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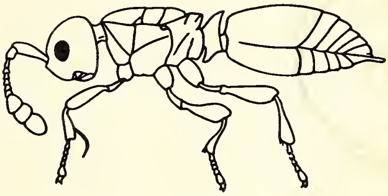

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PSYCHE

Vol. 85 March, 1978 No. 1

WEBS OF *MIAGRAMMOPES* (ARANEAE: ULOBORIDAE) IN THE NEOTROPICS

By Y. D. Lubin[1], W. G. Eberhard[2], and G. G. Montgomery[1]

Introduction

Uloborid spiders (*Uloborus* sens. lat.) typically construct orb webs composed of non-sticky threads (radii, frame threads, hub, and temporary spiral) which support a sticky spiral made of cribellar or hackled silk. Specialization of the web in the uloborid genus *Miagrammopes* has involved the reduction of its structural complexity together with changes in its operation as an insect trap. The one described web of an unidentified species from Natal, South Africa is reduced to a single horizontal capture thread (Akerman 1932). In this paper we describe the webs of six more species of *Miagrammopes* and the prey capture behavior of the spiders, revealing a substantial range of variation in simple web design within the genus.

We studied *M. simus* on Barro Colorado Island, Panama Canal Zone during the wet season of 1976. At no time was this species common. In May and June, 1977, *M,* sp. 1 (ca. *unipus*) was studied in a bamboo (*Guadua angustifolia*) thicket in the Cauca valley near Cali, Colombia where it occurred in abundance. In August, 1977, *M. intempus* Chickering and *M.* sp. 2 were found in Valle, Colombia. The former was common in some places on hanging moss on exposed roots and low branches near the Rio Anchicayá at 400 m elevation, while the latter was found in brush near the Rio Tuluá at 1100 m elevation. A small tree in a clearing on Finca La Selva

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near Puerto Viejo, Heredia Province, Costa Rica, had substantial populations of *M.* sp 3. *M.* sp. 4 was found on low vegetation in January and February, 1978, in mid-elevation wet forest in Guatopo National Park, Miranda State, Venezuela. Individuals of the last four species were observed in the field on only one or two days each, but in all cases more extensive observations had already been made on the other species, and it was thus possible to make critical observations allowing comparisons among all six species. *Miagrammopes* sp. 1–4 appear to be either undescribed species or females of species known only from males. Voucher specimens of these and of the two previously described species are deposited in the Museum of Comparative Zoology, Harvard University.

THE WEBS

M. simus

The web typically consisted of a single vertical capture thread about 1 m long, attached above to a short, horizontal resting thread strung under a leaf, and below to the ground or a leaf or twig (Fig. 1a). The capture thread was covered with sticky, cribellar silk along the central 50 to 60 percent of its length, and one or more very fine, more or less horizontal threads often connected it to other supports. Both end portions of the capture thread were non-sticky. For an individual whose webs were measured periodically, the lengths of sticky and non-sticky sections in new webs were (in cm; lengths of sticky portions underlined): 20:50:30, 4:50:30, 6:52:34, 7:60:32, and 7:60:34. One adult female which had been starved for seven days made a web with two vertical capture threads and several thin, non sticky lines between them.

One *M. simus* was seen laying sticky, cribellar silk on a non-sticky, vertical thread which was already in place. The spider moved slowly up the thread, combing out silk with legs IV until it was about 5 cm below the resting thread, then ran up and assumed the resting posture.

Individuals of *M. simus* rested under the horizontal thread and held onto the broken end of the capture thread with one leg I and one leg II, while the other legs held the resting thread (Fig. 1b). Tension was exerted on the vertical capture thread both by pulling it up with leg I and by backing up and pulling in the resting thread with the fourth pair of legs. The spider which constructed a web with two

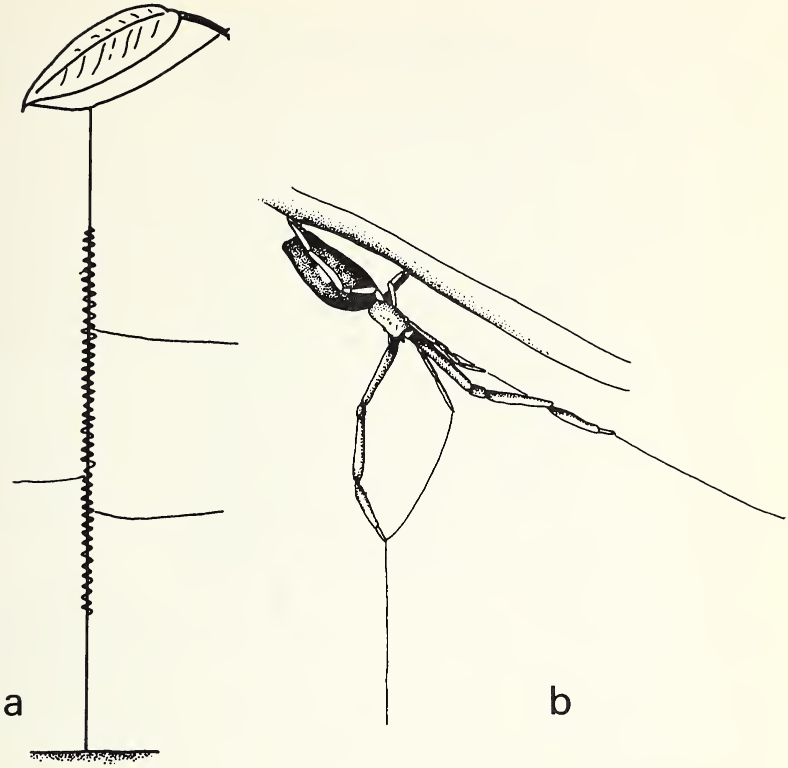

Figure 1. a) Typical web of *Miagrammopes simus,* showing the horizontal resting thread under a leaf, the vertical capture thread with sticky segment and thin, non-sticky, horizontal threads; b) posture of *M. simus* as it holds its web and waits for prey.

capture threads rested in essentially the same position; the leg I holding the horizontal resting thread was in position to monitor vibrations from the second capture thread.

When disturbed, or when hanging from a resting thread with no capture thread present, *M. simus* assumed a stick-like, cryptic posture, orienting along the resting thread with the first and second pair of legs held straight forward and the fourth pair held straight behind. The small third pair of legs held the resting thread or the substrate, but were pressed close to the body and did not break the stick-like outline.

M. sp. 1 (ca. *unipus*)

The web of this species differed in that there was usually more than one capture thread attached to a single horizontal resting thread (Fig. 2). The average was 2.4 capture threads and some webs had up to five (Table 1). There was no apparent relationship between the number of capture threads in the web and the size of the spider that constructed it. The capture threads were usually not perfectly vertical and were often in different planes with angles of less than 90° between them. They were shorter and thinner than the capture threads of *M. simus* and it was necessary to powder them with cornstarch in order to count them. The horizontal resting thread was always under a thin twig rather than a leaf, as in webs of *M. simus.*

In some webs of *M.* sp. 1 there were one or more very slack, nonsticky, horizontal threads connecting the multiple capture threads. Because of their looseness and their variable location and orientation, these lines were at first thought to be incidental (perhaps floating threads made by other spiders), but their presence in many webs of both this species and *M. simus* argues otherwise.

Web construction appeared to be similar to that of *M. simus.* One spider was seen laying cribellar silk while moving up along a vertical thread which was already in place. The spider advanced slowly, combing out silk continuously with legs IV and attaching it to the thread periodically with brisk dabs of the abdomen. Total construction time for one capture thread was about 3 minutes.

At night, *M.* sp. 1 assumed a capture position similar to that of *M. simus,* resting under the horizontal thread and holding a capture thread with legs I and II (Fig. 1b). During the day it either held the capture thread in the same way, or, more often, assumed a more cryptic resting posture. The spider positioned itself near one end of the resting thread which it broke and spanned with its body. It held one end with one or both pairs of front legs, and then pulled in the line behind it with the hind legs (and, occasionally, the

Table 1. Numbers of sticky capture threads in 66 webs of *Miagrammopes* sp. 1 (ca. *unipus*) and 22 webs of *M.* sp. 3.

	Number of Capture Threads					
Number of Webs	1	2	3	4	5	6 or more
M. sp. 1	15	21	22	6	2	0
M. sp. 3	4	5	3	3	6	1

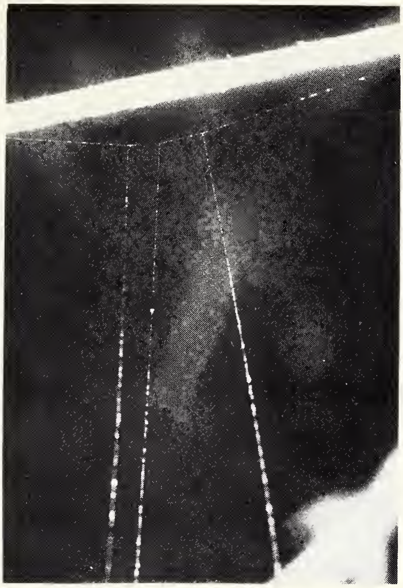

Figure 2. Typical web of *Miagrammopes* sp. 1 (ca. *unipus*) showing horizontal resting thread under twig and three capture threads.

line in front of it with legs I). The result was to draw the spider close to the twig. When adopting the cryptic posture, the spider reached out briefly with legs II and III to pull itself closer to the twig, then positioned legs II against legs I, holding the broken end of the resting thread, and legs III against the sides of the abdomen. In this position it was nearly invisible (see Fig. 3).

M. sp. 2

The web of one adult female was found in the morning (the spider was without a web at 2100 the night before), and was similar to some of the webs of *M.* sp. 1. The spider rested pressed to the undersurface of a branch, at the end of a horizontal thread about 3 cm long that was strung under the branch (Fig. 3). She held the broken end of the horizontal thread with one leg II and kept it tense by pulling in the thread with her hind legs, as described for *M. simus* and *M.* sp. 1. A single, vertical, capture thread (invisible until powdered) was attached near the other end of the horizontal thread. The lengths of the non-sticky and sticky portions of the capture thread were 7:$\underline{53}$:40.

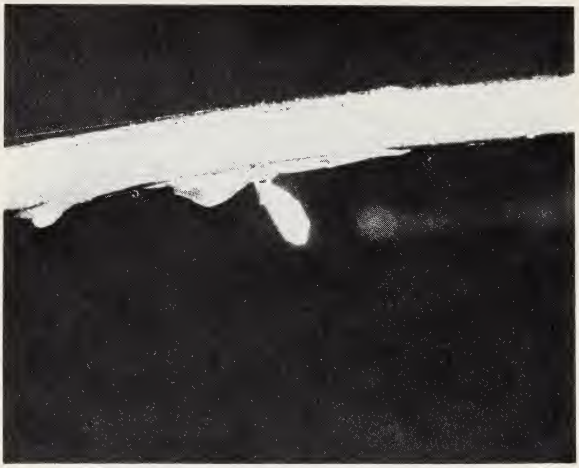

Figure 3. *Miagrammopes* sp. 2 in cryptic posture as it feeds and holds the non-sticky resting thread.

M. intempus

Webs of this species were variable and most were different from those of other *Miagrammopes* species. One mature female held both a horizontal and a vertical sticky thread with her front legs, and a single, short, non-sticky line with her rear legs (Fig. 4). A second female also held two capture threads, but both were at an angle rather than being either horizontal or vertical. The first spider was induced to move forward along the horizontal thread several times and her return to the waiting position was observed carefully (Fig. 4). Each time she tensed the sticky threads by pulling them in with her front legs; she did not move her hind legs. Another individual, on a web which was similar except that the horizontal thread did not appear to be sticky, held the sticky vertical thread in the same way that *M. simus* held the capture thread and tensed it by pulling thread with both front and hind legs. Still other individuals with single, horizontal, sticky threads (Fig. 5) failed to pull in silk as they assumed the waiting position. One vertical thread had several very fine, loose, horizontal lines attached to it, similar to those shown in Fig. 1a for *M. simus*.

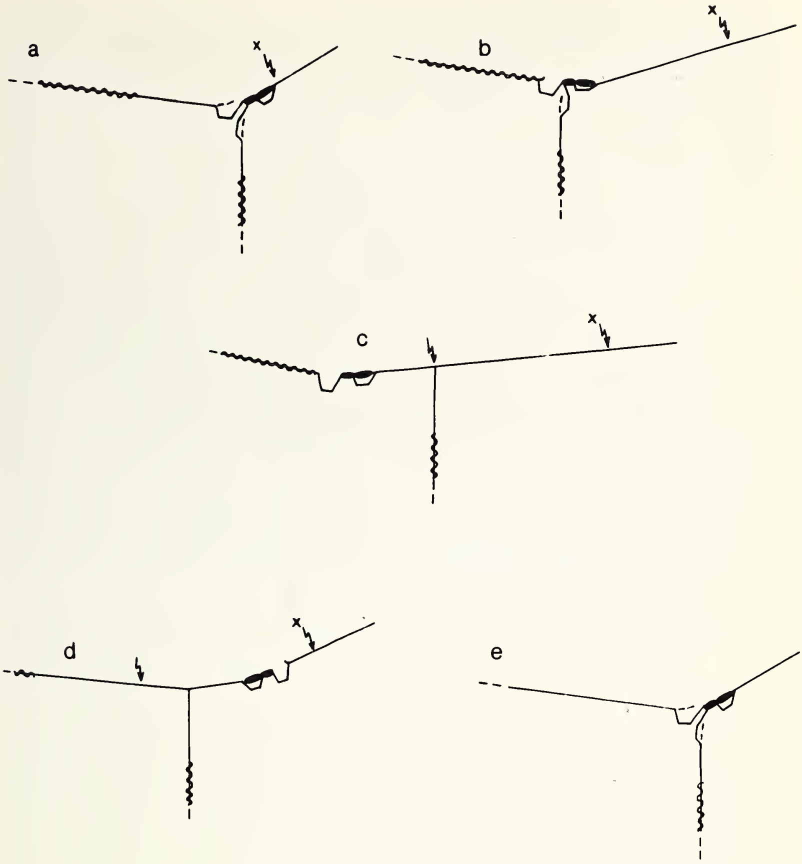

Figure 4. Movements of a female *M. intempus,* illustrating how thread attachments are manipulated. Letters mark spots on horizontal thread. The spider rested (a) holding both sticky lines with its front legs, and a third, short, non-sticky line with its hind legs at point *x* (the ends of the capture threads were not drawn as they could not be seen). When lured out onto the horizontal sticky line, the spider carried the vertical thread for some distance (b), then attached it to the horizontal line and continued on (c). When she returned, she shifted the point of attachment of the vertical thread again (d), then turned around and pulled in the line with her front legs and resumed her original position (e). The shifts in attachment were extremely rapid; the actual motions involved could not be followed, and the shifts were noticed only by comparing thread positions before and after the spider passed by.

M. sp. 3

The webs of this species were similar to those of *M.* sp. 1 in having variable numbers of capture threads (Table 1). The sticky lines were not all attached to a non-sticky line at one end, however, but rather radiated in several directions from a more or less centrally placed thread (Fig. 6). The spider rested on this thread, often breaking one of the capture threads and holding it as described for *M. simus* (Figs. 1b and 6). This position was also similar to that of *M. intempus* in that the spider held a non-sticky line behind it and a sticky line in front of it. In other cases the spider rested holding only the non-sticky thread with both front legs. The sticky threads differed from those of other species of *Miagrammopes* in being relatively short (all less than 25 cm) and sticky all the way to the lower end. The webs were found at night and were gone the next morning.

M. sp. 4

Webs of *M.* sp. 4 had one or two capture threads (invisible until powdered or sprayed with water), 20 to 40 cm long each. The captured threads were vertical or nearly vertical, but not necessarily parallel or in the same plane. Of 9 spiders found during the day, three had two capture threads each, three had a single capture thread, and three had no capture thread. As in *M. simus,* the resting thread was generally under a leaf and often placed at an angle. Spiders with capture threads rested with one leg I holding a vertical thread (see Fig. 1b) and adjusted the tension both by pulling in the resting thread with legs IV and the capture thread with leg I.

Spiders without capture threads rested in a cryptic position similar to that of *M. simus.* Often after going into the cryptic posture (and particularly when disturbed), the spider bounced up and down on the resting thread in a rhythmic motion reminiscent of rocking motions of stick insects (Phasmidae). The significance of these movements is not known.

