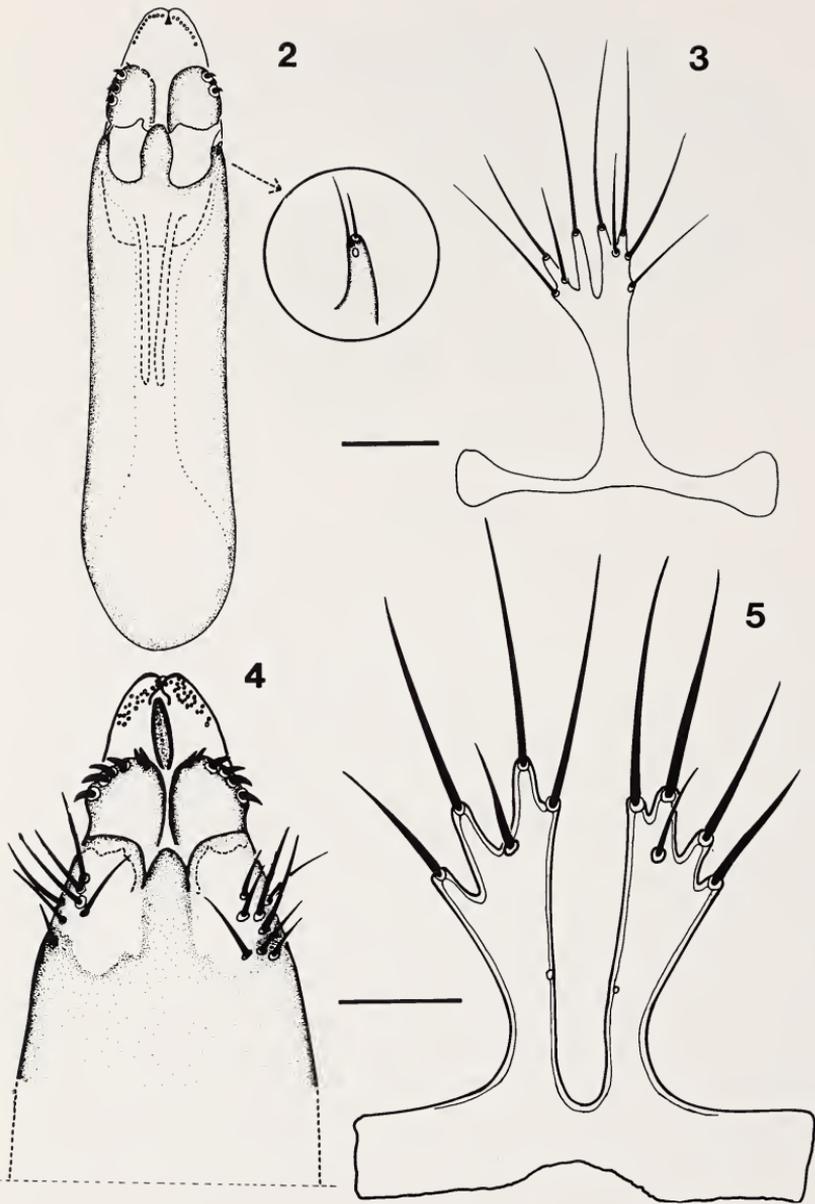


Fig. 1. *Krombeinius saunior*, lateral habitus.

Description:

Head: supraclypeal area smoothly convex, without horn or ridge; scrobal cavity deep, extending to lower ocular line or to middle of clypeus; clypeus and supraclypeal area separated by distinct suture or by faint line; inner orbits carinate; frontal carina separating the median and posterior ocelli; malar sulcus absent; malar region with strong oblique costae; posterior ocellus located high on vertex, POL approximately equal to OOL; labrum with a single narrow stalk, expanded distally with 7 digits, each with a terminal seta, and with pair of sessile setae not associated with digits, strongly excised medially [$n = 1$, *K. eumenidarum*, Fig. 3].

Mesosoma: dorsum of pronotum smoothly convex, without transverse elevations; pronotum massive, about one-third length of mesoscutum, not narrowed medially; mesothoracic spiracle located between pronotum and sidelobe of mesoscutum; postspiracular sclerite fused to the pronotum but delimited by surface sculpture; postspiracular sclerite less than one-half width of adjacent pronotal panel, with many or a single puncture; notauli distinct; scutellum vaulted, jutting over propodeum and base of metasoma; apex of scutellum acuminate, or truncate or with a distinct spine; propodeum with median area foveate, or with a short median ridge, sub-



Figs. 2-5. 2,3 *Krombeinius eumenidarum*. 2. Male genitalia. Inset: enlargement of paramere. 3. Labrum. 4,5. *Euperilampus triangularis* (Say). 4. Apex of male genitalia. 5. Labrum. [Scale lines 0.1 mm.]

median areas with weak transverse rugae or aciculate; basitarsomere not conspicuously lengthened. Forewing with marginal vein longer than postmarginal, postmarginal vein long, about 3 times length of stigmal vein, stigmal vein making either a right or oblique angle with marginal vein.

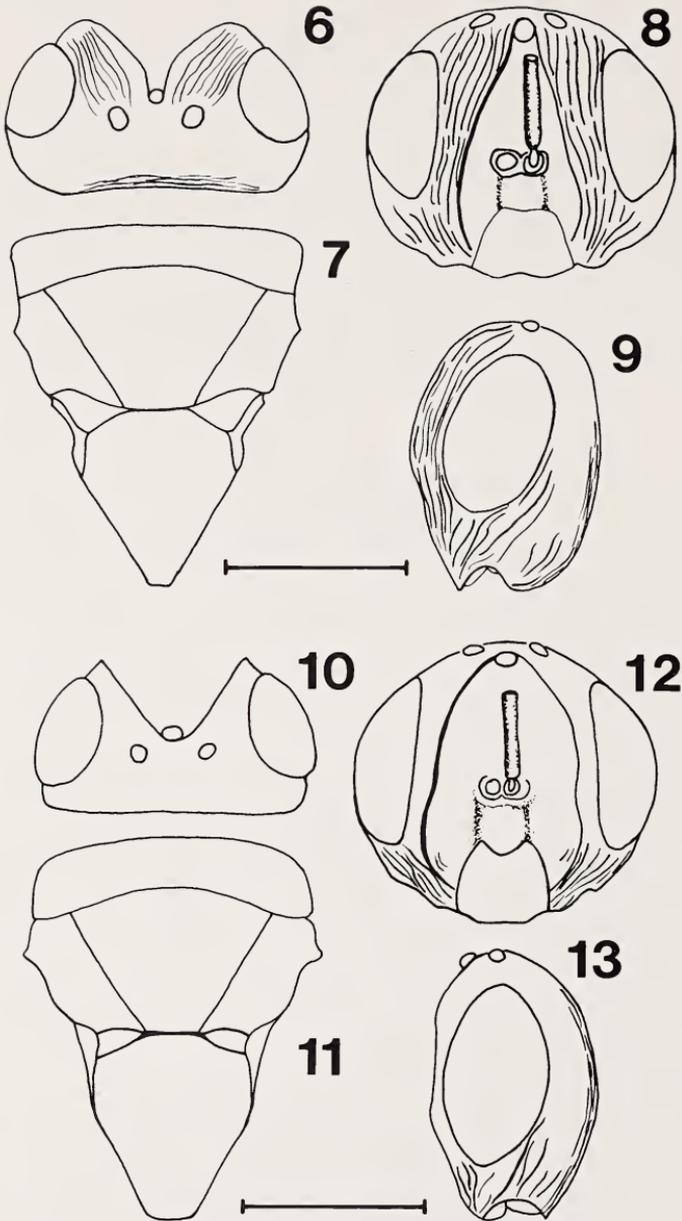
Metasoma: petiole short, transverse, the tergum forming a ridge along anterior face of gaster, sternum shifted posteriorly; gaster triquetrous, T2 and T3 fused, covering most of dorsum; T2 without distinct basal fovea; T3 much longer than T2, subquadrate, slightly wider than length along midline; ovipositor ventral, not upturned, sheaths not distinctly exerted; male genitalia with distinct parameres [$n = 1$, *K. eumenidarum*, Fig. 2].

Discussion:

The male genitalia of *Krombeinius eumenidarum* (Fig. 2) are similar to those of species of *Perilampus*: the parameres are distinct, and strong setae are distributed on these lobes. This configuration occurs throughout the Chalcidoidea (see Domenichini 1953) and is regarded as plesiomorphic. In *Euperilampus* a derived condition is found (Darling 1983): distinct parameres are lacking, and the basiparamere has a patch of strong setae distributed on transparent areas laterad of the ventral lobe (Fig. 4).

The labrum of *Krombeinius eumenidarum* (Fig. 3) has a narrow central stalk, not found in other perilampid genera (Riek 1966; Domenichini 1969; Darling, unpublished). However, the labrum does share synapomorphies with species of *Euperilampus* (Fig. 5) including a reduced number of digits (7 or 8), a pair of smaller, sessile setae not associated with digits, and a strong median excision. The narrow stalk distinguishes the labrum of *Krombeinius* from those of *Euperilampus*, and is postulated as an autapomorphy of *Krombeinius*. All other perilampid labra are 10–12-digitate, and not as strongly excised medially.

The host association of the type species of *Krombeinius* [larva of Vespidae: Eumeninae] is different from that of any other described perilampid, although solitary Sphecidae are attacked by some *Perilampus* species (e.g., *Perilampus nitidus*, primary parasitoid of *Ectemnius paucimaculatus*. Krombein 1964, as *P. canadensis*). This behavioral character is regarded as an additional autapomorphy for the genus *Krombeinius*.



Figs. 6-13. 6-9. *Krombeinius eumenidarum*. 6. Head, dorsal. 7. Mesosoma, dorsal. 8. Head, frontal. 9. Head, lateral. 10-13. *K. megalaspis*. 10. Head, dorsal. 11. Mesosoma, dorsal. 12. Head, frontal. 13. Head, lateral. [Scale line 1 mm.]

Krombeinius sauion n.sp.

(Figs. 1, 14–17)

Type Locality: Philippines, Mindanao, Surigao.

Type Material: Holotype: Female [Baker Collection, USNM].

Etymology: The specific epithet is a noun in apposition, Greek for "javelin", and is a reference to the elongate spine on the scutellum of this species.

Diagnosis:

This species can be immediately recognized by the prominent spine at the apex of the scutellum (Figs. 1, 15). The apex of the scutellum is truncate in *K. eumenidarum* (Fig. 7) and *K. megalaspis* (Fig. 11).

Description:

Female: Length, 5.4 mm. Black, except tegula and flagellum brown, mandible reddish-brown, apex of foretibia and spur, and tarsi yellow; wings hyaline, veins darkened.

Head: length of malar space 0.34 eye height; OOL 0.95 POL; maximum width of scrobe 0.56 head width; head transverse, width: height = 1.17; inner and outer orbits costate, costae convergent on clypeus; scrobal cavity deep and wide, extending below lower ocular line and delimiting clypeus and supraclypeal area; clypeus transverse, width:height = 1.31, polished and covered with long setae; clypeus not delimited by sutures, upper margin indicated by a faint line, tentorial pits distinct, lower margin weakly emarginate; ocular-ocellar region with costae radiating from posterior ocellus; vertex with strong costae at posterior margin; supraclypeal area glabrous, height 0.51 clypeus height; lateral wall of scrobe merging smoothly with face; lower tooth of mandible pointed at apex; base of mandible with weak punctures; labio-maxillary complex short. Antenna: scape narrowly linear, length 8.5 maximum width; pedicel and funicular segments subequal in length (18 versus 14,15,17,16,15, 15,13;F1–F7); pedicel 0.21 scape length; anellus 0.43 length of F1; F1 elongate, remaining flagellomeres transverse; clava 0.25 length of funicle.

Mesosoma: pronotum massive, PN:MSC = 0.34, lateral pronotal collar not regularly convex, suggesting bumpy shoulders; scutellum acuminate with a long spine, SC:MSC = 1.75; dorsum of pronotum

punctate-reticulate, punctures coalesced to form weak irregular transverse costulae medially; midlobe of mesoscutum and scutellum weakly punctate, becoming punctate-reticulate along notauli; side-lobe of mesoscutum smooth along notauli, laterally punctate-reticulate; notauli distinct; scutellum in lateral view tapering abruptly towards apex (Fig. 1; cf. Figs. 1,2 in Bouček 1978); underside of scutellum mostly coriarius, with shallow convergent grooves; propodeum vertical, medially about twice as long as metanotum, with weak median ridge, submedian areas with transverse costulae, callus reticulate-rugose; width of postspiracular sclerite 0.44 width of adjacent pronotal collar, with about 10 foveae; axilla reticulate above, costate below; axillula smooth. Forewing: submarginal:marginal:postmarginal:stigmatal veins as 64:17:12:4; stigmatal vein making a right angle (90 degrees) with marginal vein.