PREY CAPTURE

We observed in detail prey captures made by four *M. simus,* two *M.* sp. 1, and one *M. intempus.* Insects that we gave to the spiders as prey included fruitflies (2–3 mm long), moths (3–7 mm long), and ants (3–5 mm long). In general, the sequences of prey capture behavior were similar, but the spiders moved so rapidly that stop-

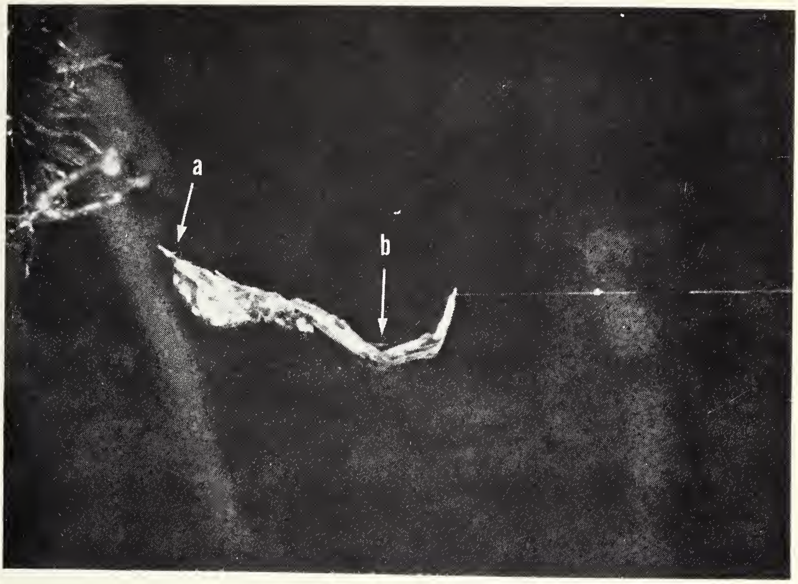

Figure 5. *Miagrammopes intempus* female holding a single thread web. Note the loose line just anterior to the tip of leg IV(a), and leg II holding the end of the capture thread (b).

action analysis of video-recording was needed to permit adequate analysis. Only *M. simus* was video-taped, using a SONY AV-3400 videorecorder and a macro lens. The descriptions below are based mainly on analyses of these video-recordings.

Stage I: Prey detection — jerking the capture thread

When an insect was placed on the capture thread, the spider responded by jerking the thread, The spider quickly flexed her lower leg I, which held the capture thread, and immediately extended it again. The maximum distance travelled by the tip of the leg on an upward jerk was 0.3 leg length (about 2.8 mm), and the quickest jerks were accomplished in less than 1/60 second (the time span of a single "frame" of the video-recording). It is tempting to think that jerking functions in gauging the weight or size of the prey, as seems to be the case in other uloborids (Eberhard 1969). Spiders with multiple capture threads (both *M.* sp. 1 and *M. simus*) jerked only the thread on which prey had been placed.

Figure 6. *Miagrammopes* sp. 3 on its web, as seen from below and slightly to the side. The brighter threads are sticky (the web was not powdered). Note that the spider has broken the end of the capture thread and holds it with the front legs bent to the side in a manner similar to that shown for *M. simus* (Fig. 1 b).

Stage II: Entanglement of the prey — sagging the line

The spider sagged the capture thread by dropping the loose silk it had pulled in with its hind legs, and perhaps also letting out additional dragline. At almost the same time it manipulated the capture thread with a series of complex movements of leg I (Fig. 7a) which resulted in the prey being jerked rapidly back up and down again (Fig. 7b). Whereas the jerks in stage I displaced a fruitfly only 5–6 mm, sagging the capture thread caused the prey to drop 26–33 mm in less than 1/30 second. As the prey dropped, it was often displaced sideways as much as 6 mm (due to air currents?). Rapid and repeated sagging of the capture thread resulted in the formation of one or more loops of silk that enveloped the prey. Such loops were seen in the capture threads of both *M. simus* and *M.* sp. 1.

The mechanism responsible for the formation of these loops is not clear. One possible explanation is that, due to the relatively higher air resistance and lower weight of the silk, the prey drops more rapidly than the silk during a sag, and therefore falls into the silk below it (Fig. 8a). An alternative explanation (Fig. 8b) is that, at the end of a sag, when the spider jerks the line up again, the prey is "snapped" back upward and accelerated more than the silk just above it so that it "runs into" the thread above it. The second of these hypotheses is more appealing since 1) it would work with non-vertical capture threads whereas the first would not, and 2) we saw two instances in which a loop clearly formed in the thread just above the prey. In any event, the spider is somehow able to entangle the prey from a distance by manipulating the capture thread.

Stage III: Immobilization of prey-wrapping

After manipulating the capture thread to cause one or more sags,

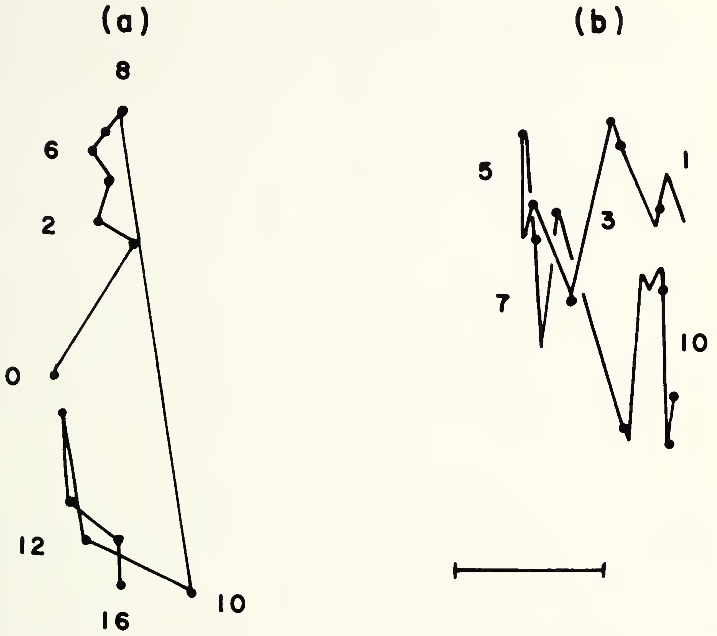

Figure 7. a) Movements of the tip of leg I of a female *Miagrammopes simus* as she sagged the capture thread. Points are locations of the tip of leg I holding the capture thread, taken from a video-taped sequence with "frames" 1/60 sec apart. In frames 3–5 the tip of the leg remained in the same spot. In frames 9 and 11 the tip of the leg was not visible; these points are not shown in the figure. b) Movements of a prey on the capture thread while the thread is being sagged and jerked back up and down, taken from a video-taped sequence (as above). Numbers refer to segments of the path of movement of the prey on the line during consecutive 1/60 sec intervals. Scale marker represents 10 mm.

the spider attached a dragline to the resting thread and moved rapidly down the capture thread, pulling in the capture thread and wadding it up loosely with legs II as it moved. It touched the prey one or more times with legs I, probably receiving tactile and chemical clues as to the identity of the prey, and then turned 180° and began wrapping. The wadded up capture thread was transferred to legs III and wrapped onto the prey, probably thereby increasing the effectiveness of the initial wraps.

While wrapping, the spider faced away from the prey, holding the capture thread just above the prey with one leg I and the prey itself with legs II and III. After 20–30 seconds of wrapping, the spider cut the capture thread just above and below the prey. It then rotated the prey package rapidly with legs II (and the palps?) while continuing to wrap by pulling silk out from the spinnerets and throwing it onto the prey with legs IV (rotation-wrapping in the nomenclature of Robinson and Olazarri 1971). While wrapping the prey, the spider spanned the gap between the two ends of the capture thread, holding each end with one leg I as do other uloborids (Marples 1962).

Stage IV: Transport of prey to the feeding site

The wrapped prey was transferred to the palps, and the spider attached a dragline to the thread she had laid on her way down and then to the broken end of the capture thread. After thus repairing the web, she ran up to the resting thread, holding the prey in the palps. Once on the resting thread, the spider transferred the prey to the third pair of legs and again wrapped it. She wrapped as described above, rotating the prey package with legs II while hanging from the resting thread with legs I. After wrapping as long as 5 minutes, the spider transferred the prey back to the palps, turned facing away from the capture thread, and pulled the resting thread with legs I as though testing the tension. She then turned 180° and resumed a resting posture with one leg I monitoring the capture thread. As in other uloborids, the prey package was held "overhead" in the palps and chelicerae while the spider fed (Fig 3) and re-wrapped several times during the process of feeding. Feeding often lasted an hour or more.

Variations in the prey capture sequence

We saw several modifications of the basic prey capture sequence in *M. simus*. Small dolichoderine ants were rejected by a spider

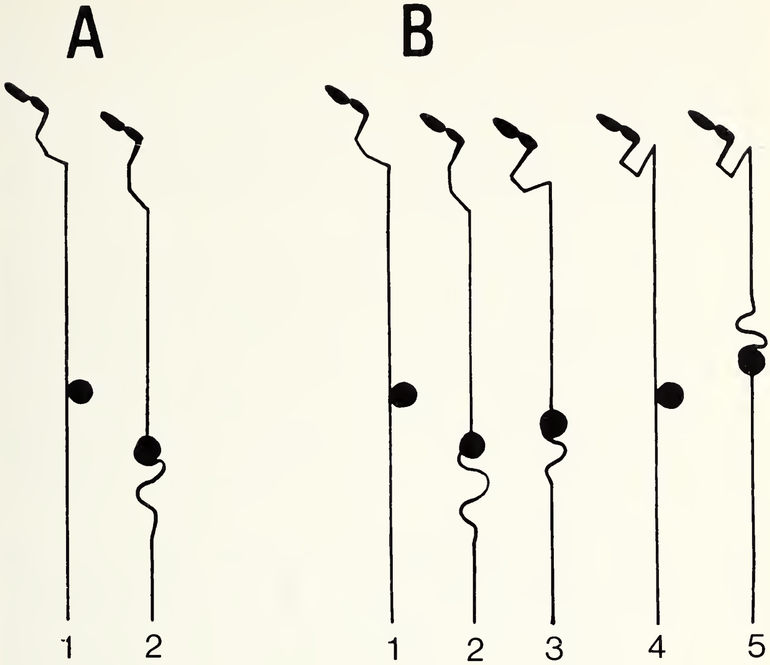

Figure 8. Two possible mechanisms which could result in prey becoming entangled as a result of sagging behavior. A) The prey drops faster than the line below it, and thus becomes entangled. B) The prey's momentum, acquired when the spider jerks the line up after a sag, causes it to become entangled in the line just above it. This hypothesis depends on the thread below the prey being extensible.

on four occasions. Each time the spider jerked and sagged the capture thread several times, ran a short distance down the capture thread, wadding it up as it went, and then cut the line above the ant and ran back up to the resting thread. These ants were thus recognized from a distance, perhaps by their strong alarm odor. After an ant was rejected, the wadded-up section of the capture thread was manipulated in the mouthparts for several minutes (feeding?), then dropped. Rejection of prey thus resulted in destruction of the capture thread. A new thread was often built within a few hours.

Three other ants, two *Camponotus* sp. and one *Ectatoma* sp., all about the same size as the spider (6–7 mm long), were attacked successfully, but modifications of the capture sequence occurred in all three trials. In two, the spider dropped the lower portion of the capture thread after wrapping the prey instead of re-attaching it to the dragline. In these trials, the spider did not rotate-wrap the prey, but cut it out after the initial wrap and carried it directly back to the resting thread. In all three trials, the ants were carried up to the resting thread dangling from the spinnerets on a 1.5 to 2 cm thread which was held with one or both legs IV. After reaching the resting thread, the spider pulled the prey in with legs IV and rotate-wrapped it.

Live moths of about the same length as the spider escaped readily from the capture thread by fluttering down it, leaving behind a conspicuous trail of scales stuck to the cribellar silk. We observed four complete prey capture sequences with moths and saw no major modifications in prey capture behavior, such as those seen with some araneids (Robinson 1969, Robinson et al. 1971). In three of the trials, the spider discarded the remaining capture thread after wrapping; as with the ants as prey, the rotate-wrap stage was omitted from these captures.

These observations suggest that the decision to retain or discard the remaining capture thread is made early in the attack sequence, and is perhaps related to the size of the prey. If the capture thread is to be abandoned, it may be advantageous for the spider to delay rotation-wrapping until it reaches the resting thread, where it is less exposed to visual predators. This explanation is not entirely satisfactory, however, since if rotation-wrapping is not necessary at the capture site (it would seem most necessary for just those large prey for which it is omitted), it would seem advantageous to perform all rotation-wrapping at the more protected resting thread.

Capture sequences with multiple prey

Capture of small prey such as fruitflies caused little damage to the capture thread, because the repair of the thread left the remaining sticky portion intact. When presented with a second or third prey, the spider rushed down the capture thread holding the first prey in its palps, and attacked the new prey in the usual manner. Second prey were wrapped together with the first prey and carried up to the resting thread in the palps in one large package, or wrapped separately and carried up hanging from the spinnerets, then wrapped with the first prey.

After only a few prey items were captured, the spider destroyed the remaining capture thread by dropping the lower end of the thread after wrapping the prey instead of attaching it to the dragline. The capture thread was destroyed even when a substantial portion remained undamaged, suggesting that the catching capacity of the thread does not limit the number of prey items the spider will attack. Since *Miagrammopes* does not attach prey at the feeding site (this is also true of *Uloborus diversus* — Eberhard 1967), it is likely that the size of the prey package the spider can hold in its palps limits it to capturing only a few insects in succession.

Prey capture in *M.* sp. 2, *M. intempus, M.* sp. 3, and *M.* sp. 4

Attack and prey capture behaviors of *M. intempus, M.* sp. 2, *M.* sp. 3, and *M.* sp. 4 were similar to those described above, involving dramatic sags of the capture thread as the spider approached the prey, wrapping of the prey at the capture site, and continued wrapping after the spider returned to the resting thread.

One *M.* sp. 3 responded to a vibrating tuning fork held nearby by quickly tightening the capture thread, either by pulling it in with leg I or by pulling in the resting thread with leg IV. Four attacks of *M. intempus* were observed, and in all cases the spider sagged the capture thread before encountering the prey, then attacked it by wrapping. One insect, an odorous pentatomid bug, was tapped repeatedly with the front legs before being wrapped and discarded. In one sequence it was possible to ascertain that the sticky capture thread was wadded up as the spider approached the prey, and was laid onto it as wrapping began.

Prey species captured

Prey taken from webs of an unidentified *Miagrammopes* sp. in Bayano, Panama which constructed a web with a single capture thread like that of *M. simus* included the following insects: 1 wasp, 1 winged ant, 2 nematocerous flies (1 psychodid), and 1 unidentified. An additional 29 prey collected as *M.* sp 1 fed on them included 14 winged ants of two species, 3 wasps, 2 nematocerous flies, 2 other flies, 1 beetle, and 7 unidentified insects. Four flies were collected as *M.* sp. 3 fed on them: 2 nematocerans of probably different families, a dolichopodid fly, and one acalyptrate. One small beetle was taken from an immature *M.* sp. 4. These lists make it clear that the spiders prey on a wide variety of insects, and are not specialists on any one group.

REPRODUCTION

The egg sac and its web

The egg sacs of *M. simus, M.* sp. 1, *M.* sp. 3, and *M. intempus* were tubular and elongate, two to four times the length of the spider, and very similar in color to the adult female. The egg sacs of *M. simus* and *M.* sp. 1 were brown, while those of *M.* sp. 3 and *M. intempus* were lightly coated with green silk. The sacs were thin-walled, with no fluffy silk inside, and the outlines of the eggs, which were arranged in one or two rows, were clearly visible.

The females stayed by the egg sacs during the day, either in a stick posture in line with the sac (Fig. 9) or holding one end of it with leg I, as seen in some *M.* sp. 1. In these positions both the spider and the egg sac were difficult to recognize; they looked like a dead twig. One *M. simus* female remained with an egg sac containing 52 eggs for 2 weeks in an outdoor cage. During this time she did not construct a capture thread. One *M.* sp. 1, however, nightly abandoned the daytime cryptic posture and laid several more or less horizontal, radial lines, suspending the sac by one end from the "hub" of this tiny web (Fig. 10). A single jagged loop of sticky silk was laid and the spider rested under the hub. When a

Figure 9. Daytime posture of a *Miagrammopes* sp. 1 (ca. *unipus*) female with an egg sac.