Metasoma: T2 smoothly concave with weak coriarius sculpture; T2 with sparse setae, without punctures, border between T2 and T3 indicated by a suture, laterotergite glabrous; T3 massive and convex, about twice length of T2 along midline, length about equal to maximum width (22 versus 25), evenly covered with long setae except along T2 border and along margins of tergite, without punctures.

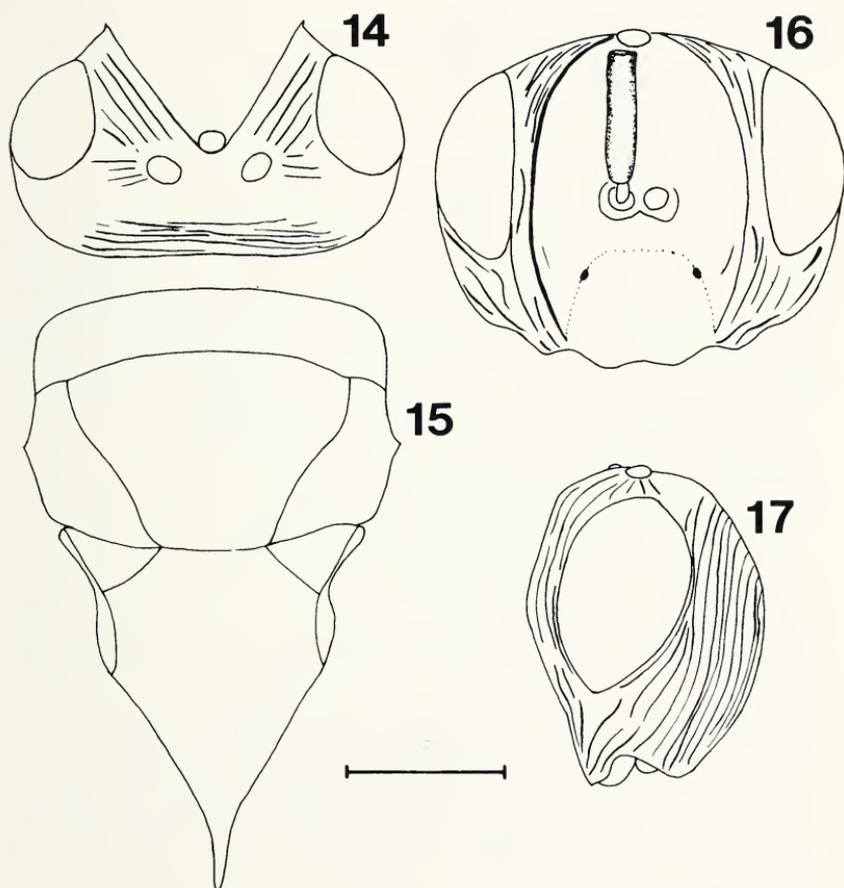
Male: Unknown.

Discussion:

Krombeinius saunion is more closely related to *K. eumenidarum* than to *K. megalaspis*. Synapomorphies of these two species are: the stigmatal vein making a right angle with the marginal vein (oblique in *K. megalaspis* and outgroup: *Euperilampus* and *Perilampus*); clypeal-supraclypeal margin weak or indistinct (separated by distinct suture in *K. megalaspis* and outgroup: *Euperilampus* and *Perilampus*); lateral pronotal collar suggesting bumpy shoulders (regularly convex in *K. megalaspis* and outgroup: *Euperilampus* and *Perilampus*); and postspiracular sclerite with many foveae (a single fovea is found in *K. megalaspis*, and in the ancestral species groups of *Euperilampus*, Darling 1983). Considering *Euperilampus* as the outgroup, the following similarities of *K. eumenidarum* and *K. saunion* are regarded as plesiomorphic: propodeum medially about twice as long as metanotum (equal to metanotum in *K. megalaspis*; autapomorphy); scutellum, in lateral view, not strongly convex, tapering gradually towards the apex (highly convex in *K. megalaspis*, Bouček 1978: Fig. 2; autapomorphy).

K. saunion and *K. eumenidarum* also have the inner orbits with strong costae (Figs. 8,9,16,17), whereas the inner orbits of *K. megalaspis* are smooth (Figs. 12,13). I consider the costate inner orbits to be a synapomorphy of *Euperilampus* + *Krombeinius*. As such I interpret the smooth orbits of *K. megalaspis* as an autapomorphic reversal. A similar reversal in this character is indicated in the *Euperilampus* cladogram (Darling 1983).

There remain some difficulties in justifying the current composition of the genus *Krombeinius*. The numerous characters separating



Figs. 14-17. *Krombeinius saunion*. 14. Head, dorsal. 15. Mesosoma, dorsal. 16. Head, frontal. 17. Head, lateral. [Scale line 1 mm.]

K. eumenidarum + *K. saunion* from *K. megalaspis* question the inclusion of *K. megalaspis*. A revised classification would create a monobasic new genus for *Perilampus megalaspis*, and would allow *Krombeinius* to be defined by the synapomorphies of *K. eumenidarum* + *K. saunion*. Recalling that the proposed synapomorphies of *Krombeinius* (structure of the labrum; host association) are not known for *K. megalaspis*, it would not be surprising if this species were to be excluded at some later date. Clearly, more material and associated biological information are essential to re-evaluate the composition of *Krombeinius*, and any nomenclatural changes at this time would be premature.

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A DESCRIPTION OF THE
ECTAL MANDIBULAR GLAND IN THE PAPER WASP
POLISTES FUSCATUS (HYMENOPTERA: VESPIDAE)*

BY H. A. DOWNING AND R. L. JEANNE
Department of Entomology
University of Wisconsin
Madison, Wisconsin 53706

While the ectal mandibular gland is a source of queen substance in both honey bees and bumble bees (Butler and Simpson, 1958; van Honk et al., 1980), little is known about this gland in the vespids. In *Vespula* and *Polistes* spp. the mandibular gland consists of 50 to 70 ducted gland cells opening into a reservoir which in turn is said to empty into the oral cavity at the base of the mandible (Hermann et al., 1971; Spradbery, 1973; Landolt and Akre, 1979). Nedel (1960), however, found that the mandibular gland of *V. germanica* (F.) opens anterior to the anterior condyle and thus to the front of the face. He describes a small brush of mechanoreceptors on the mandible.

Because the mandibular gland is so much smaller in wasps than in bees, Spradbery (1973) suggested that it probably has no social function in wasps. However, the fact that this gland is the largest of the cephalic exocrine glands in wasps and the discrepancies in the literature concerning the locus of the gland opening caution against such a conclusion. The purpose of the present study is to investigate the morphology of the ectal mandibular gland in *Polistes fuscatus* with reference to possible gland function.

METHODS

Micrographs of the exterior opening of the ectal mandibular gland were taken using the JELCO JSM-U3 scanning electron microscope. Quarter sections of female wasp heads containing the ectal mandibular gland were fixed in Kahle's solution and embedded in Spurr Low-Viscosity embedding media (Polysciences) following the methods of Spurr (1969). Sections 2 μ thick were cut with a glass

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knife on a Porter-Blum-Microtome MT-1 (Sorvall®), stained using Mallory's Azure II-Methylene Blue (Richardson et al., 1960), and examined using a light microscope.

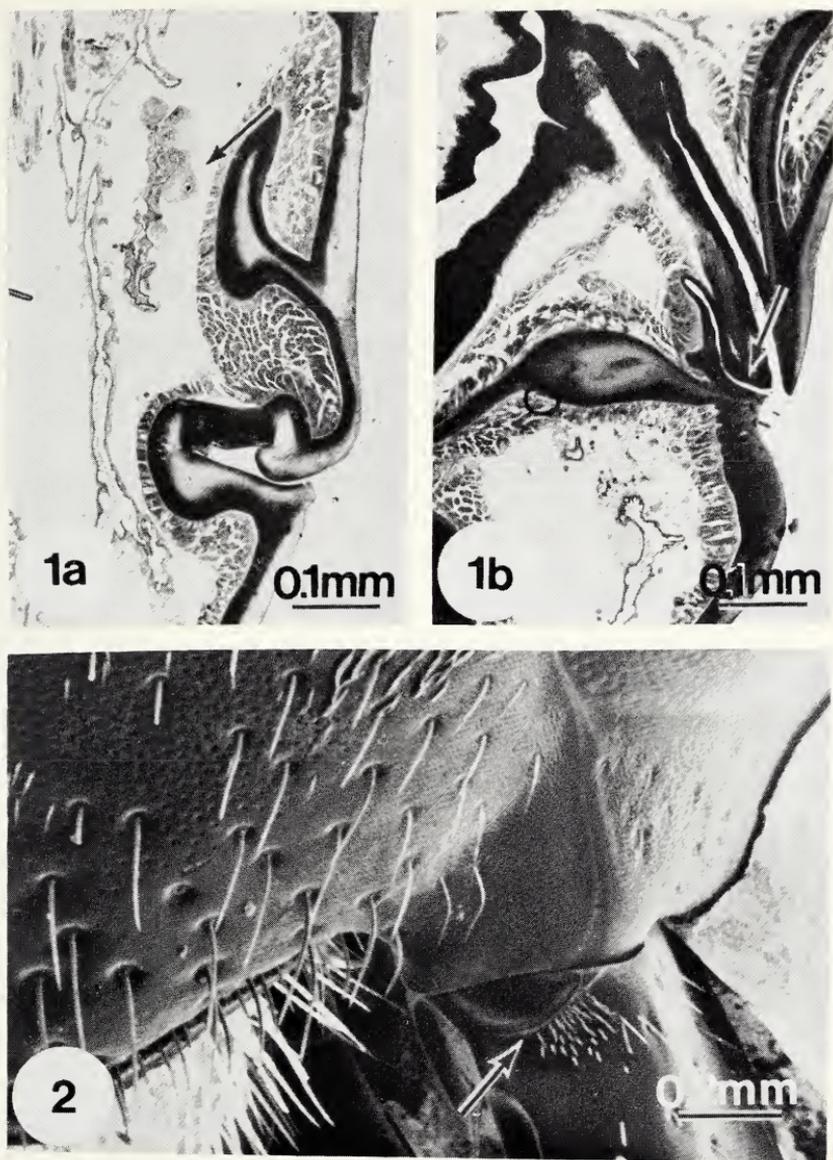
RESULTS AND DISCUSSION

The ectal mandibular gland in *P. fuscatus* females is similar to the ectal mandibular gland Nedel (1960) described for *V. germanica*. The gland reservoir, which lies appressed to the gena, opens at the base of the mandible via a long, flattened, sclerotized duct. Gland cells can be seen on the outer surface of the reservoir (Figure 1a). The sclerotized duct of the reservoir opens on to the mandibular surface just above a brush of bristles (Figure 1b). The bristles may be mechanoreceptors and may also serve to increase the surface area for evaporation of the glandular secretion. A scallop of cuticle extends ventrally from the gena, covering the brush when the mandible is closed. When the mandible is opened even slightly the brush is exposed on the front of the face (Figure 2).

The position of the ectal mandibular gland opening suggests a social rather than a physiological function. Because it does not open into the mouth, this gland is probably not a source of digestive enzymes or nest construction material. *P. fuscatus* colonies are initiated by one or more overwintered female gynes, which work together to raise the brood. Aggressive interactions result in the formation of a dominance hierarchy in which the most dominant individual is the egg-layer for the colony (Pardi, 1948). The dominant female must maintain a certain level of aggression in order to retain her dominant status, but her elevated rank is communicated by chemical cues originating in the head (Downing, 1982). Dominant wasps frequently chew on the head and thorax of their subordinates, and when threatening other females will lunge toward them with open mandibles. The ectal mandibular gland opening is exposed at these times, suggesting that it may be the source of chemical signals important for the communication of status during aggressive interactions.

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Figs. 1-2. Fig. 1. Ectal mandibular gland histology. Sagittal sections through a) reservoir (arrow points to gland cells at the top of reservoir) and b) reservoir duct, showing duct opening to the mandibular brush (arrow). Anterior is to the right. Fig. 2. Ectal mandibular gland opening, frontal view. SEM micrograph of the exposed mandibular brush, located just below the opening of the ectal mandibular gland (arrow). The mandible is in an open position. Clypeus is on the left, compound eye in the upper right.

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SPIDERS LIVING AT WASP NESTING SITES:
WHAT CONSTRAINS PREDATION BY MUD-DAUBERS?

BY MARTIN S. OBIN¹

The nests of mud-daubing wasps (Hymenoptera: Sphecidae) are excellent sources of spiders (Peckham and Peckham, 1898; Rau, 1935; Muma and Jeffers, 1945; Dorris, 1970). Females of these solitary wasp species construct mud nests during the late spring and summer. They provision each brood cell with a number of spiders which they capture and paralyze by stinging. The wasp lays an egg on one of these spiders and, upon hatching, the larva consumes all the spiders within the brood cell. When development is complete, the new adult wasp chews a hole in its brood cell and emerges. A cell in the nest of mud-daubers such as *Sceliphron caementarium* or *Chalybion californicum* may contain in excess of 25 spiders. It seems likely then that mud-dauber predation may be a significant factor influencing population dynamics and evolution of those spider genera taken as prey (see also Eberhard, 1970). But this view of wasp and spider interactions is incomplete. The same sites at which mud-daubers nest are also used by both wandering and web-building spiders for capturing prey and tending eggs. Mud-dauber nests themselves are often used by spiders for these activities. In fact, among the group of spiders active at mud-dauber nesting sites are species that are regularly taken as prey by those same spider-hunting wasps. Intrigued by this fact, I initiated field studies that addressed the following questions:

1. What groups of spiders are found living at nesting sites of mud-daubers?
2. What is the nature of the interactions between wasps and spiders at these sites?
3. If wasps do not hunt spiders at nesting sites, what factors constrain them from doing so?

¹Department of Zoology, University of Florida, Gainesville, FL 32611

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MATERIALS AND METHODS

Procedure. Nesting sites and mud nests of three species of sphecoid wasp were observed during the summer of 1980. Three groups of spiders were collected. These were: (a) active spiders within 2 meters of wasp nesting sites, (b) active spiders on or next to mud-dauber nests, and (c) paralyzed spiders from inside 110 old nests. Spiders were identified and their total body lengths measured. No attempt was made to census every spider at each site, as this would have proven impossible for genera such as *Tidarren* and *Filistata* which were numerous, mobile and often reclusive. In addition, encounters between spiders and wasps were observed and recorded.

The Wasps. *Sceliphron caementarium* (Drury) (Sphecinae: Sceliphirini) constructs individual cells of mud collected at the edges of ponds and streams. The nests are provisioned primarily with Araneidae, Thomisidae and Salticidae (Muma and Jeffers, 1945) and then sealed off with mud. Groups of contiguous cells are often covered by additional layers of mud and may appear as oval or oblong masses of up to 30 cells (see Muma and Jeffers, 1945 for plates of relevant mud-daubers and their nests). *Trypoxylon politum* Say (Larrinae: Trypoxylini) builds long, tubular nests from mud gathered at sites similar to those frequented by *Sceliphron*. The "pipe organ" nests usually contain between 3 and 5 cells, each provisioned with Araneidae of the genera *Neoscona* or *Eustala* (Muma and Jeffers, 1945; H. J. Brockmann, pers. comm.). Rather than constructing its own nest, the blue mud-dauber, *Chalybion californicum* (Saussure) (Sphecinae: Sceliphirini) either modifies and seals existing old cells of *Sceliphron* and *Trypoxylon* or cleans out and reprovisions recently completed cells. Dry mud from nearby nests is softened by mixing with water stored in the wasp's crop. The wet mud is then manipulated and used for sealing nests. *Chalybion* specializes in hunting small Theridiidae and Araneidae (Muma and Jeffers, 1945).

The Study Sites. Three sites in Alachua County, Florida were selected. Two were located in the Paynes Prairie State Preserve and were designated Boat House (BH) and Garage (G). Both sites had females of all three species actively building and provisioning nests. The boat house site had a 10 m × 25 m × 1 m high shaded crawl space with an unfinished pine ceiling, dirt floor and open sides. The

structure was within 5 m of a lake and was surrounded on three sides by a lawn dotted with palms and turkey oak. A dense stand of palmetto and hardwoods was located ca. 100 m distant. The Garage site was located 150 m from the lake shoreline and was next to a small plot of palmetto-hardwood forest. Wasp nests covered the exterior walls of this painted wood structure and were exposed to ambient light. The third site, Rocky Creek (RC) was two cement bridge tunnels where State Road 121 crossed Rocky Creek. During the study, the water level was sufficiently low such that the sand bottom of the creek was exposed throughout most of the two tunnels. The tunnel entrances were fringed with tall grass, occasional shrubs and *Eupatorium* sp. Light levels inside the tunnels were the lowest among the 3 sites. The area surrounding the site was composed of cleared agricultural plots interspersed with thickets and small stands of oak and pine.

RESULTS

Table 1 lists the spiders observed at the 3 sites. Prey species are distinguished from non-prey species and web spiders from wandering spiders.

Web-Building Spiders. Eighty-three web spiders were collected, representing 12 genera in 4 families. Ten genera were taken as prey by the mud-daubers nesting at the study sites. Species of three genera of spiders were found living in open mud cells from which wasps had emerged earlier in the season. Males and females of *Metazygia wittfeldae* (McCook), *Filistata hibernalis* Hentz and *Oecobius annulipes* (Lucas) were removed from inside old nests of *Sceliphron* and *Chalybion* that were constructed over or close to seams and cracks in walls. Of 11 cells containing *M. wittfeldae*, 8 also contained egg cases. Two old cells with adult pairs and spiderlings inside were also noted. Genera of Araneidae and Theridiidae positioned webs either close to nesting sites (*Argiope*, *Nephila*, *Micrathena* and *Neoscona*) or within 10–15 cm of active nests (*Leucauge*, *Tetragnatha*, *Tidarren*, *Latrodectus* and *Achaearanea*). Webs of *Argiope aurantia* Lucas were found only at Rocky Creek, where the tall grass and bushes at the tunnel entrance afforded suitable habitat. The distribution of *Micrathena sagittata* (Walckenaer) appeared similarly limited by habitat, as webs were confined to the wood's edge behind the Garage site.

Wandering Spiders. Five families were collected, totalling 43 spiders in 8 genera. Five of these genera are common prey items of mud-daubers. A *Xysticus* sp. was discovered inhabiting an inactive *Sceliphron* nest and a female *Platycryptus undatus* (De Geer) occupied a half-completed *Sceliphron* cell, constructed a retreat and positioned herself at the entrance. Species of *Phidippus* and *Thiodina* climbed over nests, but did not remain on these structures. However, species of *Dolomedes* were frequently noted on the outside of mud nests. They remained motionless for hours during the day and appeared to achieve an enhanced crypsis against the nest background.

Spider Size. Seventy-six specimens belonging to genera taken as prey by mud-daubers were collected at the 3 sites. Of these, only 9 exceeded the upper size range of congeners found paralyzed in wasp cells (Table 1). The 2 *Argiope* listed were also larger than conspecifics (N=3) that could not be handled (i.e., were repeatedly dropped after immobilization) by *Sceliphron*. These spiders were 15.0, 16.5, and 16.8 mm long respectively. Two spiders dropped by *Chalybion* were 15.3 mm [*Pisaurina undulata* (Keyserling)] and 14.6 mm long [*Peucetia viridans* (Hentz)]. The largest *P. undulata* provisioned by *Chalybion* was 11.8 mm (N=3), and the largest *P. viridans* was 13.8 mm (N=14). Extensive data for *Trypoxylon*, generously provided by Dr. H. J. Brockmann, indicated that the heaviest of 289 *Neoscona* provisioned by *Trypoxylon* during June and July weighed 0.2400 grams. Spiders dropped by provisioning females exceed this weight on 12 occasions, ranging in weight from 0.2537–0.4236 g. (Spiders were weighed to the nearest 0.1 mg.)

Wasp-Spider Interactions. Surprisingly, predation by mud-daubers on spiders living at nest sites was never observed. Brockmann (pers. comm.), who has spent over 3,000 hours observing wasps under bridges near Gainesville, has also never observed a single case of a wasp preying on a spider near the nesting site. Wasps repeatedly walked or flew within several centimeters of potential prey, displaying no observable taxes or predatory movements. In 2 separate incidents, female *Sceliphron* that had strayed into webs of *Tidarren sisypoides* (Walckenaer) freed themselves after stinging the overly eager spider. In neither instance did the wasp show any further interest in the potential prey item, although in both cases the spider

Table 1. Summary of spiders active at nesting sites. Live spiders were collected on or inside mud-dauber nests (1), within 15 cm of nests (2) or within 2 m of the nesting site (3). Table includes the upper size range of spider prey paralyzed in nests and the number of conspecifics at nest sites exceeding this range. (Size = length inclusive of chelicerae). C = *Chalybion californicum*; S = *Sceliphron caementarium*; T = *Trypoxylon politum*.

Active spiders	Site and location of spiders	Wasp predator	Size range (mm) of prey (paralyzed in nests)	No. of active spiders exceeding prey size range/total no. active spiders collected. (Sizes of those exceeding size range are included.)	Observed preying on mud-daubers
PREY SPIDERS					
Web spiders					
Araneidae:					
<i>Argiope aurantia</i>	RC; 3	C, S	5.2–13.8 (N = 32)	2/3 (18.5 mm, 19.7 mm)	Yes
Lucas					
<i>Leucauge venusta</i>	BH; 2	C	4.5–7.1 (N = 16)	0/4	No
(Walckenaer)					
<i>Metazygia wittfeldae</i>	BH, G, RC; 1,2	C, S	6.2–8.4 (N = 13)	0/11	No
(McCook)					
<i>Micranthena sagittata</i>	G; 3	C	4.7–8.0 (N = 9)	1/6 (8.5 mm)	No
(Walckenaer)					
<i>Neoscona domicilliorum</i>	BH; 3	C, S, T	4.6–12.0 (N = 24)	0/5	Yes
(Hentz)	BH; 3	C, S	4.8–9.6 (N = 7)	1/7 (18.0 mm)	Yes
<i>Nephila clavipes</i> (L)					
<i>Tetragnatha guatemalensis</i>					

Table 1. Continued

Active spiders	Site and location of spiders	Wasp predator	Size range (mm) of prey (paralyzed in nests)	No. of active spiders exceeding prey size range/total no. active spiders collected.	Observed preying on mud-daubers
O. P.-Cambridge	BH; 2	C, S,	8.1-10.6 (n = 6)	0/3	No
<i>Tetragnatha pallescens</i>					
F. P.-Cambridge	G; 2	C	10.1-10.3 (N = 2)	0/1	No
Theridiidae					
<i>Achaearanea tepidariorum</i> (C. L. Koch)	BH, G, RC; 2	C, S,	4.2-6.3 (N = 10)	0/7	Yes
<i>Latrodectus mactans</i> (Fabricius)	BH, G; 2	C, S	6.7-9.3 (N = 3)	1/4 (10.8 mm)	Yes
<i>Tidarren sisypoides</i> (Walckenaer)	Bh, G, RC;	C, S	4.3-4.6 (N = 4)	3/96.8 mm, 7.4 mm, 9.7 mm)	Yes
Wandering Spiders					
Anyphaenidae:					
<i>Anypha velox</i> (Becker)	BH; 3	C, S,	7.8-10.2 (N = 3)	0/2	No
Salticidae:					
<i>Phidippus audax</i> (Hentz)	G, RC; 1, 2	C, S,	5.0-7.9 (N = 7)	1/9 (9.3 mm)	No
<i>Phidippus regius</i> (C. L. Koch)	G, 2	C, S,	6.1-9.2 (N = 3)	0/2	No

<i>Playcryptus undatus</i> (De Geer)	G; 1	S ¹		No
<i>Thiodina iniquies</i> (Walckenaer)	G; 1, 2	C, S	7.3-8.6 (N = 3)	No
Thomisidae: <i>Xysticus</i> sp.	BH; 1	S ¹		No
NON-PREY SPIDERS				
Web Spiders				
Filistatidae				
<i>Filistata hibernalis</i>				
Hentz	BH, G; 1, 2			Yes
Oecobiidae				
<i>Oecobius annulipes</i> Lucas	G; 1			No
Wandering Spiders				
Lycosidae:				
<i>Lycosa punctulata</i>	BH, G, RC;			No
Hentz	1, 2			
Pisauridae:				
<i>Dolomedes albineus</i>	BH, RC;			Yes
Hentz	1, 2			
<i>Dolomedes okefinoakensis</i>	BH, RC;			Yes
Bishop	1, 2			
Salticidae:				
<i>Plexippus paykulli</i>	BH; 1, 2			No

¹Not found provisioned in this study, but found paralyzed in nests by Muma and Jeffers, 1945.