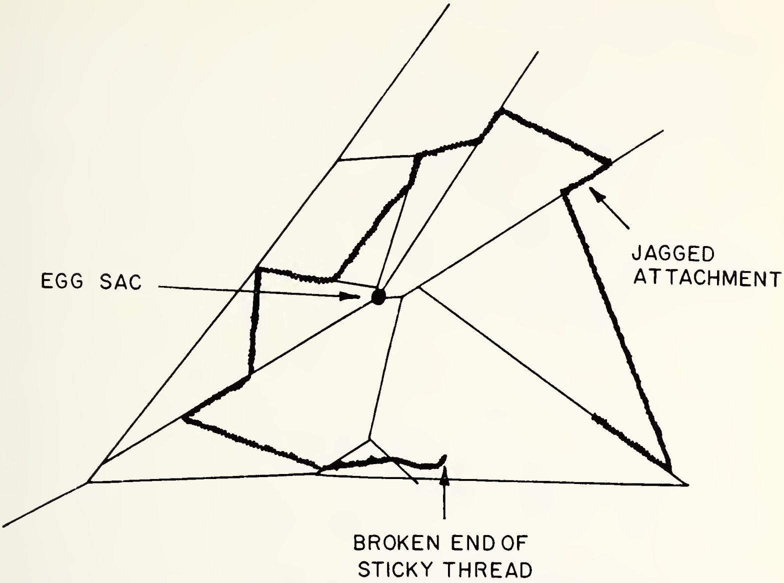

Figure 10. Egg sac web spun at night by a *Miagrammopes* sp. 1 (ca. *unipus*) female. The horizontal web is seen from above, with the tubular egg sac hanging down from the "hub." One end of the sticky "spiral" hung free and had probably been connected to the radius just to its right. The spider rested near the hub, out of contact with the egg sac.

small insect was placed on the sticky silk, the spider attacked and fed on it. During the day this rudimentary orb was gone, and the spider was back in the cryptic posture at the end of the egg sac.

Emergence of spiderlings

We observed emergence of spiderlings from one egg sac of *M.* sp. 1. The spiderlings were first seen one evening easing themselves through several ragged holes in the sac. They left behind, inside the empty sac, empty egg shells each with a pink moulted skin stuck to it. These second instar spiderlings (terminology of Hite, et al. 1966) were relatively inactive and stayed on the sac itself, holding their anterior legs in an unusual position (Fig. 11). The next morning, they had all moulted again, and the cast skins remained on the surface of the egg sac while the spiderlings wandered actively in the vial, holding their legs normally. These spiderlings (third instar) had fully developed cribella and calamistra.

Uloborids do not have functional cribella until after their first moult outside the egg sac (Wiehle 1931) and thus cannot produce sticky silk as newly emerged second instar spiderlings and cannot make functional, adult-type webs until after the second moult. Second instar spiderlings of *Uloborus* spp. spin orb webs made of dense sheets of fine threads, lacking the sticky spiral of the adult web (Wiele 1931, Szlep 1961, Eberhard 1977a). Spiderlings of *M.* sp. 1 solve the same problem by going through the second moult on the outside of the egg sac before dispersing; they thus have functional cribella before spinning their first webs.

DISCUSSION

The webs of the *Miagrammopes* species in this study are basically similar in having one or a few simple, sticky capture threads that are held under tension, sometimes with a few additional fine, non-sticky threads attached to them. The spiders' attack behaviors all involve suddenly sagging the capture thread. Details of placement of the capture and resting threads, and the spiders' web tensing behavior are variable among the species, and even to some extent among individuals of some species. Two of the characteristics described for *M.* sp. 1 appear to be unique among spiders — the double moult of the young before leaving the egg sac, and the special feeding web of the female near her egg sac.

The web of *Miagrammopes* species from Natal was similar to some of the webs of *M. intempus* and *M.* sp. 3 in having a single horizontal capture thread without a separate resting thread (Akerman 1932). The presence of additional fine threads attached to the capture thread was not noted in webs from Natal, but they would almost surely have gone unnoticed unless the webs were powdered. Web construction behavior was similar in the Natal species. The spider sat at one end of the completed capture thread, facing it; the thread may have been broken with the spider bridging the gap with its body (e.g. Marples 1962), but Akerman's drawing shows an intact line. The thread was held under tension by pulling it in with legs IV as do all six species of this study and was also quickly sagged when prey hit it. The single, horizontal, capture thread web may represent a further simplification of an already simple web, with a single sticky thread taking the place of both the horizontal resting thread and the vertical capture thread.

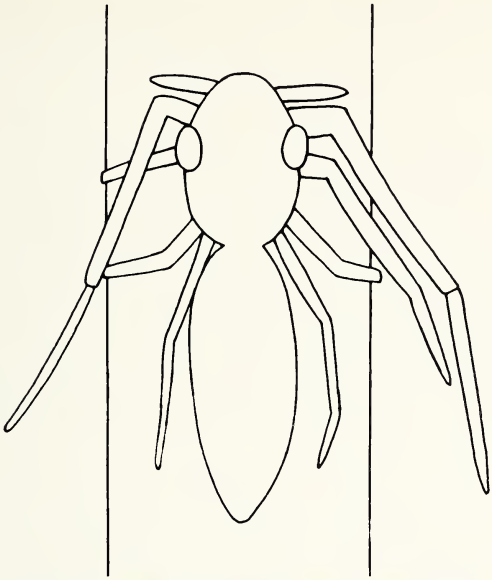

Figure 11. Typical leg positions of second instar *Miagrammopes* sp. 1 (ca. *unipus*) as they rested on the outside of the egg sac.

Although uloborids in general seem to construct their webs in the early morning (e.g. Eberhard 1972, Lubin and Eberhard unpubl.), *Miagrammopes* are more variable. Thus, while *M. simus, M.* sp. 1, and *M.* sp. 4 tend to have webs up early in the morning, they, as well as the species from Natal (Akerman 1932) sometimes build at other times, and *M. intempus* and *M.* sp. 3 commonly build in the evening. An unidentified species in New Guinea which spins single, horizontal threads also tends to build at night (Robinson and Robinson 1974, M. Robinson, pers. comm.). Readiness to build at different times of the day might be expected in view of the rapidity with which new webs can be made and the small investment of material which they represent. The tendency to discard webs support this idea.

Kaston (1964) suggested that the reduced web of *Miagrammopes* is derived from a *Stegodyphus*-type web (Eresidae) which consists of irregularly spaced radii with connecting sticky threads. A web similar to that of *Sybota* (Uloboridae) seems to us a more likely precursor of a *Miagrammopes*-type web. *Sybota producta* (Sim.)

lays cribellar silk directly on the radii and frame threads of orb-like webs which lack a sticky spiral (Wiehle 1931). The spider apparently does not manipulate tensions in the web once it is built (Wiehle 1931: Figs. 14 and 17). Such a web might conceivably become reduced to a web like that of *M.* sp. 1 by loss of frame and auxiliary spiral threads and reduction of the hub to a single resting thread. On the other hand, the jagged pattern of the sticky spiral found in the egg sac webs of *M.* sp. 1 suggests an affinity with *Uloborus* (sens. lat.) or *Hyptiotes* (Uloboridae). Spiders of both these genera commonly lay a jagged, sticky spiral on the periphery of the orb (McCook 1889, Eberhard 1972, Eberhard, unpubl.). An unidentified species of *Uloborus* (*sensu strictu*) builds an essentially identical egg sac web (Eberhard, in prep.), and *Uloborus diversus* also places sticky silk around its egg sacs (Eberhard 1969).

The most likely adaptive advantage of a single thread capture web would seem to be its near invisibility to prey, since at least some flying insects can detect and avoid webs (Bristowe 1941, Robinson and Robinson 1970, 1973, Lubin 1973, Buskirk 1975, Eberhard in prep., Lahman and Zuniga in prep.). This is apparently ruled out, however by the fact that at least two species (*M.*sp.3 and the New Guinea species) and perhaps a third (*M. intempus*) usually build their webs at night when visibility is probably unimportant.

Another possible advantage would be that predators using webs as cues to the presence of prey would be unlikely to detect webs of *Miagrammopes*. Some predators may use webs in this way, though some are known not to (Eberhard 1970). The significance of the very thin, slack lines attached to the capture threads remains even more of a mystery.

The obvious disadvantage of a single thread capture web is the low probability of a flying insect striking the web. Robinson and Robinson (1976) suggested that the numerous nematocerous flies which tend to rest on non-sticky spider threads might try to alight on *Miagrammopes* capture threads and thus become entangled. Indeed Akerman (1932) noted a number of "gnats" caught by the *Miagrammopes* species in Natal. Some nematocerous flies were among the prey collected in this study, but many other kinds of small insects were collected as well. Certainly the webs of *Miagrammopes* are not specialized to the extent of exclusively or even principally capturing nematocerous flies which alight on them. Some other spiders with reduced webs use chemical attractants for specific kinds of prey (Eberhard 1977b), but the wide variety of captured prey rules out this prey capture technique for *Miagrammopes.*

SUMMARY

The webs of six species of *Miagrammopes* (Uloboridae) studied in Panama, Colombia, Costa Rica, and Venezuela have only one or a few sticky capture threads. *Miagrammopes simus* and *M.* sp. 2 have one vertical capture thread attached to a non-sticky, horizontal resting thread. *Miagrammopes* sp. 1 (ca. *unipus*) builds from 1 to 5 near-vertical capture threads, and *M. intempus, M.* sp. 3, and *M.* sp. 4 use one or more capture threads that vary in their spatial arrangement. Webs are pulled taut by pulling in silk with either the front legs or the hind legs or both. The spiders assume highly cryptic postures during the day as they rest on their webs or near the egg sac.

Attack and prey capture behavior in all species involves rapid jerking and sagging of the capture thread by the spider, resulting (in at least two species) in the prey becoming entangled in one or more loops of sticky thread before the spider arrives to attack.

Second instar spiderlings of *M.* sp. 1 do not disperse, but moult a second time on the surface of the egg sac. Thus they construct webs only after they have fully formed calamistra and cribella and are capable of producing sticky silk. A mature female *M.* sp. 1 constructed nocturnal egg sac webs that were reminiscent of small uloborid orb webs.

The adaptive advantage of the reduced web of *Miagrammopes* is unclear. Many species of small insects are taken as prey and chemical attractants do not seem to be used.

ACKNOWLEDGEMENTS

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REVISION OF THE SOUTH TEMPERATE GENUS *GLYPHOLOMA* JEANNEL, WITH FOUR NEW SPECIES (COLEOPTERA: STAPHYLINIDAE: OMALIINAE)*

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Introduction

The southern temperate silphid genus *Glypholoma* Jeannel was transferred to the staphylinid subfamily Omaliinae by Newton (1975), and *Lathrimaeodes* Scheerpeltz (originally placed in the Omaliinae) was then synonymized with it. Newton (op. cit.) also presented additional descriptive information, a new locality record, and some discussion of the affinities of *Glypholoma* within the Omaliinae. Since that time, four new species of the genus have come to our attention, including one from Australia which greatly enlarges the known range of *Glypholoma* (previously only parts of Chile and Argentina). The discovery of these new species and the availability of a wealth of material of the type species, *pustuliferum* Jeannel, for detailed study led to our decision to revise the genus.

Methods

Measurements, made with an ocular micrometer in a Leitz binocular dissecting microscope, are defined as follows:

Length: measured in lateral view from front of (closed) mandibles to apex of abdomen (excluding genitalia if exserted, and attempting to estimate "normal" degree of contraction of abdomen).

Width: maximum body width, across closed elytra at widest point (usually near middle).

Head width: in dorsal view, maximum width including eyes.

Head length: measured along midline from anterior margin of labrum to level of centers of ocelli, viewed perpendicular to line of measurement.

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Antennal length: from constriction between scape and its basal articulatory process to apex of last antennal segment.

Ocellar diameter: measured antero-posteriorly in dorsal view.

Pronotal width: maximum width.

Pronotal length: along midline from base to apex, viewed perpendicular to line of measurement.

Elytral width: same as Width, above.

Elytral length: measured along suture from apex of scutellum to a line tangent to elytral apices.

Prosternal process length: measured along midline from a transverse tangent to the anterior margin of the procoxal cavities to apex of prosternal process.

Procoxal length: measured in ventral view between transverse tangents to anterior and posterior faces of procoxae.

Mesosternal length: along midline from anterior margin to apex of mesosternal process.

Mesosternal process length: along midline from transverse tangent to anterior margin of mesocoxal cavities to apex of mesosternal process.

Mesocoxal length: measured in ventral view between transverse tangents to anterior and posterior margins of mesocoxal cavities.

Mesosternal procoxal cavity length: along midline from anterior margin of mesosternum to a line connecting the posterior edges of the cavities.

Metasternal length: along midline between extremities of intercoxal processes.

Metasternal antecoxal sutures: measured from lateral limit to lateral limit.

Metasternal width: between posterolateral corners of metasternum.

Hind coxal length: lateral edge to posteromesal corner.

Hind femoral length: including trochanter, from posteromesal corner of coxa to most distal point of femur.

Hind tibial length: along mesal side (not including any spines or setae).

Hind tarsal length: from point of insertion of tarsus on tibia to tarsal apex, not including claws or empodial setae. The dividing line between the fourth and fifth hind tarsal segments was taken to be the point of insertion of the fifth segment on the fourth.

Abdominal segments are numbered according to their morphological origin. (The first segment visible ventrally is therefore the third segment.)

Mean length and width are given for each species, ± one standard deviation.

Preparation of specimens for scanning electron microscope pictures consisted of clearing heads, mouthparts, and prothoraces in hot 1 N potassium hydroxide, critical-point drying all parts except elytra, and coating with gold-palladium mixture. Cleared and dissected specimens of *pustuliferum* and *rotundulum* and of the aedeagi of other species were examined under dissecting and compound microscopes.

Drawings were made with the aid of a camera lucida attachment on a Leitz binocular dissecting microscope.

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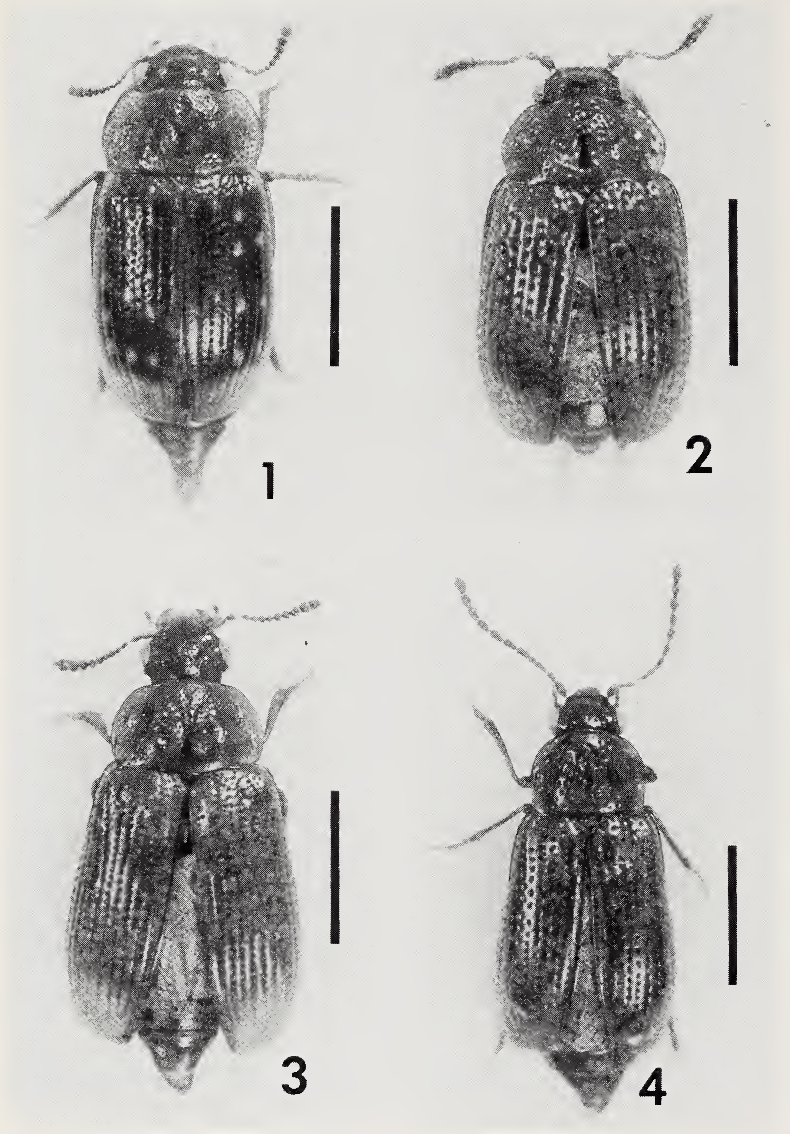
This study probably would not have come about were it not for S. B. Peck's extensive collecting in Chile and his kindly making this material available to us; he later generously provided us with a multitude of Australian specimens as well.

Specimens were borrowed from the following institutions (abbreviated in the text as indicated) and we extend our thanks to the curators involved for their cooperation in lending specimens.

CAS	California Academy of Sciences, San Francisco, California, U.S.A. (D. H. Kavanaugh)
CNC	Canadian National Collection, Ottawa, Ontario, Canada (J. M. Campbell)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
NMVM	National Museum of Victoria, Melbourne, Victoria, Australia (A. Neboiss)

Specimens are also deposited in the following collections:

ANIC	Australian National Insect Collection, Canberra, A.C.T., Australia
ANMT	A. F. Newton, Jr. and M. K. Thayer, Cambridge, Massachusetts, U.S.A.
FMNH	Field Museum of Natural History, Chicago, Illinois, U.S.A.
SBP	S. B. Peck, Ottawa, Ontario, Canada



Figs. 1–4. *Glypholoma* spp. 1. *G. pustuliferum.* 2. *G. pecki,* holotype. 3. *G. temporale,* holotype. 4. *G. tenuicorne,* holotype. Scale lines = 1.0 mm.

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Glypholoma Jeannel

Glypholoma Jeannel, 1962: 482; Newton, 1975: 53. Type species: *Glypholoma pustuliferum* Jeannel, 1962: 483, by original designation and monotypy.

Lathrimaeodes Scheerpeltz, 1972: 58; (placed in synonomy by Newton, 1975: 54). Type species: *Lathrimaeodes pustulipenne* Scheerpeltz, 1972: 59, by original designation and monotypy.

Diagnosis: Separable from other known Omaliinae by the excavate hind coxae, each elytron with eleven more or less distinct striae, male genital segment with a small "button" internally at the anterior end of sternite 9, and visible dorsal pleural-coxal articulation in the

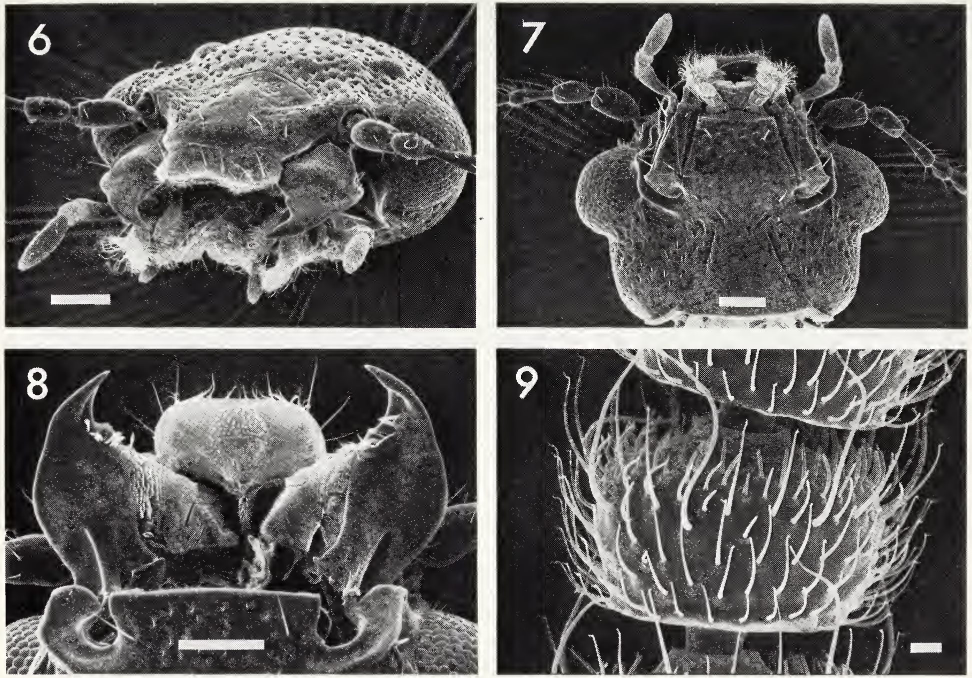
Fig. 5. *Glypholoma rotundulum*. Scale line = 1.0 mm.

prothorax. In addition, the combined presence of all of the following characters serves to distinguish *Glypholoma* from other Omaliinae. (Some other genera share one or a few of these characters with *Glypholoma,* but no other genus examined possesses all of these characters as *Glypholoma* does.)

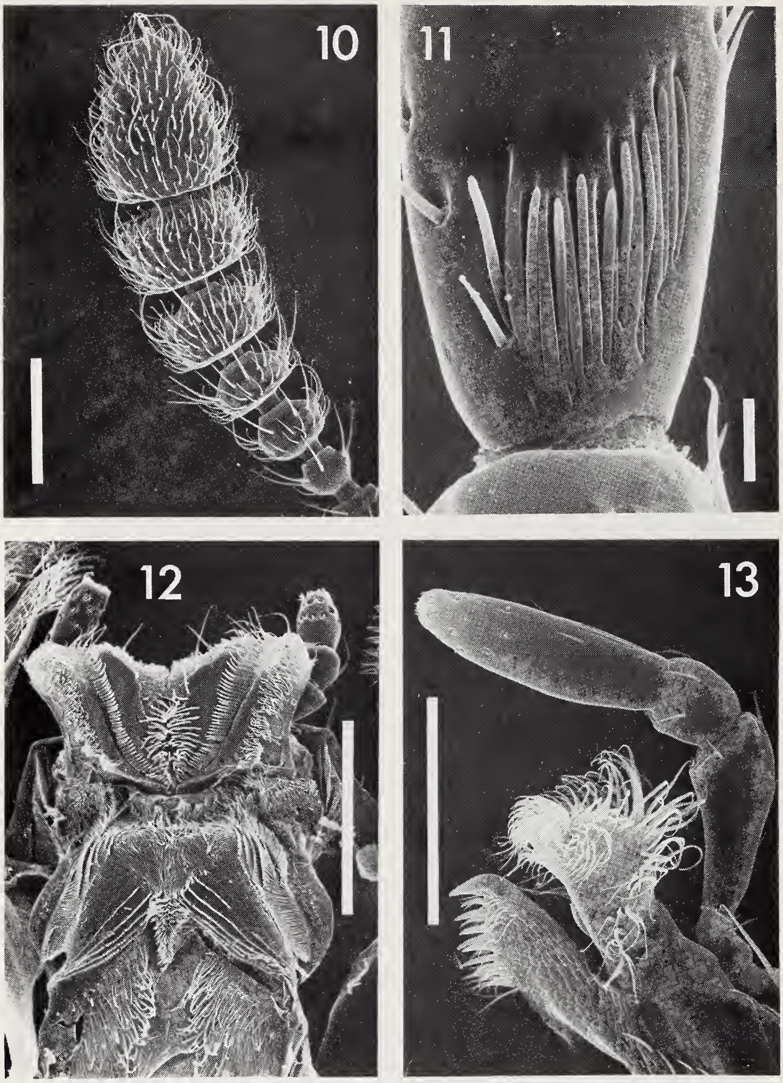
1. Gular sutures widely separated, minimum separation equal to 0.12–0.18 times the head width.
2. Prothoracic pleural-sternal articulation present.
3. Procoxa with mesal articulating groove.
4. Mesosternal procoxal cavities long, 0.40–0.75 times the total mesosternal length.
5. Hind femur relatively short, ranging from 0.92–1.05 times hind coxal length.
6. Deflexed lateral portion of elytron short, only 0.64–0.67 times as long as total length of elytron (measured in lateral view).
7. Humeral margin of elytron serrulate.
8. Median lobe of aedeagus with membranous part of basal bulb allowing dorsal-ventral instead of lateral-lateral contraction and expansion.
9. Epistomal suture present and complete (although with or without median stem).

Description: Ovoid (narrower posteriorly) to more or less oblong in dorsal view, slightly to strongly convex dorsally in cross section. Sparsely pubescent to nearly glabrous on dorsal surface, widely spaced macrosetae on alternate intervals of elytra in a fairly characteristic pattern (pattern varies some among the species; see figs. 26, 29). Microsculpture lacking on dorsal surface of head, pronotum, and elytra. Length 2.1–3.5 mm, width 1.0–1.5 mm.

Head capsule about as in fig. 58, lacking postocular ridge, temples, and nuchal constriction except in *temporale,* which has temples and a lateral nuchal constriction (fig. 57). Head about 1.8 times as wide as long, about 0.58 times as long as pronotal length, with pair of distinct ocelli on dorsal surface (see especially fig. 6); no anteocellar grooves or pits. Epistomal suture with internal reinforcing ridge present, angulate or arcuate, with or without median stem. Antennae usually about 1 to 1.5 times as long as head width, varying from filiform (*tenuicorne,* about 2.2 times head width) to having a moderately developed club of about three to five segments; basal five to eight antennal segments glabrous except for a few



Figs. 6–9. *Glypholoma pustuliferum*. 6–7. Head, anterior oblique and ventral views, respectively. 8. Mandibles and epipharynx, ventral view. 9. Tenth antennal segment. Scale lines: fig. 9 = 0.01 mm; others = 0.1 mm.



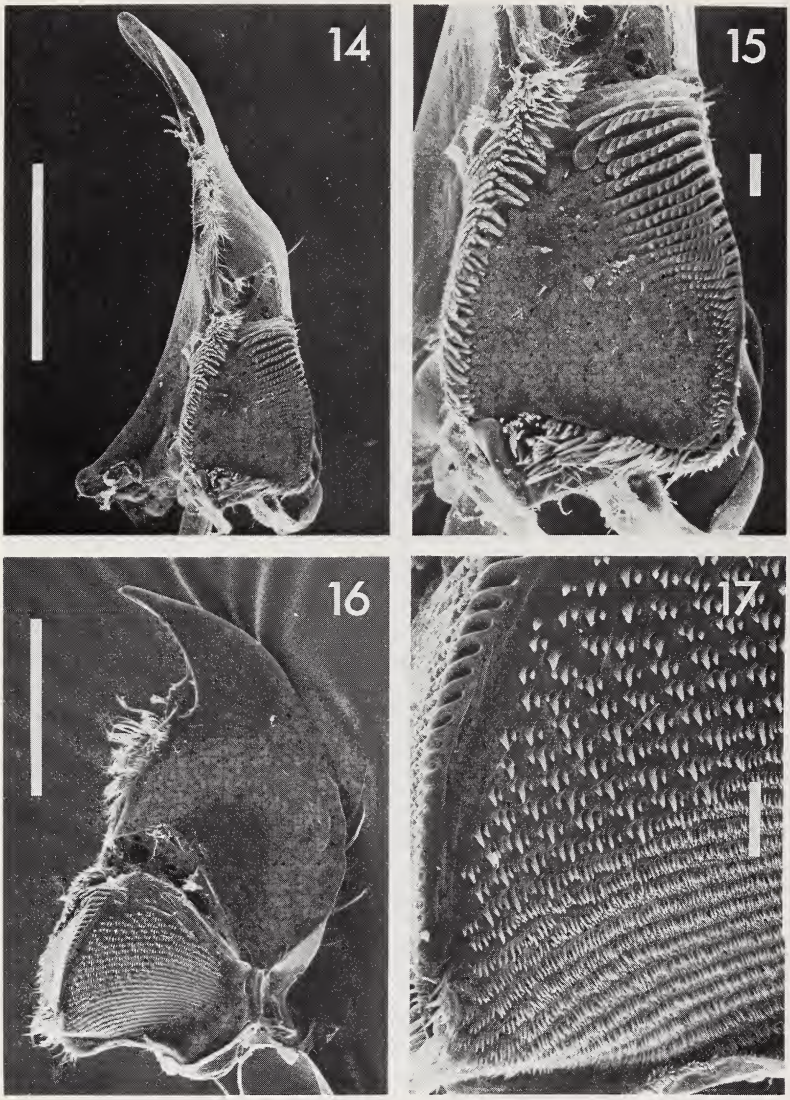
Figs. 10–13. *Glypholoma pustuliferum*. 10. Apical antennal segments. 11. Base of fourth maxillary palpal segment, external view. 12. Hypopharynx and labium, dorsal view. 13. Left maxilla, ventral view. Scale lines: fig. 11 = 0.01 mm; others = 0.1 mm.

scattered long setae. Apical antennal segments simple, without apical gutters or invaginations (see figs. 9, 10), with fairly dense short setae in addition to scattered long setae (see fig. 10, compare basal segments, fig. 7).

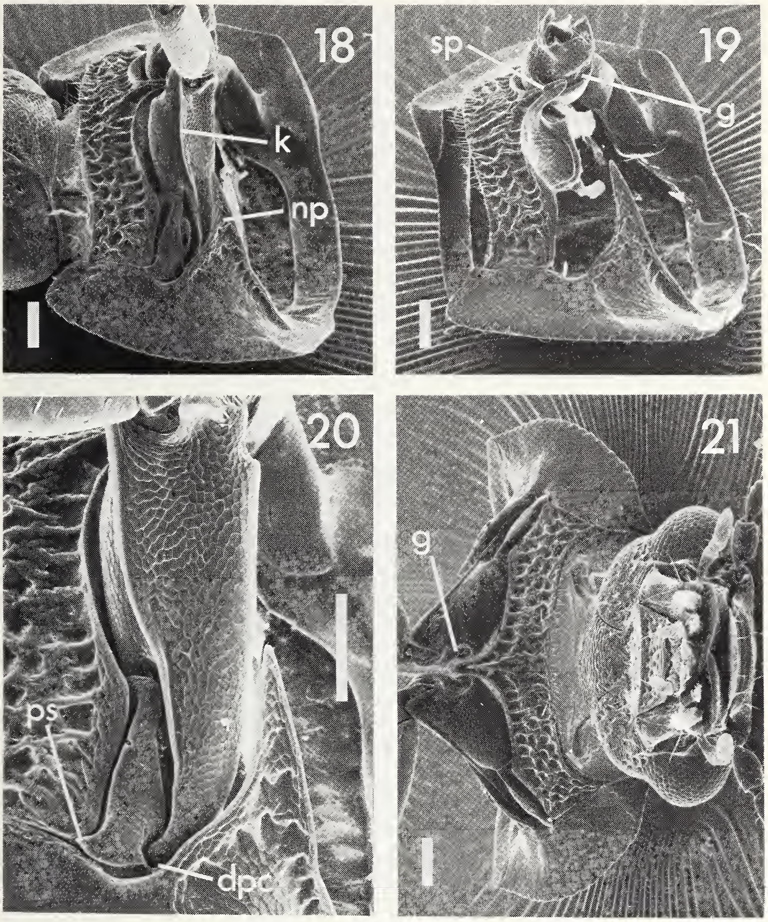
Labrum transverse, narrowly rectangular to slightly bilobed anteriorly, ventrally as in fig. 8. Mandible (of *pustuliferum* and *rotundulum,* at least) without preapical teeth, with a medial setose area about midway from base to apex and a well-developed molar lobe (see figs. 8, 14–17). Molar lobe apparently articulating dorsally and ventrally with mediobasal area of mandible proper. Maxilla more or less as in fig. 13, the palp generally filiform with fourth (apical) segment 2.5 to 5 times as long as third, a group of sensilla as in fig. 11 on its dorsolateral surface near the base. Hypopharynx (of *pustuliferum* and *rotundulum,* at least) about as in fig. 12. Labium apparently bilobed, with three-segmented palps arising from separate palpigers; segments of palp subequal in length and width (see fig. 7, also Newton, 1975, fig. 3). Mentum large and trapezoidal; gular sutures separate, their minimum separation 0.12 to 0.18 times the head width (see fig. 7).