Table 1. Continued

Active spiders	Site and location of spiders	Wasp predator	Size range (mm) of prey (paralyzed in nests)	No. of active spiders exceeding prey size range/total no. active spiders collected (Sizes of those exceeding size range are included.)	Observed preying on mud-daubers
O. P.-Cambridge	BH; 2	C, S,	8.1-10.6 (n = 6)	0/3	No
<i>Tetragnatha pallescens</i>					
F. P.-Cambridge	G; 2	C	10.1-10.3 (N = 2)	0/1	No
Theridiidae					
<i>Achaearanea tepidariorum</i> (C. L. Koch)	BH, G, RC; 2	C, S,	4.2-6.3 (N = 10)	0/7	Yes
<i>Latrodectus mactans</i> (Fabricius)	BH, G; 2	C, S	6.7-9.3 (N = 3)	1/4 (10.8 mm)	Yes
<i>Tidarren sisypoides</i> (Walckenaer)	Bh, G, RC;	C, S	4.3-4.6 (N = 4)	3/96.8 mm, 7.4 mm, 9.7 mm)	Yes
Wandering Spiders					
Anyphaenidae:					
<i>Aysha velox</i> (Becker)	BH; 3	C, S,	7.8-10.2 (N = 3)	0/2	No
Salticidae:					
<i>Phidippus audax</i> (Hentz)	G, RC; 1, 2	C, S,	5.0-7.9 (N = 7)	1/9 (9.3 mm)	No
<i>Phidippus regius</i> (C. L. Koch)	G, 2	C, S,	6.1-9.2 (N = 3)	0/2	No
<i>Platycryptus undatus</i> (De Geer)	G; 1	S ¹			No
<i>Thiodina iniquies</i> (Walckenaer)	G; 1, 2	C, S	7.3-8.6 (N = 3)	0/3	No
Thomisidae:					
<i>Xysticus</i> sp.	BH; 1	S ¹			No
NON-PREY SPIDERS					
Web Spiders					
Filistatidae					
<i>Filistata hibernalis</i> Hentz	BH, G; 1, 2				
Oecobidae					
<i>Oecobius annulipes</i> Lucas	G; 1				Yes
Wandering Spiders					
Lycosidae:					
<i>Lycosa punctulata</i> Hentz	BH, G, RC; 1, 2				No
Pisauridae					
<i>Dolomedes albineus</i> Hentz	BH, RC; 1, 2				Yes
<i>Dolomedes okefinokensis</i> Bishop	BH, RC; 1, 2				Yes
Salticidae:					
<i>Plexippus paykulli</i>	BH, 1, 2				No

¹Not found provisioned in this study, but found paralyzed in nests by Muma and Jeffers, 1945.

was paralyzed. Rather, after extricating themselves, both flew to nearby vegetation and groomed intensively before returning to their nests.

However, a number of spiders were observed preying on mud-daubers. Wasps carrying very large prey or those having just left the nest sometimes blundered into webs situated directly in the flight path of the wasp. All 3 species of wasp were found entangled in webs of either *Argiope aurantia*, *Neoscona domiciliorum* (Hentz), *Latrodectus mactans* Fabricius, *Tidarren sisypoides*, *Nephila clavipes* (Linnaeus), or *Filistata hibernalis* Hentz. Fourteen wasps were observed wrapped or trapped in webs. These included *Trypoxylon* (7), *Sceliphron* (5) and *Chalybion* (2). One of the *Sceliphron* noted was an emerging adult that was trapped in the sticky threads of *F. hibernalis* that covered its cell. *Micrathena* webs, positioned less than 0.5 meters off the ground, were too low to intercept wasps in flight. Smaller spiders such as *T. sisypoides* and the smaller individuals of *L. mactans* and *N. domiciliorum* did not always attack wasps caught in webs. These spiders retreated out of the range of the struggling wasp on 5 occasions. Biting or wrapping were delayed until the wasp had exhausted itself and was quiescent. In contrast, two *A. aurantia* observed at Rocky Creek immediately descended from the hub, wrapped the prey, inflicted a "short bite" (Robinson, 1969) and then returned to the hub before further wrapping commenced. One *Sceliphron* and 3 *Trypoxylon* were dispatched in this manner. Predation on wasps by spiders is not restricted to web-builders. Brockmann (pers. comm.) has observed attempted predation on mud-daubers by a *Dolomedes* sp. which leapt off a tunnel wall while attempting to grab a *Trypoxylon* hovering nearby. The spider was unsuccessful and pulled itself up the wall by the dragline. It is possible that large, mobile spiders of this type are preying on male *Trypoxylon* that sleep in the mud nests during the night.

DISCUSSION

Barns, old houses, bridges and the vegetation surrounding them afford appropriate habitat for many groups of spiders. The mud-daubing wasps are similarly attracted to such sites, for when water and mud are available, these sites provide favorable nesting substrate. It is not surprising therefore to observe spiders and spider-hunting wasps living in close proximity. It is noteworthy, however,

when these spiders (76 of 107 collected in our study) are prey species of the nesting wasps, for it suggests that these spiders escape predation. This study addressed that question in particular.

Why Mud-Daubers Do Not Hunt at Nest Sites. The inability of mud-daubers to recognize and capture prey living amongst them poses interesting questions. As demonstrated by Tinbergen (1935) for the solitary wasp *Philanthus triangulum* (Fabricus), successful predation may involve the hierarchical sequencing of various "appetitive behaviors" (Craig, 1918), each controlled by a specific releasing stimulus. In *Sceliphron*, for example, visual releasers such as spider-sized objects on a contrasting background are known to release a predatory pounce from a wasp in flight (Eberhard, 1970), but it is highly probably that wasp search images vary between habitats. Conspecifics hunting in the canopy and those hunting in the leaf litter may respond to learned visual cues appropriate to the particular microhabitat being searched. It is possible then that mud-daubers were catching spiders against backgrounds different from those presented to them at the 3 study sites. This might explain in a proximate sense why we observed no wasps attacking spiders at these sites. One might also propose that mud-daubers require a minimum light level to activate particular behaviors of the predatory sequence. However, nests at the Garage site were not in shade, and no hunting by wasps was observed. Are spiders at nest sites too large for mud daubers to immobilize and provision? The data strongly suggest otherwise, as less than 12% of potential prey collected during the study exceeded the upper range of spiders found paralyzed in wasp nests (Table 1).

One ultimate explanation of why "leave the nest site" appears to be a behavioral rule for foraging mud-daubers posits the importance of spider predation on wasps. Spiders that have previously encountered a wasp may be more likely to successfully defend themselves from subsequent wasp attack, and the probability of attacking a spider that has previously encountered and successfully handled a wasp may be greater close to or at nest sites than it is at a distance from such sites. Moreover, it is possible that spiders may learn to recognize characteristic vibrational signatures of mud-daubers. Such pretactile prey determination has been hypothesized (Robinson and Mirick, 1971), although Suter (1978) could not identify such a mechanism in the araneid *Cyclosa turbinata* (Walckenaer).

It is also possible that by not hunting at nest sites, mud-daubers more effectively conceal the location of their nest. Such a mechanism has been proposed to explain why raptors usually do not hunt near their own nests (Durango, 1949). Mud-dauber larvae fall prey to a variety of parasitoids and inquilines (Rau and Rau, 1916; Krombein, 1967). Hunting away from the nest site can reduce the probability of parasitization if the following assumptions are met: (1) The parasite encounters the host species at sites where the host species hunts; (2) The parasite trails the host species back to the nest; (3) The host species can evade the trailing parasite, the probability of so doing increasing with the distance over which the host species is trailed.

Certain host-parasite systems involving mud daubers and sarcophagid flies meet the above assumptions. Flies in the tribe Miltogrammini are larviporous parasites of many aculeates, including sphecid wasps (Allen, 1926). The genera *Amobia* and *Senotainia* include species of mud-dauber parasites that follow prey-laden wasps to their nests (Chapman, 1959; Cole, 1969). The adult flies are nectivorous, and it is likely that they encounter foraging wasps on vegetation. Prey-laden mud daubers often fly at reduced speeds, and their maneuverability is similarly impaired (Obin, pers. obs.). They are presumably easier to follow at such times. Furthermore, a wasp with prey assures a trailing fly that the wasp is nesting, that a cell is being provisioned and is consequently open, and that there will be food available in that cell. Sarcophagid flies have been observed trailing *C. californicum* females to their mud nests over distances of 3–5 m. The pursued wasps often took circuitous routes to their nests, and in certain instances left the site altogether before reaching their nest (Obin, unpublished data). Whether such behavior results in successful evasion is not known, but it does suggest that wasps may require flight distances greater than those observed in order to evade trailing Miltogrammini. If so, selection may, on average, favor wasps that do not hunt close to their nest.

Interactions between spiders and mud-daubers may not be exclusively antagonistic, and the selective advantage accruing to wasps that do not hunt at nest sites may be a consequence of a site-specific mutualism between these two traditional enemies. During the study, various parasites of mud-daubers were observed in webs at nest sites. These included bombyliid and sarcophagid flies as well as

chrysidid and mutillid wasps. These observations suggest that spider predation may reduce the parasite load at mud-dauber nest sites. Since mud-daubers are usually adept at recognizing and maneuvering on webs and retreats (Eberhard, 1970; Coville, 1976), spiders at nest sites may pose only a limited threat to wasps. We have observed individuals of all three species of wasp successfully nidify and provision nests positioned such that the wasp flew through or walked behind a web on each trip to and from the nest. Wasps became entangled in webs when their regular flight path was disrupted during agonistic encounters or when they attempted to provision very large spiders. Empirical evaluation of the relative costs (e.g., probability of predation, costs associated with increased flight distance to foraging patches) and benefits (reduced parasitism) of hunting away from the nest site is in progress. One predication of the "reduced parasitism" hypothesis is that a small percentage of mud daubers at any site may "cheat"—i.e., may occasionally prey on spiders at nest sites. Relative to other wasps in the population, these wasps would enjoy reductions in the time and energy costs of hunting and transporting prey, while at the same time benefitting from the "parasite umbrella" afforded by spiders active at nest sites. The relative frequencies of cheating and non-cheating (hunting away from nest sites) may perhaps be maintained by frequency-dependent selection (Fisher, 1930) in an Evolutionarily Stable Strategy (Maynard Smith and Price, 1973).

The Effects of Prey Size and Availability on Mud-Daubers. Various authors have suggested that spider size constrains prey collection by *Chalybion* (Muma and Jeffers, 1945), *Sceliphron* (Muma and Jeffers, 1945; Eberhard, 1970) and *Trypoxylon* (Cross et al., 1975). Selection should favor wasps that minimize both the risks and metabolic cost of (1) immobilizing and (2) transporting large spiders. Do wasps refrain from attacking large prey that they can incapacitate but not readily transport, or is the upper range of prey size found in nests a reflection of the wasp's inability or reluctance to paralyze prey above a certain size? Measurements of spiders dropped by provisioning mud daubers indicate that the wasps successfully incapacitate spiders that exceed the upper range of prey size noted in nests, but fail in their ability to transport or cache them.

The data differ from those of Muma and Jeffers regarding prey selection by *Chalybion* and *Sceliphron*. In their study in Maryland, the theridiid *Latrodectus mactans* constituted 25% of all prey taken by *Chalybion*. Locally, *L. mactans* is provisioned less frequently, comprising less than 5% of all prey taken. These differences may be due in part to the availability of more prey species in Florida. Spiders not found in Maryland nests but taken by *Chalybion* and *Sceliphron* in Florida include *Tetragnatha guatemalensis* O. P.-Cambridge, *Tetragnatha pallescens* F. P.-Cambridge, *Pisaurina undulata*, *Mecynogea lemniscata* (Walckenaer), *Gasteracantha cancriformis* (Linnaeus), and *Tidarren sisyphoides*. *M. lemniscata* and *G. cancriformis* were also found provisioned in *Sceliphron* cells. Maryland constitutes the northern most distribution for *M. lemniscata* (Kaston, 1978). *G. cancriformis* ranges only as far north as North Carolina (Levi, 1978). The distribution of *T. sisyphoides* in North America is restricted to the southern United States and Mexico (Levi, 1955).

Nest Sites as Spider Habitat. Mud-dauber nest sites may be particularly good habitats for some spiders. Benefits to spiders at such sites include the following:

1. Mud nests afford environmentally buffered refugia and brood chambers and may provide cryptic backgrounds.
2. Additional prey is available, including the wasps themselves, other spiders (Tolbert, 1975), mites and hymenopterous and dipterous parasites of mud-daubers, "renting" Arthropods that use empty mud-dauber cells (Dermaptera, lepidopterous larvae and non-sphelid wasps) and nest associates such as Psocoptera.
3. The risk of predation from wasps nesting at these sites is reduced.

Although somewhat counter-intuitive, the probability of wasp predation appears to be lower for spiders living at sites where wasps nest. The greatest threat may exist for smaller, naive individuals, and a small cost is probably incurred by those spiders whose web is damaged after intercepting a wasp. However, the benefits of living amidst mud-daubers may outweigh these potential costs. Associations of predator and prey at predator nests sites are not without precedent. Nesting of passerines with raptors has been reported

(Durango, 1949; McGillivray, 1978; Parker, 1981). Since raptors hunt away from their nests, traditional prey species nesting close by appear less threatened (Brown and Amadon, 1968; Parker, 1981).

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AGATHIDIODES PORTEVIN,
NEW SYNONYM OF STETHOLIODES FALL
(COLEOPTERA: LEIODIDAE: ANISOTOMINI)*

BY ALFRED F. NEWTON, JR.
Museum of Comparative Zoology
Harvard University, Cambridge, Mass. 02138

Examination of type material of many obscure genera of Leiodidae for a work in preparation on the suprageneric classification of the family has revealed a new generic synonymy in the tribe Anisotomini (=Agathidiini).

Stetholiodes Fall, described for a single species *S. laticollis* Fall from Indiana, USA (Fall 1910), has recently been redescribed by Wheeler (1981) who discussed the close relationship of the genus to *Agathidium* Panzer.