Pronotum 1.5 to 1.8 times as wide as long, about 0.35 times as long as elytra; widest point variable, from posterior corners to just behind middle; with complete sharp lateral margins, explanate in at least basal half; lacking lateral foveae with internal pillars. Postcoxal process of pronotum acutely triangular, apparently a bar to coxal flexation (see figs. 18, 20). Prosternum with or without median longitudinal keel; prosternal intercoxal process extending one-half to two-thirds of the (antero-posterior) length of the procoxae. Procoxa with external longitudinal keel and mesal transverse articulating groove (see figs. 18–21). Protrochantin exposed, shorter than postcoxal pronotal process, dorsal pleural-coxal (trochantinal-coxal) articulation visible, pleural-sternal articulation present (the last possibly absent in *tenuicorne*), as in fig. 20.

Mesosternum 0.5 to 0.6 times as long as metasternum, with a nearly acute process (except in *rotundulum,* see figs. 35, 37) extending between the mesocoxae for four to seven tenths of their length (figs. 34, 36). Mesosternal process not medially longitudinally carinate. Anterior part of mesosternum with cavities for reception of procoxae 0.4 to 0.75 times as long as whole mesosternum.



Figs. 14–17. *Glypholoma pustuliferum,* right mandible. 14–15. Mesal view, whole mandible and molar surface, respectively. 16–17. Dorsal view, whole mandible and part of mola, respectively. Scale lines: figs. 14, 16 = 0.1 mm; figs. 15, 17 = 0.01 mm.

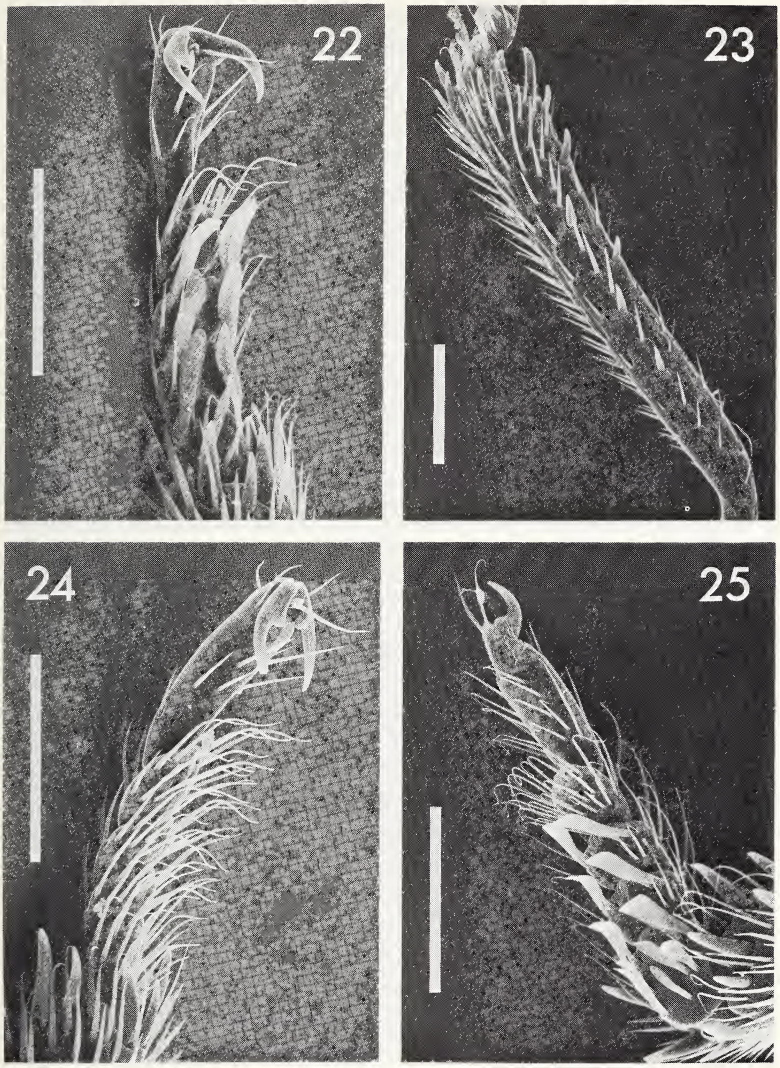


Figs. 18–21. *Glypholoma pustuliferum.* 18–19. Prothorax, ventrolateral view, with and without procoxa and trochantin, respectively. 20. Right procoxa and surrounding area, ventrolateral view, with coxa rotated anteriorly. 21. Prothorax and head, anteroventral view. dpc = dorsal pleural-coxal articulation; g = mesal articulating groove of coxa; k = external coxal keel; np = postcoxal process of pronotum; ps = pleural-sternal articulation; sp = prosternal intercoxal process. Scale lines = 0.1 mm.

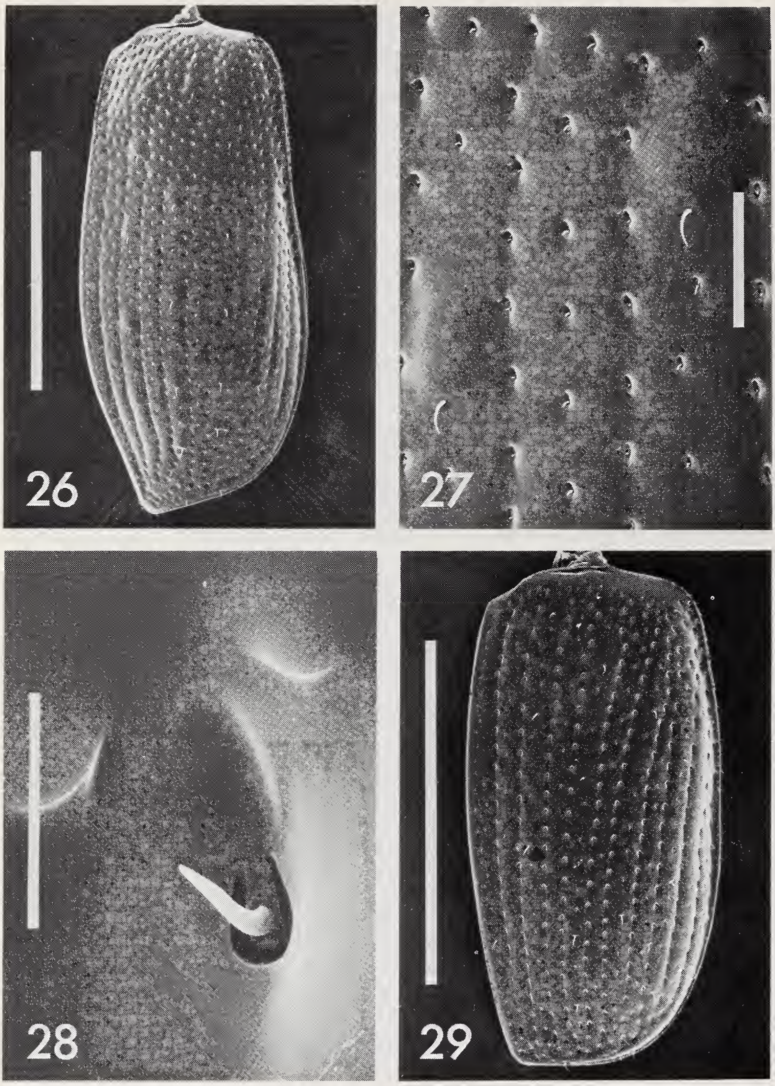
Mesepisternal-mesepimeral suture present; mesosternal-pleural suture present posteriorly, but disappearing anteriorly, apparently with fusion of the two sclerites (except in *tenuicorne,* where it may be complete). Metasternum with short anterior process meeting mesosternal process between mesocoxae, short process with bifid apex between metacoxae, and antecoxal sutures as in fig. 59 (*temporale* only) or 60. Metacoxae excavate, i.e. with posterior face vertical and entire postero-ventral margin explanate (fig. 38).

Legs rather slender; tibiae only slightly, if at all, wider at apex than at base, usually with some small spines on the external surface (slightly fewer to slightly more than in fig. 23), meso- and metatibia generally with more spines than protibia, the sexes usually similar within each species. Hind coxa and femur subequal in length, hind tibia about 0.9 times as long as femur, hind tarsus 0.5–0.7 times as long as tibia. All tarsi with five segments, hind tarsus with last segment one-third to two-thirds as long as first four together. Bisetose empodium between bases of tarsal claws (see fig. 39).

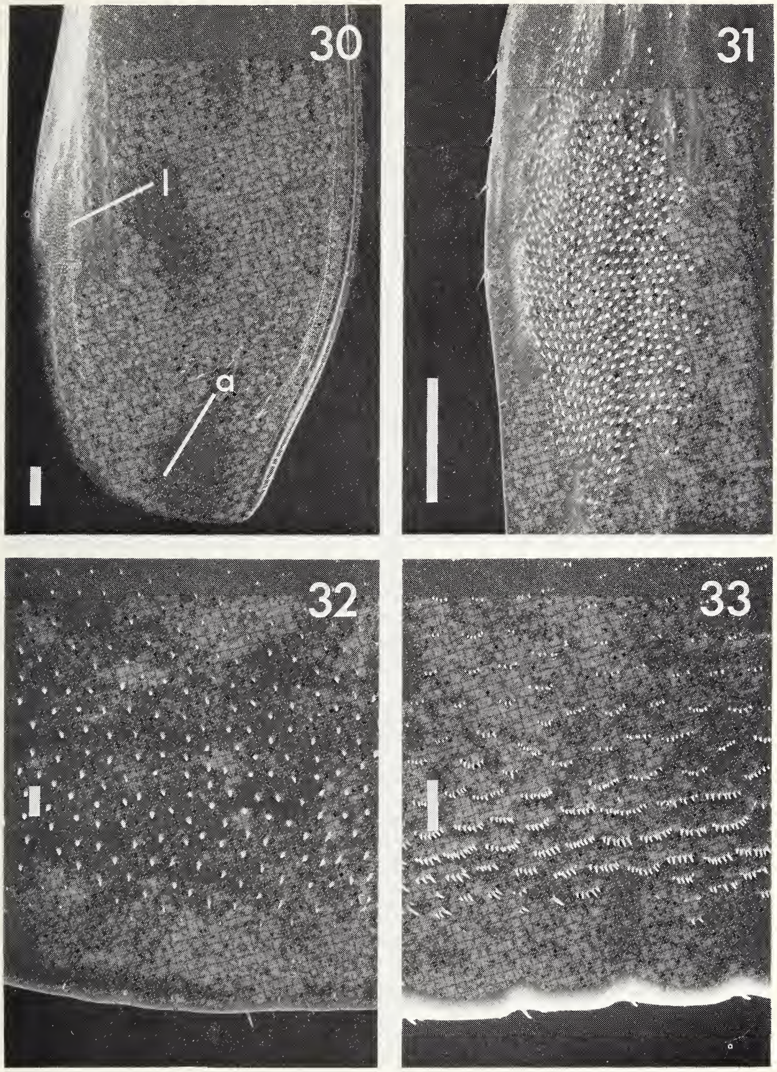
Elytra together about three-quarters as wide as long, each with eleven punctate striae (most clearly delimited in the middle section, more confused anteriorly and posteriorly) which are impressed between the punctures except in *tenuicorne*; eleventh stria (adjacent to epipleural keel) somewhat irregular. Macrosetae present on alternate intervals, associated in some species with raised pustules and/or spots; (except perhaps in *tenuicorne?*) intervals finely punctate between macrosetae (see figs. 26, 27, 29). Elytron with epipleural keel complete, serrulate in humeral region, intersecting with upturned lateral edge of elytron at about two-thirds the distance from elytral base to apex. Elytron covering abdomen through segment 5 or 6, with apparent elytral-abdominal interlocking patches on the internal elytral surface just antero-mesal to the confluence of the epipleural keel and elytral edge (see figs. 30, 31) and on the lateral area of abdominal segment 3 (see fig. 46). (Whole complex seen in detail only in *pustuliferum* and *rotundulum*; elytral patch present in all species except possibly *tenuicorne*; because of the limited number of specimens available of three of the species, an exhaustive search for the abdominal patches could not be made.) Elytron with patch of small single or grouped teeth near apex of ventral surface (as in figs. 30, 32, 33). Wings covering abdomen through tergite 3 when folded, except in brachypterous individuals



Figs. 22–25. *Glypholoma* spp., prolegs. 22–24. *G. pustuliferum;* 22, male tarsus, oblique ventral view; 23, male left tibia, posterior view; 24, female tarsus, oblique ventral view. 25. *G. rotundulum,* male tarsus, oblique ventral view. Scale lines = 0.1 mm.



Figs. 26–29. *Glypholoma* spp. 26–28. *G. pustuliferum,* right elytron; 26, dorsolateral view; 27, detail of fig. 26, including two pustules; 28, strial puncture (detail of fig. 26). 29. *G. rotundulum,* right elytron, dorsolateral view. Scale lines: figs. 26, 29 = 1.0 mm; fig. 27 = 0.1 mm; fig. 28 = 0.01 mm.

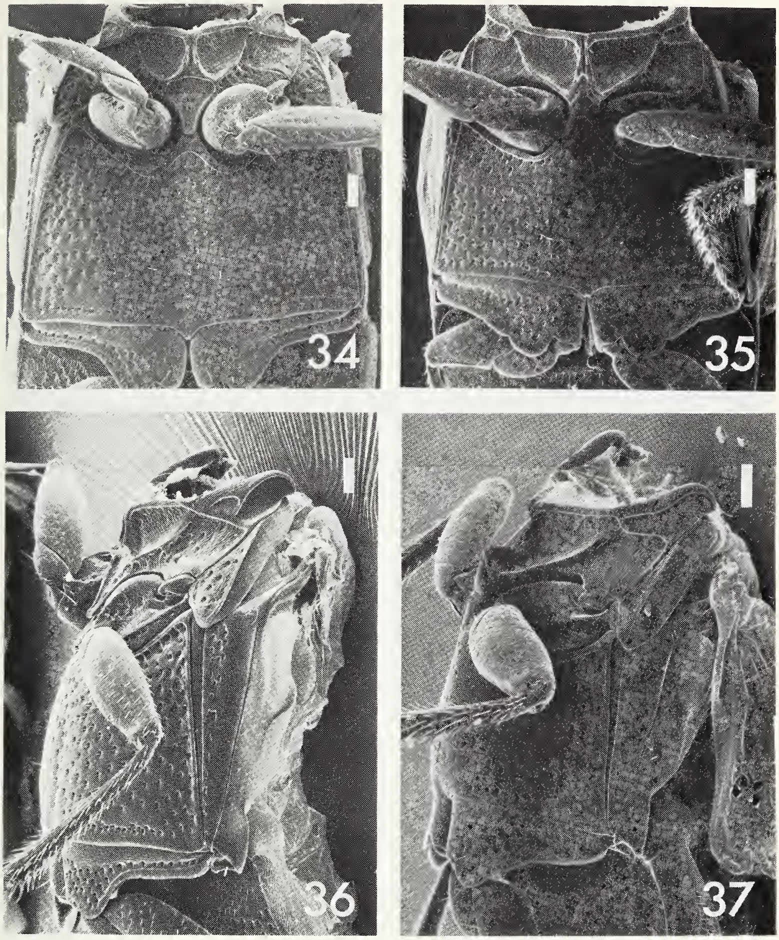


Figs. 30–33. *Glypholoma* spp., internal elytral surface. 30–32. *G. pustuliferum;* 30, overall view; 31, detail of lateral area ("l" in fig. 30); 32, detail of apex ("a" in fig. 30). 33. *G. rotundulum,* same view as fig. 32. Scale lines: figs. 30, 31 = 0.1 mm; figs. 32, 33 = 0.01 mm.

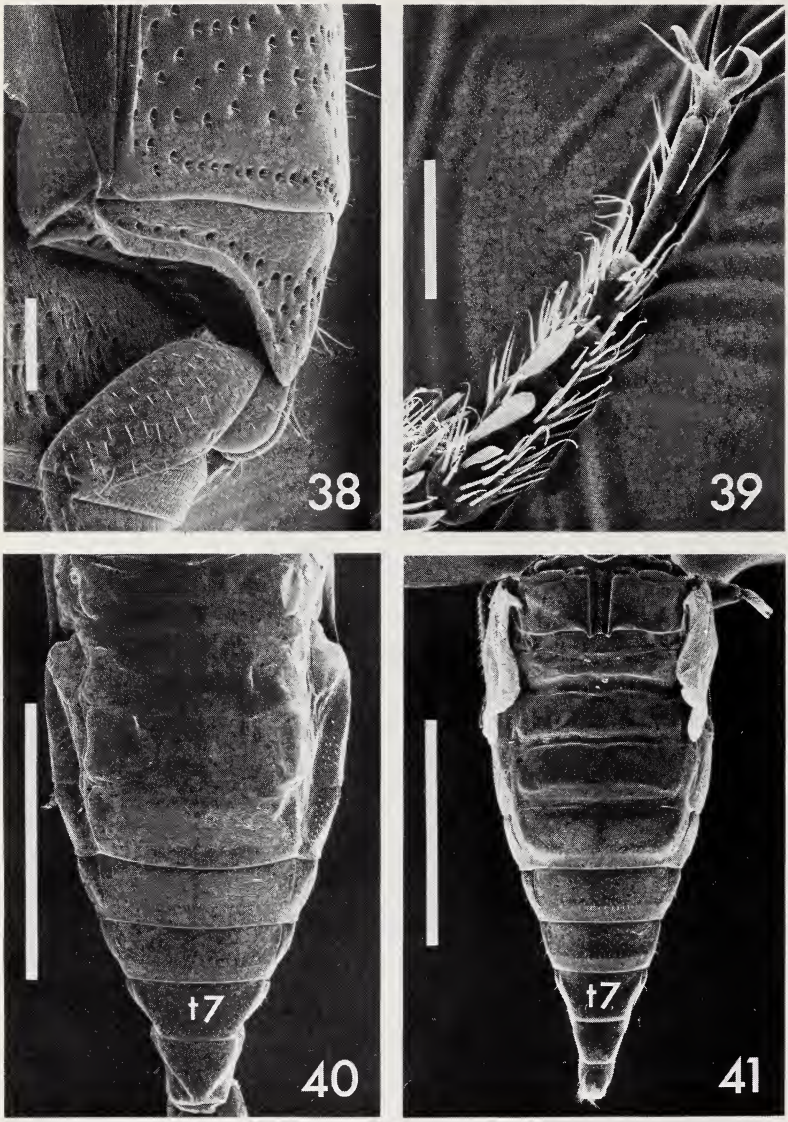
of *rotundulum,* in which the wings only reach the apex of tergite 2 and are not folded. Distinct anal flap present on wings of *pustuliferum* and *rotundulum,* probably in other species also. Folding pattern of fully-developed hind wing similar to that illustrated for *Anthobium* (=*Eusphalerum*) *sorbi* by Forbes (1926: fig. 33), the first transverse fold being a hinge by which the costal margin is turned about 90°. (In an individual, the hinges of the two wings usually form slightly different angles.)

Abdomen with most of segment 8 and part of genital segment exposed; first visible sternite is sternite 3. Tergites 4 or 5 to 8 fairly well to well-sclerotized, spiracles located in tergites 4 or 5 to 8, in membrane beside tergites 1 to 3 or 4; one pair of paratergites on each of segments 3 to 6 or 7, may be partly or entirely fused with sternites laterally (as almost complete fusion in fig. 47); tergite(s) 4 or 4 and 5 with paired patches of medially-directed microtrichia which cover about half to nearly all of the surface of the tergites (figs. 40–43); tergite 7 with an apical fringe ("palisade fringe" of some authors) as in fig. 45. Intersegmental membranes with a brick wall pattern of irregular plates as in fig. 44, some dorsal plates with posterior teeth as shown. Sternite 2 extending up around sides of abdomen slightly, but in *tenuicorne* appearing to be membranous, its limits therefore not determinable. Sternites 2 and 3 with small intimately associated intercoxal processes, more or less as in fig. 48, sternite 3 (at least in *pustuliferum* and *rotundulum*) with a transverse fold across its middle one-fourth to one-half about at posterior margin of intercoxal process (this area not visible in other species because of telescoping of abdomens). Sternite 3 without distinct coxal cavities, metacoxae simply protruding parallel to sternite's surface; at least in some species with a ridge near basal margin and, like sternites 4 to 5 or 6, a curved ridge just inside each lateral margin. Sternite 8 with anterior median projection (see figs. 49, 61–65) associated with a gland system, similar to that described by Klinger and Maschwitz (1977). In at least three species (*rotundulum, pecki, pustuliferum*) gland reservoir extending anteriorly as far as anterior margin of segment 5.

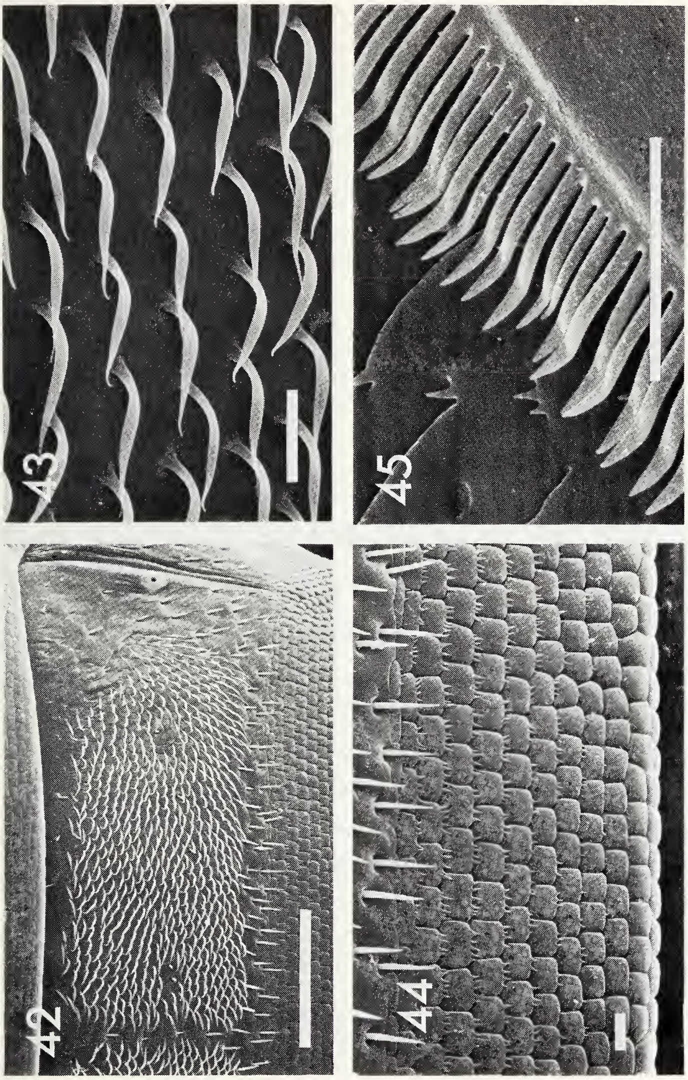
Male: Peg setae apparently absent from trochanters, femora, and tibiae; first four segments of protarsus slightly broadened, spatulate setae in pairs on segments 1 to 3 of protarsus (figs. 22, 25), and singly on first two (possibly three in *pecki*) segments of mesotarsus



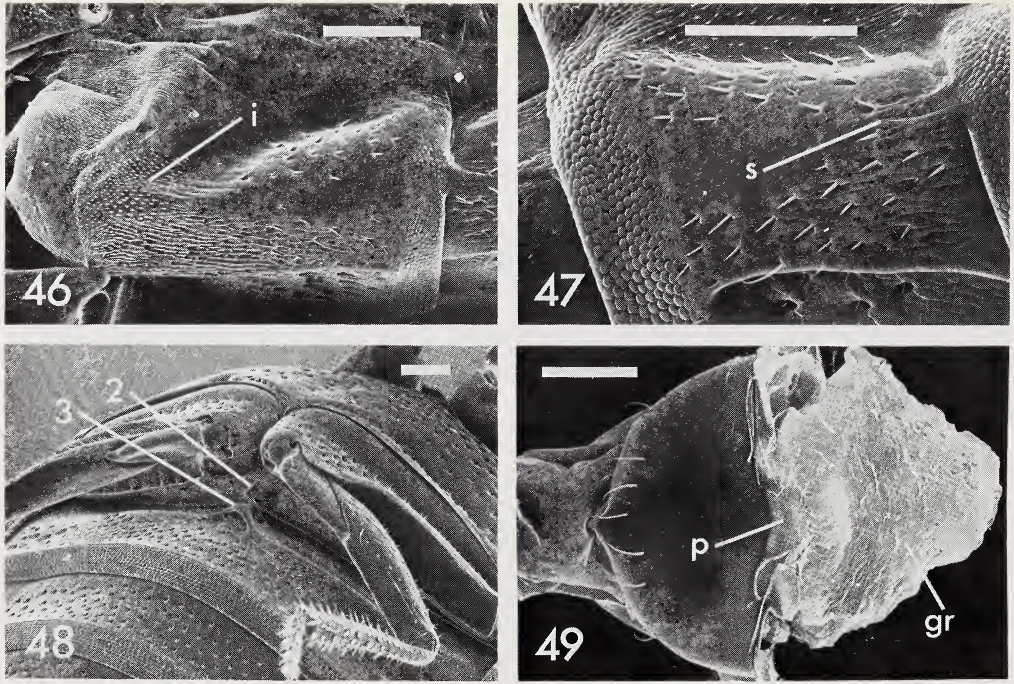
Figs. 34–37. *Glypholoma* spp., pterothorax. 34, 36. *G. pustuliferum,* ventral and oblique lateral views, respectively. 35, 37. *G. rotundulum,* ventral and oblique lateral views, respectively. Scale lines = 0.1 mm.



Figs. 38–41. *Glypholoma* spp. 38–40. *G. pustuliferum;* 38, metasternum and right metacoxa, lateral view; 39, male left mesotarsus, ventral view; 40, abdomen, dorsal view. 41. *G. rotundulum,* pterothorax and abdomen, dorsal view. t7 = tergite 7. Scale lines: figs. 38, 39 = 0.1 mm; figs. 40, 41 = 1.0 mm.



Figs. 42–45. *Glypholoma pustuliferum*, abdomen. 42–43. Microtrichial patch on tergite 5 (right side). 44. Intersegmental membrane between tergites 5–6. 45. Apical fringe of tergite 7, oblique anterior view. Scale lines: fig. 42 = 0.1 mm; others = 0.01 mm.



Figs. 46–49. *Glypholoma pustuliferum,* abdomen. 46. Segment 3, left lateral view, showing presumed elytral interlocking patch (i). 47. Segment 4, right lateral view, showing vestige of suture (s) between paratergite (above) and sternite (below). 48. Abdominal base, oblique ventral view, showing intercoxal processes of second (2) and third (3) segments. 49. Sternite 8, dissected out, ventral view, showing anterior projection (p) and gland reservoir (gr). Scale lines = 0.1 mm.

(see fig. 39). Genital segment with tergite 9 narrowly continuous across dorsal midline, tergite 10 short, sternite 9 attenuate, fairly well sclerotized in posterior one-third or so, only lightly sclerotized anteriorly, with a small cylindrical protuberance on internal surface near anterior end (see figs. 66–75). Aedeagus of general staphylinid type (median lobe with basal bulb, small dorsal median foramen, ventro-apical median orifice); parameral side of aedeagus facing dorsally within abdomen; small basal piece present as a more or less C- or U-shaped strap on dorsal side of basal bulb (often very lightly sclerotized and difficult to see); basal bulb of median lobe lightly sclerotized, with a membranous band around the abparameral side, presumably allowing dorsal-ventral bellows-like contractions; internal sac with dense armature of short, fine spines; apex of median lobe a finger-like projection, even with or slightly shorter than apices of parameres; parameres with or without subapical setae (see figs. 76–85).

Female: Pro- and mesotarsus without spatulate setae, as in fig. 24. Genitalia (based on *pustuliferum* and *rotundulum,* except as noted) about as in Newton, 1975, figs. 8–10: sclerotized spermatheca apparently absent, sternite 9 present, tergite 9 divided into two lateral sclerites, tergite 10 U-shaped; proximal gonocoxites separate, about half as long as distal gonocoxites; in all species in which females are known, distal gonocoxites separate, each bearing at its apex a short stylus with 1 (or 2?) long apical seta(e) and one or more subapical setae.

Immature stages unknown.

Range: Southern Chile and Argentina south to Tierra del Fuego; Victoria, Australia; see maps, figs. 50, 51.

KEY TO THE SPECIES OF *GLYPHOLOMA* JEANNEL

1. Antenna filiform (fig. 56); elytra without raised pustules; dorsal surface uniform in color; body form as in fig. 4 .... *G. tenuicorne* n.sp.
   Antenna with gradual apical club (figs. 52–55); elytra with or without raised pustules; dorsal surface with various color markings; body form otherwise (figs. 1–3, 5) 2
2. Elytra with raised pustules on alternate intervals (fig. 26) .3
   Elytra without raised pustules (fig. 29) 4

3. Postocular lobe present (fig. 57); metasternal antecoxal sutures long, about three-fourths the width of the metasternum (fig. 59); elytral pustules concolorous with surrounding area .. .. *G. temporale* n.sp.
   Postocular lobe absent (fig. 58); metasternal sutures short, no more than about one-third the width of the metasternum (fig. 60); elytral pustules lighter in color than surrounding area .... *G. pustuliferum* Jeannel
4. Antennal segment 11 about 4× as long as segment 10 (fig. 52); mesosternal process a simple angulate projection between mesocoxae (cf. figs. 34, 36); pronotum with lateral margins explanate, dorsal surface uneven; dark median spot on vertex of head, dark median streak on pronotum, no markings on elytra................................ *G. pecki* n.sp.
   Antennal segment 11 not more than about 2.5× as long as segment 10 (fig. 55); mesosternal process an elevated pentagonal protuberance between mesocoxae (figs. 35, 37); pronotum evenly convex, not broadly explanate laterally; head and usually pronotum without markings, elytra with yellow spots on alternate intervals, sometimes with additional pale areas; usually brachypterous .... *G. rotundulum* n.sp.

Glypholoma pustuliferum Jeannel

Glypholoma pustuliferum Jeannel, 1962: 483; Newton 1975: 53–54; Szymczakowski, 1976: 424.

Lathrimaeodes pustulipenne Scheerpeltz, 1972: 59. (Placed in synonymy by Newton, 1975: 54.)

With the characters of the genus as described above.

Moderately convex dorsally, shape as in fig. 1, various shades of brown in color: head darkest, reddish-brown to nearly black (with area anterior to epistomal suture the darkest part), basal two-thirds of elytra (except lateral margins) roughly concolorous with main part of head except for much lighter yellow pustules on alternate intervals; central area of pronotum similar to elytra or slightly lighter, with pronotal and elytral margins yellow to yellowish-brown, legs and dorsum of abdomen generally about the color of the central pronotal area. Ventral body surface usually reddish-brown, with lateral pronotal margins and deflexed portion of elytra paler. Some specimens (teneral?) are yellowish to reddish-brown, nearly unicolorous, with elytral pustules only slightly paler. Very short setae (similar to that in fig. 28) sparsely distributed over body surface, legs more densely setose, especially tibiae and tarsi. Length: 3.0 ± 0.2 mm (2.6–3.5); width: 1.3 ± 0.1 mm (1.1–1.5) (N = 55).

Head capsule as in figs. 6, 7, and 58, epistomal suture with median stem (not always visible on surface). Antennal length about 1.1 times head width, first six antennal segments without dense pubescence, antennal club five-segmented, gradual (see fig. 54). Ocellar diameter about 0.095 times head width. Labrum shallowly emarginate anteriorly as in fig. 6. Maxillary palp with fourth segment about three times as long as third, the two approximately subequal in width.

Pronotum as in fig. 1, with several small shallow paramedian and lateral depressions; lateral margins explanate. Prosternum deeply pitted and rugose, but lacking microsculpture, and without median longitudinal carina (see figs. 18–21). Mesosternum with dense irregular microsculpture, cavities for reception of procoxae about half the length of the mesosternum; mesosternal process fairly narrow, blunt, extending seven-tenths of the way between mesocoxae (see figs. 34, 36). Metasternum convex with faint median longitudinal depression, surface without microsculpture but with short setae in large punctures (see fig. 36), antecoxal sutures short, extending only three-tenths the width of the metasternum (fig. 60). Protibia setose, with several small spines on outer surface (fig. 23), meso- and metatibia with slightly more spines. Hind tarsus six-tenths as long as hind tibia, fifth segment of hind tarsus two-thirds as long as first four together. Empodial setae subequal in length to tarsal claws.

Elytral striae impressed between punctures, intervals punctate and with short fine setae (in addition to macrosetae on alternate intervals; see figs. 26, 27). Pale pustules located anterior and adjacent to macrosetae. Angle formed by elytral apices at suture about 180°. Wings fully developed, with anal flap.