The genus *Agathodes* Portevin was described for a single species *A. striatipenne* Portevin from Kashmir, India (Portevin 1926). Portevin later (1944) proposed the new name *Agathidiodes* to replace *Agathodes* Portevin 1926 (not Guénée 1854). He considered *Agathidiodes* to be closely related to *Agathidium*.

Stetholiodes and *Agathidiodes* are each known only from the holotype male of the type species. Direct comparison of these two specimens (examined dry with a dissecting microscope and on temporary slides in lactophenol with a compound microscope) shows that the two species are extremely similar in all characteristics that have been used at the generic and subgeneric level in Anisotomini. I therefore propose the following synonymy:

Stetholiodes Fall
= *Agathidiodes* Portevin, NEW SYNONYMY
= *Agathodes* Portevin (not Guénée)

The two included species, *Stetholiodes laticollis* Fall and *S. striatipennis* (Portevin) (NEW COMBINATION), show slight differences in shape, sculpture, male secondary sexual characters and the shape of

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the median lobe and parameres of the aedeagus. They are thus evidently not conspecific. In *S. striatipennis* the basal three tarsomeres of the protarsus and basal two tarsomeres of the mesotarsus are dilated and bear tenent setae, while in *S. laticollis* the basal three tarsomeres of both legs are similarly modified. It should be noted that Portevin (1926) erred in describing this character for *S. striatipennis* as well as in attributing a 5-5-5 tarsal formula to this species (tarsi are 5-5-4 segmented in *S. striatipennis* and *S. laticollis*).

The genus *Stetholiodes* has been well characterized by Wheeler (1981), whose description is virtually unmodified by the addition of *S. striatipennis*. I would add that both *Stetholiodes* species lack an epistomal suture and have a supraocular carina and groove that separate the side of the head (including the eyes) from the dorsum. This last character is found in most or all *Agathidium* but is absent in *Anisotoma* and allied genera of Anisotomini. I agree with Wheeler that *Stetholiodes* is closely allied to, and possibly congeneric with, *Agathidium*. At present *Stetholiodes* appears to differ from *Agathidium* only in having nine distinct punctate elytral striae, rather than fewer or no striae, and in lacking an epistomal suture. Further study of the large and diverse genus *Agathidium* is needed to clarify the status of *Stetholiodes*.

I thank Mlle. Nicole Berti of the Museum National d'Histoire Naturelle, Paris, for loan of the holotype of *Agathidiodes striatipenne*; and Fernando Angelini, Hermann Daffner, Stewart B. Peck and my wife, Margaret K. Thayer, for commenting on the manuscript. Dr. Angelini has noted a recent collection of two males of *S. striatipennis* from Aru, Kashmir, October 1977, leg. H. Franz, now in his collection and that of Dr. Franz.

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FOSSIL TIGER BEETLES (COLEOPTERA: CICINDELIDAE): REVIEW AND NEW QUATERNARY RECORDS

BY CHRISTOPHER D. NAGANO¹, SCOTT E. MILLER²
AND ALAN V. MORGAN

INTRODUCTION

Fossil Cicindelidae are extremely rare in the stratigraphic record, probably due to the fragile nature of their exoskeleton. In this paper we summarize previous records and comment on new finds, as well as describe cicindelid specimens found in the southern California asphalt deposits which were noted, but not identified, by Pierce (1947a, 1947b).

SOUTHERN CALIFORNIA ASPHALT DEPOSITS

Both the well known McKittrick asphalt deposit in Kern County, California and the Rancho La Brea sequence, Los Angeles County, California, have produced identifiable cicindelid specimens. Pierce's specimens are deposited in the Natural History Museum of Los Angeles County (LACM). A fairly well-preserved specimen of *Cicindela haemorrhagica* LeConte (LACM Invert. Paleo. hypotype 4944) from the McKittrick asphalt deposit, retains complete markings on the elytra, and the elytral pleura still show a blue coloration similar to that of populations found along the sea coast of central San Diego County, California. A mandible (LACM Invert. Paleo. hypotype 4945) also from McKittrick, is probably a cicindelid but family placement is uncertain due to the poor condition of the specimen. Both McKittrick specimens were collected by L. Bessom from W. D. Pierce's "site 4" (LACM Invert. Paleo. Loc. 260), at a depth of 4 feet (1.3m) (Pierce 1947b, Miller and Peck, 1979). This site has not yet been radiocarbon dated, but a *Cybister* elytron taken from a depth of 3 feet (1 m) in the road cut at McKittrick has provided an

¹Natural History Museum of Los Angeles County, Los Angeles, California 90007.

²Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

³Department of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1.

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experimental sample for a ^{14}C mass spectrometer run at Chalk River Nuclear Laboratory, Ontario, Canada. The resultant age of *ca* 8,000 yr B.P. suggests that the samples are probably of Holocene age, (Miller and Peck 1979, Morgan and Morgan 1980a) or of very late Pleistocene age as stated by Pierce (1947b).

Three *Cicindela* specimens are known from Rancho La Brea; two thoraces of *C. haemorrhagica* (RLP 8779E and RLP 9014E) and a metasternum of *C. oregona* LeConte (RLP 9465E). RLP 8779E and 9465E are from Pierce's "Bliss 29" material, which was collected in 1929 by W. Bliss from the sites of pits A, B, and C. The samples are probably late Pleistocene in age, but this is questionable due to unknown locality and possible contamination (Miller and Peck, 1979). RLP 9014E is from Pierce's "Pit X", which refers to mixed material, lacking data, and of questionable age.

The Quaternary presence of *C. haemorrhagica* and *C. oregona* in southern California is not unexpected. Both are presently widely distributed in fresh and marine littoral habitats in western North America. Although these two species are not narrowly restricted to specific microhabitats, they are always found near permanent sources of water.

NEW RECORDS OF FOSSIL CICINDELIDS ELSEWHERE IN NORTH AMERICA

Beside the above mentioned localities, a rekindled interest in the examination of coleopterous faunas has recently revealed fragments of cicindelids in a number of sites in the United States and Canada (Fig. 1). All but one of these records are more recent than the last review of North American fossil insects (Morgan and Morgan 1980b). The oldest specimen which is stratigraphically interpreted as pre last interglacial (pre-Sangamon) is a partial elytral fragment which is probably of the genus *Omus* from the Mountain View Dump site near Palo Alto, California (D. Adam pers. comm. 1978, Morgan unpublished). In the Pacific northwest, a recently examined site (Nelson and Coope, 1982) from Discovery Park, Fort Lawton, Seattle, has produced the remains of *Cicindela oregona* LeConte. A large and varied assemblage accompanies this find which is from sediments previously radiocarbon dated at between 23,000 and 18,000 yr. B.P. The site pre-dates the last major (Vashon) ice advance in the area and suggests a cooler climate with more open

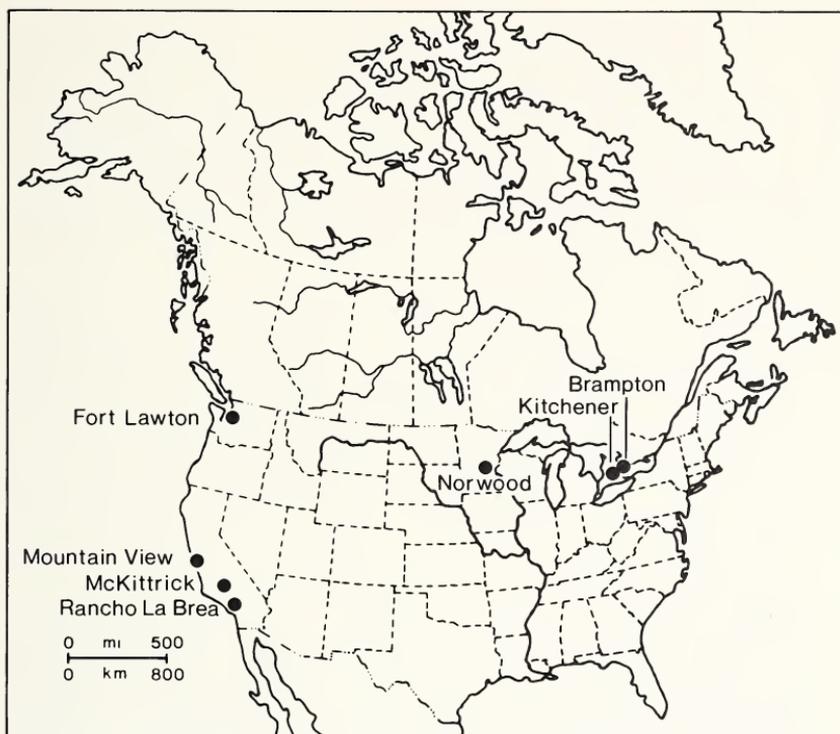


Figure 1. Location of North American sites mentioned in the text.

vegetation, an interpretation similar to that made from another 18,000 year old coleopterous assemblage from Port Moody in southern British Columbia (Miller, Morgan and Hicock, 1982).

In the central eastern section of the continent three sites post-dating the retreat of Laurentide ice have produced cicindelid remains. The Norwood site in Minnesota (Ashworth *et al.*, 1981) is a late-glacial kettle which has a sequence of silts overlain by peat dated at $12,400 \pm 60$ yr. B.P. (QL-1083). A left elytron of *Cicindela* cf. *C. sexguttata* Fabricius was recovered from the upper silt, an horizon characterized by a number of open ground beetle species. In the Canadian province of Ontario two sites at Kitchener and Brampton contain specifically identified cicindelids. The sites are approximately equivalent in age to the Norwood locality (*ca.* 12,400 to 12,000 yr. B.P.) and both slightly post-date the last major (Port Huron) ice readvance in the region. The Gage Street site, Kitchener,

produced a solitary, well-preserved mandible of *Cicindela repanda* Dejean from the basal level of a marl deposit (Schwert, 1978) found in association with open-ground but largely boreal species. The Brampton site near Toronto, is a kettle deposit from which a solitary well-preserved right elytron and mandible fragment of *Cicindela limbalis* Klug was recovered (Morgan and Freitag, 1982). Once again the cicindelid fragments were associated with a fauna resident today in open ground regions within the boreal zone (Morgan, Morgan and Motz, 1982).

The presence of cicindelids in these early deposits of late Wisconsinan sequences is not surprising. In all cases, with the exception of the California examples, the tiger beetle remains are associated with species which inhabit open ground situations. Undoubtedly the ice merely forced many cicindelid populations southward at the time of maximum advance and they remained there to successfully recolonise sandy terrain after ice retreat. Tiger beetle remains also are present due to the nature of the sediments; the very fine silts and clays which are typical of most of these sequences is ideal for the preservation of the extremely thin elytral chitin found in cicindelids. In coarse sediments, or in sequences which are organic-rich, the detritus would abrade, distort and fragment the remains to a degree where most skeletal parts would become unrecognizable.

In Table I, we have attempted to compile known fossil Cicindelidae records including those described in this paper, and we have also commented, where appropriate, on some of the early identifications.

Table I: Known Fossil Cicindelidae¹

Age	Deposit	Locality	Species	Reference
Eocene	Green River	USA: Colorado	<i>Cicindelopsis eophilus</i> Cockerell ²	Cockerell 1920
Oligocene	Baltic Amber		<i>Cf. Collyris</i> sp.	Larsson 1978
Oligocene	Baltic Amber		<i>Odontochila</i> sp.	Horn 1907
Oligocene(?) ³	Baltic Amber		<i>Megacephala carolina</i> Linnaeus	Horn 1906
Quaternary	Binagady brea	USSR: Caucasus Region	<i>C. lunulata</i> Fabricius, <i>C. campestris pontica</i> Fisch., <i>C. germanica</i> Linnaeus	Bogachev 1948
Quaternary	Fyzabad brea	Trinidad	<i>Megacephala</i> cf. <i>M. femoralis</i> Perty ⁴	Blair 1927
Pleistocene(?) ⁵	Port Kennedy	USA: Pennsylvania	<i>C. haemorrhagica</i> LeConte ⁶ ; C.sp.	Horn 1876
Pleistocene	Mountain View Dump	USA: California	<i>Omus</i> sp?	this paper
Late Pleistocene	Rancho La Brea	USA: California	<i>Cicindela oregona</i> LeConte <i>C. haemorrhagica</i> LeConte	this paper
Late Pleistocene	Seattle	USA: Washington	<i>Cicindela oregona</i> LeConte	Coope and Nelson, 1982
Late Pleistocene	Chelford ⁸	U.K: Cheshire	<i>Cicindela campestris</i> Linnaeus	Coope 1959
Late Pleistocene	Minworth ⁹	U.K: Warwickshire ⁷	<i>Cicindela</i> sp.	Coope and Sands 1966
Late Pleistocene	Low Wray Bay, Windermere ¹⁰	U.K: Westmoreland	<i>C. campestris</i> Linnaeus	Coope 1977
Late Pleistocene	Glanlynchau ¹¹	U.K: Caernarvonshire ⁷	<i>C. campestris</i> Linnaeus	Coope and Brophy 1972
Late Pleistocene	Church Stretton ¹²	U.K: Shropshire	<i>C. campestris</i> Linnaeus	Osborne 1972
Late Pleistocene	West Bromwich ¹³	U.K: Staffordshire	<i>Cicindela</i> sp.	Osborne 1980
Late Pleistocene		U.K.	<i>Cicindela sylvatica</i> Linnaeus	Coope 1979

Age	Deposit	Locality	Species	Reference
Late Pleistocene	Norwood	USA: Minnesota	<i>Cicindela</i> cf. <i>sexguttata</i> Fabricius	Ashworth et al., 1981
Late Pleistocene	Gage St., Kitchener	Canada: Ontario	<i>Cicindela repanda</i> Dejean	Schwert 1978
Late Pleistocene	Brampton	Canada: Ontario	<i>Cicindela limbalis</i> Klug	Morgan and Freitag, 1982
Holocene	McKittrick brea	USA: California	<i>C. haemorrhagica</i> LeConte	this paper

NOTES

¹Matthews' (1976 and 1977) record of a cicindelid mandible from the late Tertiary Beaufort Formation on Meighan Island has been reidentified as *Sialis* sp. (Neuroptera: Sialidae) larva (Matthews, pers. comm.).