Abdomen with tergites 4 to 8 well sclerotized, spiracles located in tergites of these segments; paratergites separated anteriorly but not posteriorly from sternites on segments 4, 5 and 6 (see fig. 47), apparently not separated from sternites on segments 3 and possibly 7. Tergites 4 and 5 with paired patches of medially-directed microtrichia as in figs. 40, 42, 43. Transverse fold on sternite 3 about one-fourth width of sternite. Sternite 8 with anterior projection as in figs. 49 and 61.

Male: Spatulate setae on protarsus as in fig. 22, three pairs on first segment, two pairs each on second and third segments, and on first two segments of mesotarsus as in fig. 39, three on first segment, two on second, only on anterior half of mesotarsal segments; genital segment and aedeagus as in figs. 66, 67, 84, 85.

Female: Genitalia as illustrated by Newton (1975, figs. 8–10).

Distribution: see map, fig. 50. (Includes records from the literature and those listed below.)

Types: *Glypholoma pustuliferum* Jeannel. Holotype (sex unknown): CHILE: Aisén Province, Chile Chico [Museo Nacional de Historia Natural, Santiago, Chile]; not seen. Paratype as listed by Jeannel, 1962.

Lathrimaeodes pustulipenne Scheerpeltz. Holotype (♂): ARGENTINA: Rio Negro Province, El Bolsón, Mt. Piltriquitron [Hungarian Natural History Museum, Budapest, Hungary]; not seen. Paratypes as listed by Scheerpeltz, 1972.

Material examined: CHILE: Malleco Prov.: 7 km W V. Portales, 1300 m, 23–24.XII.1976, S. Peck (1) [SBP]; 15 km W V. Portales, 1650 m, 22–25.XII.1976, S. Peck (2) [SBP]; 15 km W Victoria, 200 m, 28–30.XII.1976, S. Peck (2) [SBP]; 20 km E Manzanar (=30 km E Curacautin, nr. Malalcahuello), 1100 m, 19–31.XII.1976, S. Peck (106) [ANIC, ANMT, CNC, FMNH, MCZ, NMVM, SBP]; same locality, 1300–1400 m, 19–21.XII.1976, S. Peck (1) [SBP]; same locality, no elev., 19–25.XII.1976, S. Peck (16) [ANMT, CNC]; Talca Prov.: Alto Vilches, 1300 m, 10–13.XII.1976, S. Peck (3) [ANMT, SBP]; Ñuble Prov.: Las Trancas, 70 km E Chillan, 1400 m, 13–17.XII.1976 (some labeled 70 km SE Chillan 1300 m, 14–17.XII), S. Peck (15) [ANMT, CNC, SBP]; Magallanes Prov.: Punta Arenas, Feb. 1906, R. Thaxter (6) [MCZ]; Cautin Prov.: 22 km E Temuco, VI–VII.1951, M. G. Smith (2) [CAS].

Habitat: Of the material examined, ecological data are available for most of the specimens collected by Peck. Twenty-eight specimens were collected at dung traps (three collections), 35 at carrion traps (five collections), 60 from litter under carrion left for several days (one collection), and one from mushrooms on a rotting stump (with litter and moss; one collection). Most of these collections were made in *Nothofagus* forest (also two specimens from *Nothofagus-Araucaria* forest, one from *Araucaria* forest), and several of the dung and carrion traps were set near streams (S. Peck, pers. comm.). Scheerpeltz (1972), whose records are mainly small series, reports this species (as *Lathrimaeodes pustulipenne*) primarily from ground litter in forests of *Nothofagus, Libocedrus,* and other trees, and also mentions one record from an old rabbit carcass in such a forest. These beetles seem to live in forest litter, but are strongly attracted to carrion and dung. Nothing is known about their feeding habits.

Glypholoma temporale, new species

With the characters of the genus as described above.

Moderately convex dorsally, shape as in fig. 3, with central areas of pronotum and elytra brown, their lateral margins and the elytral apices yellowish, head and dorsum of abdomen between these two colors, slightly reddish; venter of body darker than dorsum, legs slightly paler than head. Head and pronotum with pale scattered short fine setae, elytra glabrous between macrosetae, tibiae and tarsi fairly densely setose. Length: 2.9 ± 0.1 mm; width: 1.3 ± 0.02 mm ($N = 6$).

Head capsule as in fig. 57, epistomal suture angulate, lacking median stem, temples and lateral nuchal constriction present. Antennal length about 1.3 times head width, first four antennal segments without dense pubescence, apical segments broader than basal, but distinct club difficult to delimit (see fig. 53). Ocellar diameter about 0.09 times head width. Labrum slightly emarginate anteriorly. Maxillary palp with fourth segment about 2.5 times as long as third, slightly wider at middle than third.

Pronotum as in fig. 3, with very shallow paramedian and lateral depressions, lateral margins explanate. Prosternal surface finely rugose, without median longitudinal carina. Mesosternum similar to that of *pustuliferum* (figs. 34, 36), with microsculpture; cavities for reception of procoxae about two-fifths the length of the mesosternum, mesosternal process narrow, extending just over half way between mesocoxae. Metasternum convex, lacking microsculpture but with large punctures containing minute setae, antecoxal sutures long, extending three-fourths the width of the metasternum (fig. 59). Protibia setose, slightly fewer spines than in *pustuliferum* (cf. fig. 23), meso- and metatibia with more spines than protibia. Hind tarsus nearly seven-tenths as long as hind tibia, fifth segment of hind tarsus half as long as preceding four together. Empodial setae longer than tarsal claws.

Elytral striae impressed between punctures, intervals finely punctate. Pustules (concolorous with surrounding area) present on alternate intervals, anterior and adjacent to macrosetae. Angle formed by elytral apices at suture slightly less than 180° (convex posteriorly). Wings fully developed.

Abdomen with tergites 5 to 8 well-sclerotized, spiracles located in tergites of these segments; paratergites clearly present and distinct on segments 4 to 6, sutures between sternite and paratergites lacking on segment 3 and (perhaps) posteriorly on segment 7. Tergites 4 and 5 with paired patches of medially-directed microtrichia, fairly similar to those of *pustuliferum* (cf. fig. 40). Sternite 8 with anterior projection as in fig. 63.

Male: Spatulate setae in pairs on protarsal segments 1–3, singly on mesotarsal segments 1 and 2, similarly to fig. 39, but exact number unknown; genital segment and aedeagus as in figs. 70, 71, 82, 83.

Distribution: see map (fig. 50).

Holotype: CHILE: Malleco Prov., 20 km E Manzanar, 19–25.XII.76 S. Peck, 1100 m, carrion + dung traps [MCZ].

Paratypes (2♂, 3♀): Same locality and date as holotype; no elevation or habitat data [ANMT, CNC, MCZ, SBP].

Habitat: In addition to the label data, the holotype was collected in moist *Nothofagus* forest near a stream (S. B. Peck, pers. comm.).

Etymology: This species name refers to the well-developed temples on the head.

Glypholoma pecki, new species

With the characters of the genus as described above.

Moderately convex dorsally, shape as in fig. 2, unicolorous yellowish-brown, except the following darker brown: spot on vertex of head between ocelli, median longitudinal line on pronotum, last three or four antennal segments, and third and fourth segments of

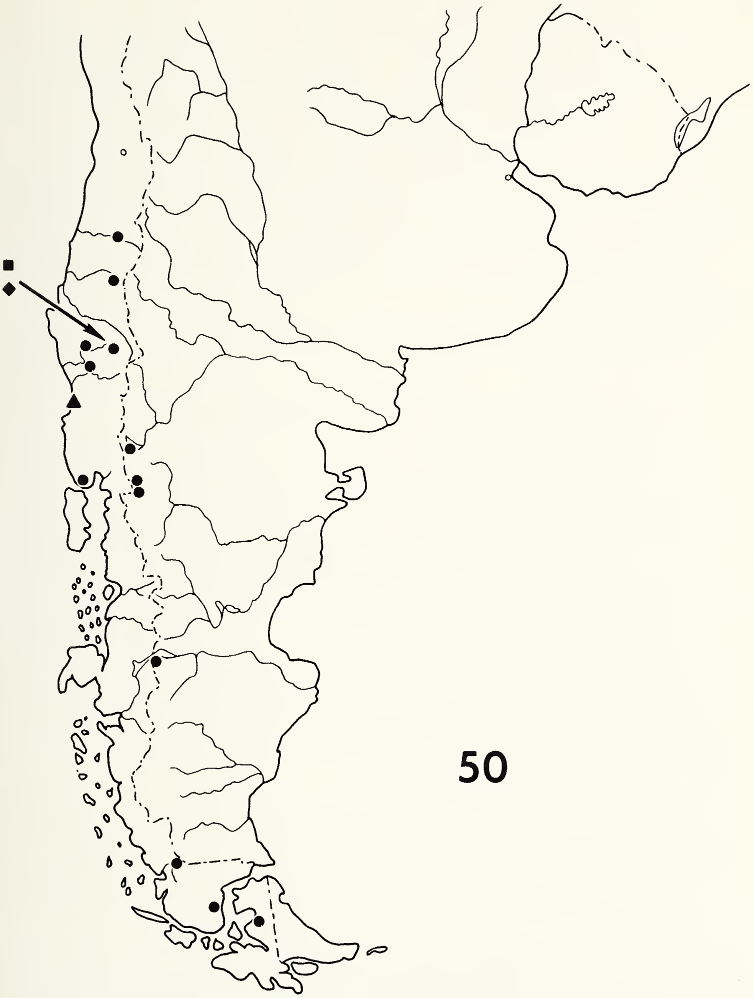


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Fig. 50. Southern Chile and Argentina, showing locality records for South American *Glypholoma* spp.: *G. pustuliferum,* dots; *G. temporale,* diamond; *G. pecki,* square; *G. tenuicorne,* triangle.

maxillary palps. Dorsal surface of head, pronotum, and elytra virtually glabrous except for elytral macrosetae. Length: 2.6 mm; width: 1.2 ± 0.03 mm (only two specimens seen).

Head capsule similar to that of *pustuliferum* (fig. 58), but eyes more prominent and epistomal suture lacking median stem. Antennal length about 1.3 times head width, first seven antennal segments without dense pubescence, antennal club three-segmented, apical segment four times as long as preceding segment (see fig. 52). Ocellar diameter about 0.08 times head width. Labrum approximately rectangular (anterior margin straight). Maxillary palp with fourth segment about 4.5 times as long as third, the two subequal in width.

Pronotum as in fig. 2, with shallow median and lateral depressions, lateral margins explanate. Prosternum coarsely punctate with median longitudinal carina. Mesosternum with dense microsculpture except on mesosternal process, cavities for reception of procoxae about half the length of the mesosternum, mesosternal process similar to that of *pustuliferum* (cf. figs. 34, 36), extending about two-thirds of the way between mesocoxae. Metathorax convex, without microsculpture, coarsely punctate with minute setae in punctures; antecoxal sutures short, extending one-fifth to one-fourth the width of the metasternum. Male protibia with a few external spines near apex, meso- and metatibia with a few more spines, female tibiae with fewer spines than male. Hind tarsus about two-thirds as long as hind tibia, fifth segment of hind tarsus three-fifths as long as first four segments together. Empodial setae subequal in length to tarsal claws.

Elytral striae impressed between punctures, elytral intervals finely sparsely punctate between macrosetae on alternate intervals. Elytra without pale spots or raised pustules. Angle formed by elytral apices at suture slightly greater than 180° (concave posteriorly). Wings fully developed.

Abdomen with tergites 5 to 8 well-sclerotized, spiracles located in tergites of these segments (possibly 4 also); sutures between sternite and paratergites apparently lacking on segments 3 to 7. Tergites 4 and 5 with paired more or less rectangular patches of medially-directed microtrichia, less extensive than those of *pustuliferum* (cf. fig. 40). Sternite 8 with anterior projection as shown in fig. 62.

Male: Spatulate setae in pairs on protarsus, number unknown, singly on first two or three segments of mesotarsus, number unknown; genital segment and aedeagus as in figs. 68, 69, 80, 81.

Distribution: See map (fig. 50).

Holotype (♂): CHILE: Malleco Prov., 20 km E Manzanar, 1100 m, 19–25.XII.1976, S. Peck, malaise trap [MCZ].

Paratype (♀): Same data as holotype [CNC].

Habitat: Both specimens were collected in a malaise trap at the edge of moist *Nothofagus* forest (S. B. Peck, pers. comm.), but this species was absent from dung and carrion traps at the same locality which produced over 100 *pustuliferum* and one *temporale.*

Etymology: This species is named after Dr. Stewart B. Peck, who collected both types as well as most of the other specimens used in this study.

Glypholoma tenuicorne, new species

With the characters of the genus as described above.

Slightly convex dorsally, shape as in fig. 4, unicolorous light reddish-brown, head and pronotum dorsally with a few scattered setae, elytra glabrous except for macrosetae, tibiae and tarsi less densely setose than in other species. Length: 3 mm; width: 1.2 mm (one specimen seen).

Head capsule generally similar to that of *pustuliferum* (fig. 58), but epistomal suture arcuate and lacking median stem. Antennal length about 2.2 times head width, first four antennal segments without dense pubescence, club lacking (see fig. 56). Ocellar diameter about 0.11 times head width. Labrum rectangular (anterior margin straight). Maxillary palp with fourth segment about 3.5 times as long as third, the two subequal in width.

Pronotum as in fig. 4, with shallow median and anterolateral depressions, lateral margins acute anteriorly, explanate posteriorly. Prosternum minutely rugose and sparsely punctate, without median longitudinal carina; pleural-sternal articulation possibly absent. Mesosternum with dense microsculpture, cavities for reception of procoxae about two-fifths the length of the mesosternum, mesosternal process similar to that of *pustuliferum* (figs. 34, 36), extending half the distance between mesocoxae; mesosternal-pleural suture possibly complete. Metasternum convex, without microsculpture, more finely punctate than *pustuliferum* (cf. fig. 34) and with most of the posterior half impunctate; antecoxal sutures short, extending one-fourth the width of metasternum. Protibia without spines externally, meso- and metatibia with only a few. Hind tarsus seven-tenths as long as hind tibia, fifth segment of hind tarsus one-third as long as first four segments together. Empodial setae subequal in length to tarsal claws.

Elytral striae not impressed between punctures, intervals impunctate except for macrosetae. Elytra without pale spots or raised pustules. Angle formed by elytral apices at suture slightly greater than 180° (concave posteriorly). Wings fully developed.

Abdomen with tergites 4 to 8 well-sclerotized, spiracles in tergites of segments 4 (or possibly 3) to 8; paratergites clearly present and distinct on segments 4 to 6, sutures between sternite and paratergites lacking on segment 3. (Structure of segment 7 uncertain.) Tergites 4 and 5 with paired patches of medially-directed microtrichia, patches slightly narrowed laterally but still occupying most of the width and (medially) the length of both tergites. Sternite 8 with anterior projection as in fig. 64.

Male: Spatulate setae in pairs on protarsal segments 1–3, number unknown, present singly on anterior half of first two segments of mesotarsus, number unknown; genital segment and aedeagus as in figs. 72, 73, 76, 77.

Female unknown.

Distribution: See map (fig. 50).

Holotype (♂): CHILE: Valdivia Prov., Corral, Dec. 1905, R. Thaxter [MCZ].

Etymology: The species name *tenuicorne* refers to the long slender antennae, apparently unique within the genus.

Glypholoma rotundulum, new species

With the characters of the genus as described above.

Very convex dorsally, shape as in fig. 5, reddish-brown to dark brown or occasionally almost black, elytra with small yellow spots on alternate intervals, a slightly larger yellow spot at each humerus, and usually a still larger subapical yellow patch on each elytron. Elytra sometimes with light areas laterally, apically, or basally (or

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Fig. 51. Victoria, Australia, with dots showing locality records for *Glypholoma rotundulum*.

various combinations of these), with the normal spots obscured in these regions. Some individuals with very small yellow spots on the pronotal margins, the maximum being an anterior paramedial pair, a lateral pair, a posterior paramedial pair, and a posterior lateral pair. Dorsal surface of body with minute to short setae (as well as macrosetae on elytra), tibiae and tarsi fairly densely setose. Length: 2.5 ± 0.2 mm (2.1–3.0); width: 1.2 ± 0.1 mm (1.0–1.3) ($N = 18$).