²As suggested by Cockerell (1920), this may not be a cicindelid.

³Thought by Cockerell (1920) to be a fake.

⁴Originally reported as 'prope *viridis*' Tatum, now a synonym.

⁵The Port Kennedy mammal fauna is considered middle Pleistocene (Kurten & Andersen 1980), but stratigraphic relationships of the insects are unknown.

⁶Willis (1967) suggests this may be a misidentification of *C. ruffiventris* Dejean.

⁷Because of county boundary revisions in many parts of England and Wales former counties (in text) have disappeared i.e. (Caernarvonshire in North Wales is now included in the new county of Gwynedd). Refer to original papers for national grid coordinates.

⁸ca. 70,000–60,000 yrs. B.P.

⁹ca. 32,000 yrs. B.P.

¹⁰ca. 13,000 yrs. B.P.

¹¹ca. 12,500 yrs. B.P.

¹²ca. 12,500–11,500 yrs. B.P.

¹³ca. 12,100 yrs. B.P.

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PREDATION ON THE WESTERN HONEY BEE,
APIS MELLIFERA L., BY THE HORNET,
VESPA TROPICA (L.)

BY MICHAEL BURGETT¹ AND PONGTHEP AKKRATANAKUL²

Hornets of the genus *Vespa* are recognized as efficient and devastating predators of honey bees, especially in tropical and subtropical biomes. Of the four species of honey bees in the genus *Apis* only *A. dorsata* Fabr., the giant honey bee, appears free from attack by hornets (Seeley et al. 1982). De Jong (1978) reviewed the records of *Vespa* predation on *A. mellifera* and *A. cerana* Fabr. Maturra and Sakagami (1973) provided a detailed description on *V. mandarinia* Smith attack behavior on *A. mellifera* in Japan.

We observed the predation and ultimate destruction of a small *A. mellifera* colony by *V. tropica* (L.) on the Kamphaeng Saen campus of Kasetsart University, Nakorn Pathom, Thailand, during a four day period in December 1981. The honey bee colony consisted of four standard frames with a comb area of ca. 7,000 cm² in a hive body with a volume of 21 l. The colony entrance was restricted to an area of ca. 3.5 cm². The colony possessed one comb approximately one-half full of capped honey, two empty combs, one comb with an active brood nest and an estimated 0.5 kg of worker bees which occupied two combs. The brood nest was infested with the parasitic brood mite *Tropilaelaps clareae* Delfinado and Baker.

Uninterrupted observations of hornet behavior at the colony were conducted on December 21 and 23 for a total of 19 h and 50 min. To facilitate the observations eight individual hornets were tagged on their thoraces with color and number coded discs. Observations were begun at 0730 h on the 21st and 0715 on the 23rd and continued until after 1700 h on both days. The ambient temperature was 16°C at the start of observations on both days and reached a maximum of 25°C by mid-afternoon.

We estimate that 25 to 35 hornets were involved in this predatory episode. One of us (P.A.) first noted the presence of a few hornets at

¹Department of Entomology, Oregon State University, Corvallis, Oregon 97331

²Department of Entomology, Kasetsart University, Kamphaeng Saen, Thailand
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the colony some ten to 12 days prior to the 21st. This would correspond to what Matsuura and Sakagami (1973) describe as the hunting phase for *V. mandarinia*. By the 21st the attack had escalated to the slaughter phase where nearly two score of hornets were concentrating upon the now weakened honey bee colony.

The hornet attack was a campaign of slow attrition for the honey bees. Usually two to five hornets would position themselves at the colony entrance. They would engage any honey bee entering or exiting the hive. The large hornets had no difficulty in seizing the bees and would maul them with their strong mandibles. The hornets would normally drop the disabled bees to the ground and only rarely was a moribund bee observed to be eaten by a hornet. The guard hornets would frequently position themselves in the entrance passageway with only their abdomens visible to the observer. These hornets would engage individual guard bees just inside the entrance and after seizing a bee, quickly drag it out and drop it off the landing board to the ground. A separate cadre of hornets would enter the colony and position themselves on the comb containing capped honey. This peripheral comb was without bees which were concentrated on the brood comb. Honey scavenging hornets would spend long periods of time within the colony uncapping honey storage cells and engorging themselves on the contents. On the 21st the average time spent by a hornet inside the colony was 22.9 ± 17.7 min ($n = 64$). Upon emerging from the hive the scavenger hornets were frequently antennated by the guard hornets, and an exchange of alimentary fluid would usually result.

Continuous observation at the colony was not conducted on December 22. However, a one m² piece of plywood was placed directly in front of the hive to facilitate an estimate of adult honey bee mortality. Between 0930 and 1415 h 119 dead honey bees had been deposited on the plywood by guard hornets. At 1420 h the colony absconded and within ten minutes had clustered on a small shrub ca. 15 m north of the hive. For the remainder of the afternoon hornets were observed for the first time exiting the hive with larvae and pupae scavenged from the brood nest. At 1930 h on the 22nd we reintroduced the swarm cluster and queen back into the hive.

Observations on the 23rd began at 0715 h. At 0834 h the colony

once again absconded. Several guard hornets were at the hive entrance during the exodus of the bees. The hornets physically engaged scores of worker bees, mauling and tossing them to the ground. The queen was seen emerging from the hive at 0838 h. She was immediately approached by a hornet which attacked her. She was able to disengage herself from the hornet at the cost of the tarsi from her left front leg. She flew to the branch of a small tree ca. three m from the hive and the worker bees began clustering around her.

With the abandonment of the hive the hornets began to concentrate on the undefended brood nest. From 0845 to 1705 h hornets were observed on 109 occasions to exit the hive with brood as prey. The time individual hornets spent inside the hive was significantly shorter, ave. 13.1 ± 11.3 min ($n = 127$), than on the 21st when bees were present to mount a defense of the colony. The number of foraging events by individual hornets showed a corresponding increase with the departure of the bees. On the 21st, with the bees present, eight marked hornets were observed to conduct 94 complete forays upon the colony for an average of 10.6 ± 6.4 trips per hornet. On the 23rd eight marked hornets completed 171 trips for an average of 21.4 ± 6.0 trips per hornet.

An examination of the hive interior on December 24 revealed that the hornets had completely removed all larvae and pupae from the brood comb. The honey storage comb contained less than an estimated 500 g of honey. Hornet traffic at the hive was considerably reduced from the previous three days. Occasional observations of the hive throughout the day revealed at most, six hornets still engorging on the remaining honey.

Apis mellifera is an introduced species to Southeast Asia (Akwatanakul 1976). The colony we observed came from stock originally imported from California in 1979. Absconding by *A. mellifera* in temperate climates is an unusual phenomenon. However, absconding by other species of tropical *Apis* is a common defensive strategy (Seeley et al. 1982). It is interesting to note that *A. mellifera* from temperate origins still retains absconding as a defense mechanism in the face of severe predation.

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THE GUILD OF SAWGRASS-INHABITING ANTS IN THE FLORIDA KEYS*

BY BLAINE J. COLE
Department of Biology,
University of Utah,
Salt Lake City, UT 84112

A guild is a group of species using similar resources in a similar manner (Root 1967). The guild of ants on which I report here uses, as nest sites, the hollow stems of sawgrass (*Cladium jamaicense*). The primary objectives of this study were to examine this guild for the purposes of: 1. ascertaining the extent to which there is evidence of competition for nest sites. 2. determining the extent to which available nest sites are filled. 3. determining whether *Solenopsis picta* (Emery) nests in association with other species.

Materials and Methods

I examined 119 dead, erect culms of sawgrass, *Cladium jamaicense*, on Sugarloaf Key in Monroe County, Florida. Data were collected between 7/29/81 and 8/3/81. Each stem had seven or more internodal regions. For the ants in sawgrass stems the following data were recorded: the species present, the inside diameter of the internodal segments occupied and the internodal segment in which the colony was housed. For *Pseudomyrmex pallida* (F. Smith) the number and location of queens were also recorded. The inside diameter of a culm was measured with a micrometer to the nearest 0.1 mm. The internodal segments were numbered with the lowest segment numbered one. The numbered segments indicated relative height on the culm. Due to individual variation in the height of *C. jamaicense*, this does not translate directly into absolute height.

Results

Out of 119 sawgrass culms examined, 34 (29%) did not have a colony of any species. The occurrences of various species as well as

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their co-occurrences with other species is given in Table 1. *Pseudomyrmex pallida* is by far the most frequent ant, found in 57 culms or 48% of the total. *Tapinoma littorale* (Wheeler) and *Solenopsis picta* are each found in approximately 10% of the total.

The co-occurrence of series are also given in Table 1. *Solenopsis picta* is found frequently with other species including *P. pallida*, *Zacryptocerus varians* (F. Smith), and *Camponotus planatus* (Roger). No other ant species co-occur with *P. pallida*. *T. littorale* is the only species frequent enough to examine statistically. If *P. pallida* and *T. littorale* assorted into culms independently of one another, the expected number of co-occurrences would be 5.75. *T. littorale* never co-occurs with *P. pallida*, a difference that is statistically significant ($X^2 = 11.0$, $p < 0.001$).

It is possible to calculate the probability that *S. picta* should be the only species that co-occurs with *P. pallida*. This calculation can be done independently of our knowledge that *T. littorale* is negatively associated with *P. pallida* ($p = 0.002$) or contingent on our knowledge of this relationship ($p = 0.02$). In either case, it is shown that if any species occurs with *P. pallida* it is likely to be *S. picta*. It is not possible to statistically demonstrate the stronger statement that *S. picta* is positively associated with *P. pallida*. Indeed, this seems not to be the case due to co-occurrence of *S. picta* and other species.

If one combines the data of *Z. varians*, *C. planatus*, *Leptothorax allardycei* (Mann) and *Pseudomyrmex elongatus* (Mayr), one can also demonstrate that this aggregate is negatively associated with *P. pallida* ($X^2 = 12.0$ $p < 0.001$). Due to the relative rarity of these species, one cannot test each species individually. This result must be considered tentative.

Table 2 gives some characteristics of the nests of the guild of sawgrass inhabiting ants. The average inside diameter and standard deviation of internodes occupied by *P. pallida* is calculated separately for that subset of the colonies that occupy a single internode and for that subset that occupy more than one internode. Nests of *P. pallida* that occupy a single internode have an inside diameter of 2.38 mm. The inside diameter of internodes occupied by *P. pallida* that are found in two internodes are 2.45 and 2.03 for the lower and upper chamber respectively. The diameter of the single nest chamber does not differ from that of the lower nest chamber of a *P. pallida* colony that occupies two chambers ($t_s = 0.53$, $p > 0.5$).

Table 1. Co-occurrence of Sawgrass Ants.

Species found:	no other ant	Co-occurring with:					Total
		P.p.	T.l.	S.p.	Z.v.	C.p.	
<i>Pseudomyrmex pallida</i>	52	—	0	5	0	0	57
<i>Tapinoma littorale</i>	10	0	—	0	1	0	12
<i>Solenopsis picta</i>	2	5	0	—	3	1	11
<i>Zacryptocerus varians</i>	2	0	1	3	—	0	7
<i>Camponotus planatus</i>	3	0	0	1	0	—	4
<i>Leptothorax allardycei</i>	0	0	1	0	1	0	2
<i>Pseudomyrmex elongatus</i>	1	0	0	0	0	0	1
Unidentified spider	1	1	0	0	0	0	2
Nothing	—	—	—	—	—	—	34

Table 2. Nest Characteristics of Sawgrass Ants

Species		Nest Characteristics		
		Inside Diameter mean (sdev, n)	Internode Occupied	# internodes occupied/ culm
<i>Pseudomyrmex pallida</i>	sgl. chamber	2.38 (.41, 39)	3.7	1.4
	lower	2.45 (.41, 13)	3.7	
	dbl. chamber			
	upper	2.03 (.37, 13)	4.7	
<i>Solenopsis picta</i>		3.41 (1.04, 12)	2.2	1.2
<i>Tapinoma littorale</i>		2.45 (.63, 15)	4.3	1.15
<i>Camponotus planatus</i>		4.73 (.82, 7)	2.3	—
<i>Zacryptocerus varians</i>		3.13 (.61, 8)	3.6	—

The average inside diameter is greatest for *C. planatus* (4.73), surprisingly large for *S. picta*, which is such a minute ant, and smallest for *P. pallida* (2.38, single chamber). The average diameter of internodes occupied by *P. pallida* and *T. littorale* does not differ significantly (t -test, $t_s = .70$, $p > 0.5$).

As shown in Table 2 the internode occupied by the nest parallels the results of internode diameter. Since larger internodes are lower

on the culm, species that inhabit internodes with large diameter also inhabit low internodes.

The number of internodes occupied per culm is given in Table 2 for *P. pallida*, *S. picta*, and *T. littorale*. *P. pallida* has a tendency to occupy more internodes per culm (1.4) than does either *S. picta* (1.2) or *T. littorale* (1.15).

In most *P. pallida* nests a queen was located. However, in 19% of the nests a queen was not seen. It is conceivable that the queen could have been overlooked in these nests. In the 46 nests in which a queen was noted, 31 (67%) had a single queen, 8 (17%) had two queens, 6 (13%) and one had four queens. When multiple queens are found in nests occupying multiple chambers, there is no tendency for the queens either to be found in a single chamber or to disperse to separate chambers. When a single queen is found in a nest occupying multiple internodes there is a tendency for the queen to occupy the higher internode.

Discussion

The guild of sawgrass inhabiting ants is a collection of species for which there is evidence that certain pairs of species compete for nest sites and certain pairs of species do not. *P. pallida* and *T. littorale* are strongly negatively associated. This pair of species was not encountered inhabiting the same sawgrass culm. *P. pallida* and *T. littorale* occupy internodes of similar physical characteristics (inside diameter, and relative height on the culm). It is less likely that the two species compete for an internode of particular character than they compete for the space of an entire culm (Levings and Traniello 1981, Cole 1982).

P. pallida shows no evidence of competition for nest sites with *S. picta*. The distributions of *S. picta* and *P. pallida* are independent of one another. These two species are found in the same sawgrass culm with *S. picta* occupying larger and lower internodes. There is little evidence to suggest that *S. picta* is found in association with other species of ants. It seems to be found frequently in association with *P. pallida* simply due to the fact that *P. pallida* is common. *S. picta* has been referred to as a thief ant which nests in close proximity to other ants and specializes in stealing brood from them. In approximately half of the cases in which *S. picta* is found in a sawgrass culm

with another species of ant, there is at least one intervening, empty internode between *S. picta* and the other species.

Of the total sawgrass culms, 71% are occupied by at least one species. Let C be the average probability that a species will colonize a sawgrass culm and E be the average probability that a colony will go extinct. Then the equilibrium fraction of sawgrass culms occupied is $C/C+E = 0.71$. One can then obtain an estimate of the rate of extinction relative to the rate of colonization as $C = 2.5E$.

If colonization takes place on an annual cycle, then one can estimate that the average lifespan of a colony which becomes established is about 2.5 years. This estimate assumes that the occupancy of sawgrass culms is at equilibrium. In addition, data from several species, each of which may not have the same demographic characteristics, are combined. This is not as bad as it seems, however, due to the fact that the bulk of the species' occurrences are of *P. pallida*. The estimate of average colony longevity is principally an estimate based on *P. pallida*.

The inside diameter and position of the lower nest chamber of *P. pallida* colonies that inhabit two internodes is comparable to the inside diameter and position of the internode occupied by *P. pallida* in a single nest chamber. This suggests that *P. pallida* move up to occupy a second internode. The fact that the queen of *P. pallida* tends to be found in the upper chamber suggests that the queen moves into the newer, smaller or higher nest chamber.

The average inside diameter of sawgrass culms occupied by *Z. varians* (3.13 mm) is not significantly different from the average inside diameter of hollow stems of red mangrove occupied by *Z. varians* (2.95 mm, Cole 1979, $n = 114$, $t_s = 0.94$, $p > 0.2$). The major workers of *Z. varians* are morphologically modified for passive colony defense (Wilson 1976, Cole 1980). It is reasonable to suppose that there is selective pressure of *Z. varians* to choose, as nest sites, hollow stems that are of a suitable size to allow the major workers to block off the stem and bulldoze out intruders.

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DEFENSIVE SPRAY MECHANISM OF A SILPHID BEETLE
(*NECRODES SURINAMENSIS*)*

BY THOMAS EISNER AND JERROLD MEINWALD
Section of Neurobiology and Behavior,
and Department of Chemistry,
Cornell University, Ithaca, NY 14853

INTRODUCTION

Although much has been learned about chemical defenses of beetles in recent years (Weatherston and Percy, 1978), few studies have been made of Silphidae, the family that includes the largest carrion beetles. As is known to anyone who has collected these insects, many silphids respond to disturbance by emitting a nauseatingly malodorous ooze from the anus. The fluid is said to be strongly alkaline in some species, and rich in ammonia (Schildknecht and Weis, 1962). In *Silpha*, a gland had been noted that opens into the rectum (Dufour, 1826; Leydig, 1859), but no chemical work had been done to determine whether specific defensive chemicals in the anal effluent might stem from the gland.

Personal observation had told us that one silphid, the so-called red-lined carrion beetle, *Necrodes surinamensis*, might be unusual. First, the beetle seemed able to eject its anal fluid as a spray rather than an ooze, which no other silphid had been reported to do, and second, the fluid gave an acidic test on indicator paper and had a stench that was overlain by a distinct aromatic fragrance.

We have now studied *N. surinamensis* in some detail. Chemical work, carried out in collaboration with others, led to the isolation of several fatty acids and terpenoid compounds, present in the spray and produced by a special rectal gland. An account of these chemical findings, which are summarized in Figure 1, will be published elsewhere. We here give details of the beetle's defensive behavior, plus a brief description of the gland, and data on the beetle's unacceptability to predators.

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PROCEDURES AND RESULTS

Necrodes surinamensis is a large beetle, about 2 cm in average body length. It occurs throughout the United States, east of the Rocky Mountains. It is mostly taken at carcasses. We collected large numbers at baits (dead fish and chickens) in the environs of Ithaca, New York, and on the grounds of the Archbold Biological Station, Lake Placid, Florida. They were maintained in the laboratory on commercial meat-based dog food preparations. Observations were made mostly on freshly captured specimens.

Spray ejection was studied by techniques previously used with other chemically protected arthropods (Eisner, 1958). The beetles were individually fastened with wax to tethers and placed in normal stance upon sheets of indicator paper (filter paper presoaked in red alkaline phenolphthalein solution, blotted off to near dryness just before use). They were then subjected to simulated attack by pinching some of their appendages with forceps or briefly touching parts of the body with a hot spatula. Their responses were immediate. No sooner had a stimulus been applied than they revolved the abdominal tip, which projects free beyond the posterior margin of the elytra, aimed it toward the site stimulated, and sprayed. As evidenced by the pattern of white spots induced by the acid fluid on the indicator paper, the discharges were accurately directed (Fig. 2A, B). The site of emission of the spray was clearly noted to be the anus. The abdominal tip is essentially a revolvable emplacement for the anal nozzle. It can be pointed in all directions, even anteriorly over the beetle's own back (Fig. 2C-F). Regions of the body stimulated were always noticeably wetted by the spray. Beetles that had remained undisturbed in confinement for several days, and were tethered without being caused to discharge (they were kept refrigerated during the tethering procedure), proved capable of spraying repeatedly, even in quick succession if a rapid sequence of stimuli was applied. The number of discharges ($\bar{x} \pm sd$) that could be elicited from such beetles was 4.9 ± 1.1 ($N = 5$ females + 3 males). Only direct contact elicited discharges. The beetles never sprayed in response to movement or tapping nearby.

The rectal gland, which is identical in both sexes, was readily exposed by dissection. It consists of a tubule and a sac (Fig. 3). The tubule lies free in the hemocoel, is long and narrow (actual measurement in a female = 18×0.2 mm) and closed at its distal end. It opens proximally into the bladder-like sac, which itself opens by

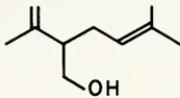
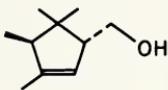
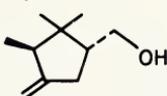
<u>Aliphatic Acids</u>		<u>μg per Beetle</u>
Caprylic acid	$\text{CH}_3(\text{CH}_2)_6 \text{CO}_2\text{H}$	25
Capric acid	$\text{CH}_3(\text{CH}_2)_8 \text{CO}_2\text{H}$	5
<i>cis</i> -3-Decenoic acid	$\text{CH}_3(\text{CH}_2)_5 \text{CH}=\text{CHCH}_2\text{CO}_2\text{H}$	5
<i>cis</i> -4-Decenoic acid	$\text{CH}_3(\text{CH}_2)_4 \text{CH}=\text{CH}(\text{CH}_2)_2 \text{CO}_2\text{H}$	5
<u>Terpene Alcohols</u>		
Lavandulol		4
α -Necrodol		14
β -Necrodol		3

Fig. 1. Substances isolated and characterized from the rectal gland of *Necrodes surinamensis*. The two terpene alcohols, α -necrodol and β -necrodol, are new natural products; *cis*-3-decenoic acid and *cis*-4-decenoic acid have not previously been reported from an insectan source. Details of the chemical procedures will be published elsewhere.

way of a narrow neck into the rectum. The tubule is surrounded by a loose meshwork of muscle fibers, clearly identifiable as such in whole mounts of the gland viewed by transmitted polarized light. Comparable compressor muscles, arranged in a thick layer, envelop the sac. The entire gland has an inner lining of membranous cuticle, which was readily isolated by treatment of the gland with 10% aqueous potassium hydroxide, and was shown to be continuous with the cuticular lining of the hindgut. In freshly dissected preparations, both parts of the gland were seen to be filled with clear fluid. The hindgut, in contrast, was usually replete with opaque fecal paste.

The compounds listed in Figure 1 had been shown to be present both in extracts of isolated glands and in samples of the spray itself. None were present in more than trace amounts in extracts of the region of the hindgut anterior to the glandular junction. It seemed reasonably certain, therefore, that the fatty acids and terpenes are products of the gland rather than the enteron. This conclusion was further supported by circumstantial evidence. Fluid squeezings from isolated glands, unlike squeezings from the hindgut, gave acidic spot

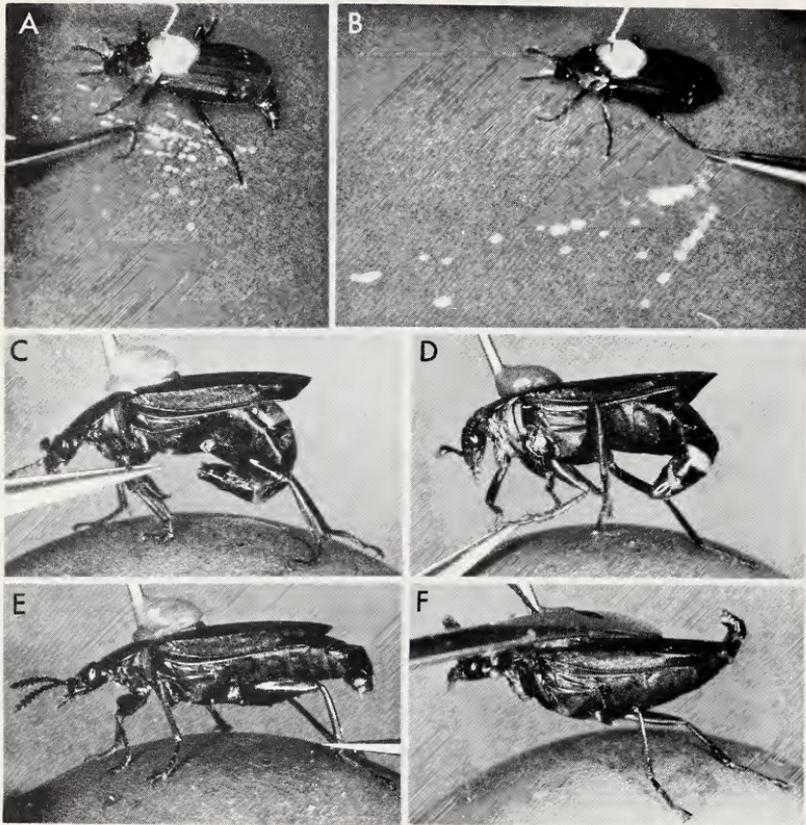


Fig. 2. A-B, Aimed discharges elicited by pinching a left midleg (A) and left hindleg (B) of *Necrodes* with forceps. The spray pattern is visible on phenolphthalein indicator paper. C-F, Directional aiming movements of the anal turret of *Necrodes*. Note that the abdominal tip is accurately pointed toward the site of application of the stimulus: (C) tibia of midleg, (D) tarsus of midleg, (E) tibia of hindleg, pinched with forceps; (F) back of beetle touched with hot spatula.

tests on phenolphthalein indicator paper and had the recognizable terpenoid fragrance of the spray.

Examination of fresh spray ejected by *Necrodes* on glass showed occasional presence of opaque material in the discharged fluid, suggesting that the secretion may sometimes be expelled with admixture of fecal paste. Since the glandular contents are forced to the outside by way of the rectum, such admixture may occur whenever the pathway of secretory egress is blocked by enteric matter. Two fatty acids not listed in Table 1, stearic acid and palmitic acid, were

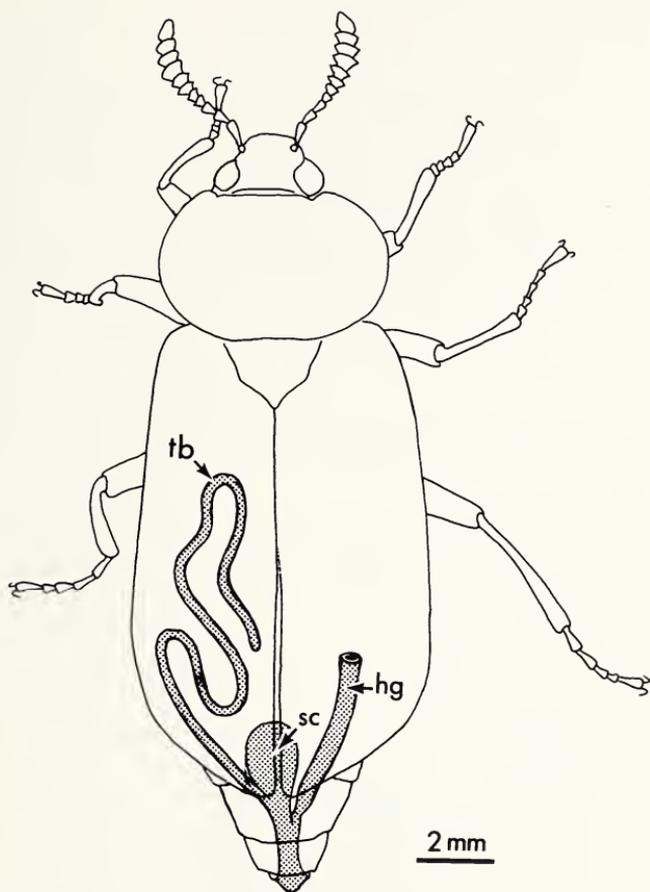


Fig. 3. Diagram of *Necrodes surinamensis* showing the position of the rectal gland (tb = tubule; sc = sac) relative to the hindgut (hg).

identified as occasionally present in the spray. Neither was detected with consistency or in substantial amounts in extracts of the gland, but they were always present in extracts of the hindgut. Their occurrence in the spray may be a further indication that rectal contents are sometimes ejected with the secretion.

Laboratory tests done with formicine ants (*Formica exsectoides*) and Swainson's thrushes (*Catharus ustulatus*) demonstrated that *Necrodes* is well protected against such predators. The tests with *Formica* involved presenting individual tethered *Necrodes* to groups of 10 ants in small glass enclosures. The ants attacked immediately, by clamping onto the beetles with their mandibles, in response to which the beetles revolved their abdominal tip and sprayed. As was particularly clear from the patterns of droplets sometimes visible on the bottom of the enclosures, the discharges were accurately aimed toward the ants. These usually released their hold quickly and fled. At varying intervals thereafter they engaged in intensive cleansing activities, which seemed all the more protracted when the ants had been heavily contaminated with spray. Five beetles were exposed to ants in this fashion for 30 min. each. None received noticeable injury.

The tests with the thrushes followed a protocol previously used with these birds in experiments with other chemically protected insects (Eisner *et al.*, 1978). *Necrodes* were offered together with mealworms (larvae of *Tenebrio molitor*, which served as edible controls) to 3 individually caged birds (all males), in 3 daily feeding sessions per bird. Mealworms outnumbered *Necrodes* 2 to 1. The insects were offered one at a time, up to a total of 14–15 per session. Sequence of presentation was such that each series of 3 consecutive items consisted of two mealworms and one randomly placed *Necrodes*. Each item was left with a bird until it was eaten, or for a maximum of 2 min. Fate of prey was scored as follows: eaten (*E*, if the insect was ingested after having been pecked no more than 3 times); eaten with hesitation (*EH*, if the insect was eaten after having been pecked more than 3 times); rejected (*R*, if the insect was ignored after having been pecked one or more times); not touched (*NT*, if the insect was not contacted by the bird during the 2 min. of presentation). Insects not touched at the end of a feeding session were not tallied, since such avoidance might have been due to satiation of the bird.

The results, lumped for the 9 feeding sessions with the 3 thrushes, are shown in Figure 4. It is clear that the birds rated *Necrodes* distinctly undesirable relative to mealworms. While the latter were all eaten outright, 74% of *Necrodes* were either rejected or left untouched. The 26% that were eaten were only taken after repeated peckings. A special point was made to check the rejected *Necrodes* for injury. None was found to bear any, and all were live when examined several days later. Although it proved impossible to determine with certainty whether *Necrodes* always sprayed when pecked or grasped by a bird, in some cases there was evidence that discharges had occurred. Streaks of spray occasionally made their appearance on the glossy floor of the cage during an attack, or birds shook their heads violently after seizing a beetle, as we have repeatedly seen captive thrushes do when attempting to take insects that spray (e.g. carabid beetles).

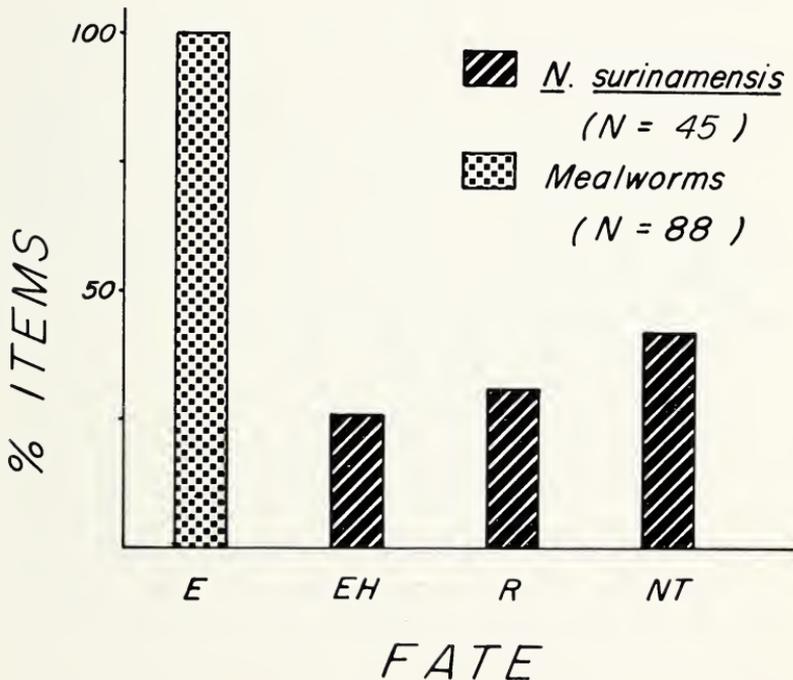


Fig. 4. Fate of *Necrodes surinamensis* and mealworms fed to three Swainson's thrushes; E = eaten; EH = eaten with hesitation; R = rejected; NT = not touched. Details in text.

DISCUSSION

The discovery of a chemical defense mechanism in an insect should come as no surprise, since such mechanisms are extraordinarily widespread among arthropods. Moreover, many insects, including a multiplicity of beetles, termites, ants, earwigs, caterpillars, and phasmids, eject their defensive secretions in the form of accurately directed jets. *Necrodes* is anomalous in that it expels its aimed secretory discharges from the anus. Other beetles that spray, such as Carabidae, also discharge from the tip of the abdomen and may aim their ejections by movement of the abdominal tip (e.g. Eisner, 1958), but their glands are integumental and open beside the anus on the body wall itself. *Necrodes* is further unusual in that it has only one gland. Exocrine defensive glands in beetles commonly occur in pairs.

It seems reasonable to presume that the gland of *Necrodes* arises developmentally as an outpocketing of the rectum. Other rectal glands in Silphidae, such as that of *Silpha*, are doubtless homologous to that of *Necrodes*. We feel this to be so despite some differences in gland morphology [In *Silpha americana* the lateral tubule is reduced to a short elaborately subdivided diverticulum (Alsop, 1970)]* and in gland chemistry (*Silpha americana*, as we shall report elsewhere, produces steroids in its gland). While in the absence of histological work little can be said about the function of the two parts of the *Necrodes* gland, the strongly muscled condition of the sac suggests that it might serve as the reservoir from which secretion is expelled for the discharge. The tubule might be strictly secretory.

It seems clear from the tests with ants and birds that *Necrodes* is relatively unacceptable to such predators. But to what extent this is attributable to the glandular components of the spray, or to enteric additives of the spray, or even to entirely different factors (carrion contamination of the beetle's body?) remains to be seen. The secretion, no doubt, plays a defensive role, but the other factors may amplify the effect. It is interesting in this connection that another common inhabitant of carrion, the staphylinid beetle *Creophilus*

*Dufour (1826) writing of *Silpha littoralis*, speaks of a rectal gland with a "vaisseau sécréteur" almost as long as the body, suggesting that he was dealing with a gland similar to that of *Necrodes*.

maxillosus, also mixes intestinal fluid with the secretion of its defensive glands (Jefson *et al.*, 1983). A diet of carrion, one might imagine, could render an insect's enteric contents potently deterrent. The ammonia reportedly present at high concentrations in the anal effluent of some silphids (Schildknecht and Weis, 1962) is probably derived from decaying ingested animal protein and may well serve for defense. To us at least, the odor of the intestinal fluid discharged by many carrion insects upon handling, or for that matter the odor of the insects themselves, is repugnant. The fragrance emitted by *Necrodes* after a discharge is transient, and certainly does not mask the intrinsic stench of the animal.

While it would have been desirable to test the various secretory components of *Necrodes* for repellency, this proved impossible due to lack of sufficient synthetic quantity of α -necrodol and β -necrodol, the two most interesting novel compounds in the mixture. It seems likely, however, that these terpenes are deterrent to insects. They are cyclopentanoid compounds, of which many are known to occur in the defensive glands of insects and in plants (Nakanishi *et al.*, 1974), and some are provenly repellent to insects (Eisner, 1964; Smolanoff *et al.*, 1975; Meinwald *et al.*, 1977; Jefson *et al.*, 1983). Fatty acids have also been reported from other arthropodan defensive glands. They may themselves be deterrent, and may also serve as surfactants. As part of a spray they may promote spread and penetration of droplets on target, a role that has been demonstrated for caprylic acid in whip scorpion secretion (Eisner *et al.*, 1961). The fatty acids of *Necrodes* may have a similar function, and may also facilitate the mixing of the apolar glandular material with the largely aqueous enteric fluid when the two are discharged together. Two of the *Necrodes* fatty acids, *cis*-3-decenoic acid and *cis*-4-decenoic acid, have not previously been identified from an insectan source. The apparent enteric, rather than glandular, origin of stearic and palmitic acid should come as no surprise, since these fatty acids are major components of animal fats and hence likely to be ingested by *Necrodes* with carrion.

Only speculation can be offered to account for the presence of lavandulol in the *Necrodes* spray. The substance has not previously been reported from insects, although it is known from plants as a major component of lavender oil (Karrer, 1958). We suspect the compound to be repellent to insects, as some low molecular terpenes

are known to be, which if true would provide some explanation for the presence of the substance in plants. An increasing number of compounds known previously only from plants is being isolated from the defensive glands of insects. In our judgment the very occurrence of such compounds as defensive agents in animals suggests that they may (sometimes at least) fulfill a similar function in plants.

Carrion insects, often crowded in their food source, undoubtedly interact in subtle competitive ways. To what extent *Necrodes*, or for that matter any other chemically protected carrion insect, makes use of its defensive glands in such interactions, remains an intriguing unknown.

SUMMARY

When disturbed, the carrion beetle *Necrodes surinamensis* (family Silphidae) ejects jets of fluid from the anus. The abdominal tip, which projects beyond the posterior margins of the elytra, serves as the revolvable turret by which the ejections are aimed. Only contact stimulation elicits discharges. The fluid is primarily of glandular origin but may contain admixed enteric matter. The gland, which consists of a tubular portion and a vesicular sac, opens into the rectum itself. Chemical work (to be reported elsewhere) has shown the secretion to contain two novel cyclopentanoid compounds (α -necrodol and β -necrodol) as well as lavandulol and several fatty acids. Two of the fatty acids, *cis*-3-decenoic acid and *cis*-4-decenoic acid, were not previously known from insects.

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