Head capsule similar to that of *pustuliferum* (fig. 58), but epistomal suture slightly arcuate medially, with short median stem. Antennal length about 1.2 times head width, first seven antennal segments without dense pubescence, antennal club three-segmented, slightly more abrupt than in *pustuliferum* (see fig. 55). Ocellar diameter about 0.08 times head width. Labrum slightly emarginate anteriorly. Maxillary palp with fourth segment about five times as long as third, its inner side slightly swollen so that fourth segment at middle is about half again as wide as third segment.

Pronotum as in fig. 5, evenly convex except for a broad shallow depression near each posterior angle, lateral margins acute anteriorly, explanate posteriorly. Prosternum coarsely punctate, with microsculpture and median longitudinal carina. Mesosternum (see figs. 35, 37) with dense microsculpture except on the raised pentagonal mesosternal process, cavities for reception of procoxae about three-fourths the length of the mesosternum, mesosternal process extending about four-ninths of the way between mesocoxae. Metasternum convex, without microsculpture but with large punctures containing very short setae, antecoxal sutures short, extending only one-fifth the width of the metasternum. Protibia setose, slightly less spinose than that of *pustuliferum,* meso- and metatibia slightly more spinose than protibia. Hind tarsus slightly less than six-tenths as long as hind tibia, fifth segment of hind tarsus half as long as first four together. Empodial setae longer than tarsal claws.

Elytral striae impressed between punctures, intervals minutely punctate and with very short setae, in addition to the usual macrosetae on alternate intervals (see fig. 29). Pale spots (but not pustules) anterior and adjacent to macrosetae. Angle formed by elytral apices at suture slightly greater than 180° (concave posteriorly). Wings greatly reduced in nearly all specimens seen, only extending over tergite 2, and not folded at rest (see figs. 37, 41), very rarely fully or almost fully developed; anal flap present.

Abdomen with tergites 4 to 8 well-sclerotized, spiracles located in tergites of segments 5 to 8, at edge of tergite 4; paratergites clearly present and distinct on segments 4 to 6, sutures between sternite and paratergites lacking on segment 3; segment 7 with sutures between sternite and paratergites fading out posteriorly. Tergite 4 with small paired patches of medially-directed microtrichia (see fig. 41), tergite 5 with or without even smaller transverse patches of same near posterior edge. Transverse fold on sternite 3 about one-half width of sternite. Sternite 8 with anterior projection as in fig. 65.

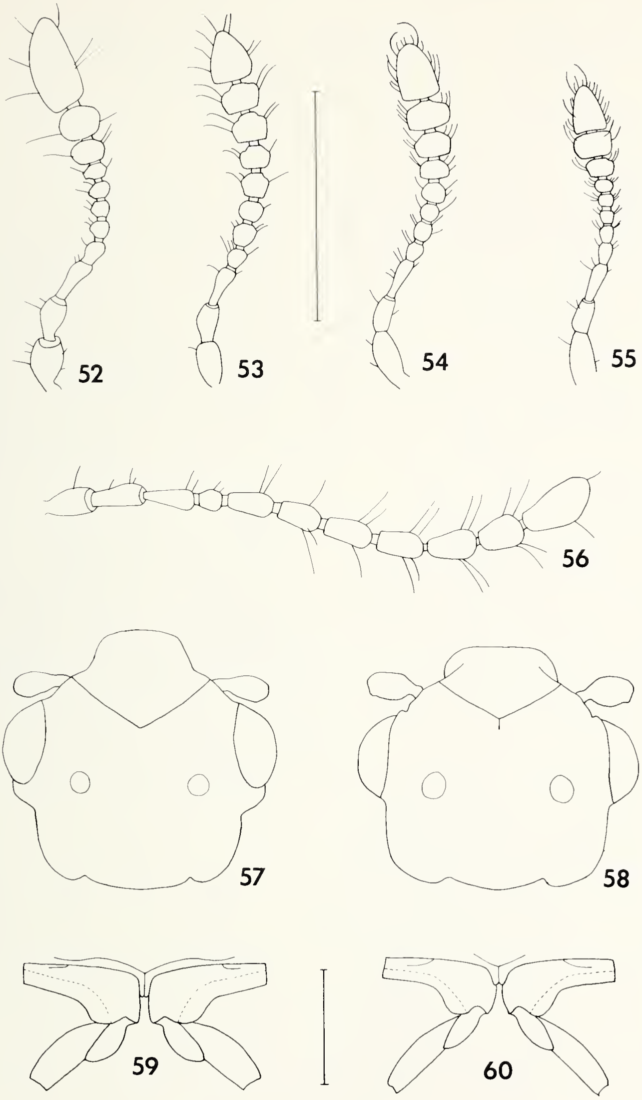
Male: Spatulate setae on protarsus as in fig. 25, five pairs on first segment, two pairs each on second and third segments, on first two segments of mesotarsus, similarly to fig. 39, but with five on the first segment and two on the second; genital segment and aedeagus as in figs. 74, 75, 78, 79.

Female: Genitalia very similar to those of *G. pustuliferum,* distal gonocoxites relatively slightly thicker.

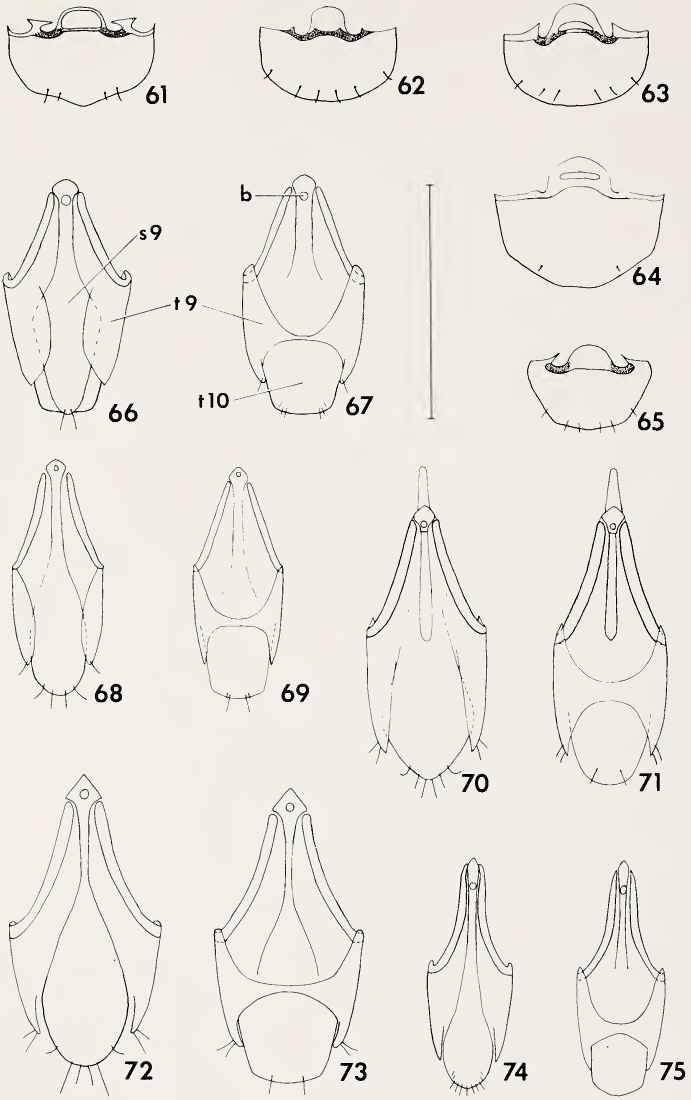
Distribution: see map (fig. 51).

Holotype (♂): AUSTRALIA: Victoria: Belgrave, F. E. Wilson, 22–5–29/Fallen leaves/F. E. Wilson Collection [NMVM].

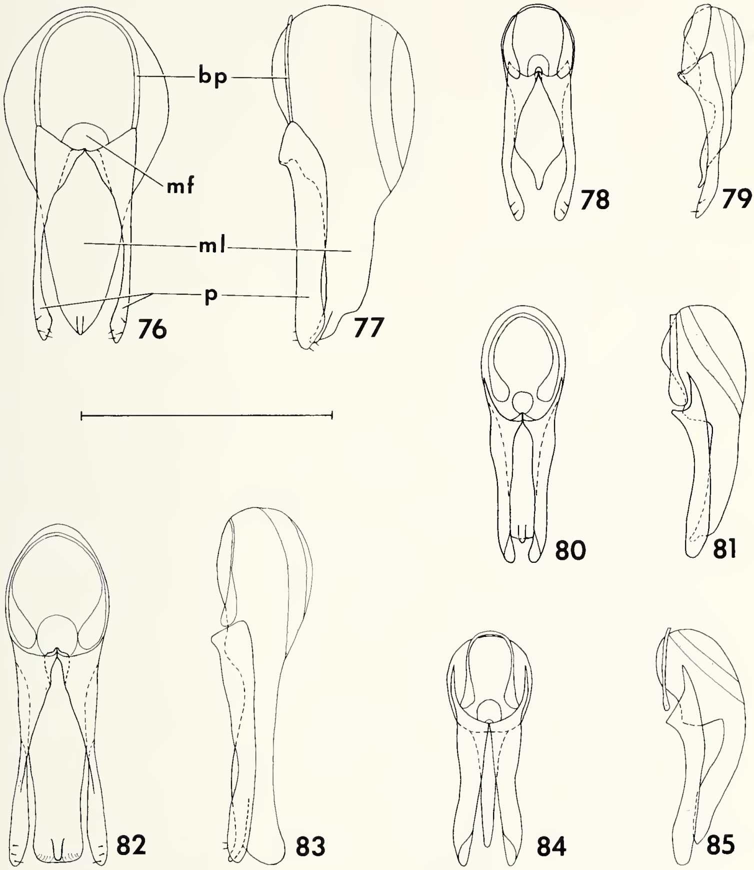
Paratypes: AUSTRALIA: Victoria: Warburton, F. E. Wilson, 4080 feet/in tussocks/F. E. Wilson Collection (3 ♂) [NMVM]; Mt. Baw Baw, summit, etc., Mar. '58, Darlington (1 ♂) [MCZ]; Warburton, Mt. Donna Buang, 1200 m, IV.28-V.7.1978, carrion traps, *Nothofagus* forest, S. B. Peck (79 ♂, 104 ♀) [ANIC, ANMT, CAS, CNC,



Figs. 52–60. *Glypholoma* spp. 52–56. Right antenna, dorsal view; 52, *G. pecki;* 53, *G. temporale;* 54, *G. pustuliferum;* 55, *G. rotundulum;* 56, *G. tenuicorne.* 57–58. Head, dorsal view; 57, *G. temporale;* 58. *G. pustuliferum.* 59–60. Metacoxae and metasternal antecoxal sutures; 59, *G. temporale;* 60, *G. pustuliferum.* Scale lines = 0.5 mm; upper one applies to figs. 52–58, lower one to figs. 59–60.



Figs. 61–75. *Glypholoma* spp. 61–65. Abdominal sternite 8, ventral view; 61, *G. pustuliferum;* 62, *G. pecki;* 63, *G. temporale;* 64, *G. tenuicorne;* 65, *G. rotundulum.* 66–75. Male genital segment, ventral and dorsal views, respectively; 66–67, *G. pustuliferum;* 68–69, *G. pecki;* 70–71, *G. temporale;* 72–73, *G. tenuicorne;* 74–75, *G. rotundulum.* b = internal cylindrical "button"; s9 = sternite 9; t9 = tergite 9; t10 = tergite 10. Scale line = 0.5 mm.



Figs. 76–85. *Glypholoma* spp., aedeagus (*in situ*), dorsal and right lateral views, respectively. 76–77, *G. tenuicorne;* 78–79, *G. rotundulum;* 80–81, *G. pecki;* 82–83, *G. temporale;* 84–85, *G. pustuliferum.* bp = basal piece; mf = median foramen; ml = median lobe; p = paramere. Scale line = 0.5 mm.

FMNH, MCZ, NMVM, SBP]; Warburton, Acheron Gap, 750 m, VI.27–30.1978, Ber.u.log bark *Euc.* + *Notho.,* S. B. Peck (2♂, 6♀) [SBP]; same locality, IV.28-V.7.1978, carrion trap, *Nothofagus* forest, S. B. Peck (4♂) [ANMT]; Tara Valley N.P., 450 m, V.10–17.1978, carrion traps, S. & J. Peck (4♂, 8♀) [ANMT]; Bulga N.P., 550 m, V.10–17.1978, carrion traps in *Nothofagus* ravine, S. & J. Peck (11♂, 12♀) [ANIC, ANMT, CNC, SBP]; same locality, V.17.1978 Ber. fungi on logs and stumps, S. & J. Peck (7♂, 5♀) [SBP]; Mt. Buffalo N.P., 1300 m, IV.22–26.1978 carrion trap, S. & J. Peck (2♂) [ANMT]; same locality, 500 m, IV.24–27.1978, wet sclerophyll forest, creek: carrion, S. B. Peck (1♀) [MCZ]; Victoria? /ex C. Oke Collection, no locality (2♂, 2♀) [NMVM].

Habitat: Ecological data are available for all but five of the 252 specimens of this species seen. Of these, 225 specimens were collected in carrion traps or at carrion (six collections), twelve from fungi on logs and stumps (one collection), eight under bark of *Eucalyptus* and *Nothofagus* logs (one collection), three in tussocks (one collection), and one among fallen leaves (presumably loose ground litter). Most of the specimens were collected in *Nothofagus* forest, and in general *Glypholoma rotundulum* seems to occur in habitats similar to those of *G. pustuliferum,* but nothing is known about the feeding habits of this species, either. These beetles seem to be notably cold-adapted. The largest collection (183 specimens) was taken in carrion traps set in snow-covered ground (S. B. Peck, pers. comm.), across which the flightless beetles must have walked.

Wing polymorphism: All specimens examined are brachypterous except the three from Mt. Buffalo, the northernmost recorded locality for the species. One of these specimens (♂) has fully-developed wings and the other two (♂♀) have wings sharply reduced beyond the costal hinge.

Etymology: The species name *rotundulum* (diminutive of *rotundum,* round) refers to the great convexity and small body size of the members of this species.

DISCUSSION

We believe that the five species here included in *Glypholoma* form a monophyletic group (in the strict, Hennigian sense) which can be defined on the basis of these characters which we presume to be uniquely derived or synapomorphic within Omaliinae: excavate hind coxae with "retractile" hind femora, each elytron with eleven more or less distinct striae, and male genital segment with a small "button" internally near the anterior end of sternite 9. Some of the species here included in *Glypholoma* have characteristics, such as the filiform antenna of *tenuicorne* and mesosternal structure of *rotundulum,* that might conventionally be used to justify the erection of new genera. Because the south temperate omaliine fauna is relatively poorly known, we feel that the use of a conservative generic concept is best at present, since this will possibly reduce the need for nomenclatural changes at the generic level as the full range of variation within the south temperate fauna becomes better known. A need for the creation of more genera may become apparent eventually; judgment of this is best reserved until at least a large proportion of the fauna (rather than the present fragments) is known.

Although not enough information is available to allow formulation of a complete phylogenetic hypothesis, a few comments can be made concerning probable relationships among the species of *Glypholoma.* Each species can be defined by an autapomorphous trait, as follows: *tenuicorne,* elytral striae not impressed between punctures; *rotundulum,* raised pentagonal mesosternal process; *pecki,* elongate antennal segment 11; *temporale,* bulging temples; and *pustuliferum,* coarsely punctured and rugose prosternum. All species but *tenuicorne* have clavate antennae (instead of filiform, which is presumably more primitive within Staphylinids) in common, and within this subgroup, *pustuliferum* and *temporale* share the apparently derived condition of raised pustules on the elytral intervals. No synapomorphies have been discovered yet which clarify the relationships among these four species any further. The availability of more material for detailed study of the three new South American species described in the present paper, and the discovery of immature stages or biological information for any species, might allow the discovery of additional synapomorphies and the development of a complete phylogenetic hypothesis.

The position of *Glypholoma* within the Omaliinae is somewhat ambiguous, largely because relationships within the subfamily as a whole are not very well worked out, especially the extra-Holarctic representatives of the subfamily. A majority of the characters distinguishing *Glypholoma* from most or all other Omaliinae are characters exhibiting plesiomorphic states in *Glypholoma.* This suggests, at least, that *Glypholoma* is a relatively primitive member of the subfamily and branched off early in the evolution of the Omaliinae. The close relationship of *Glypholoma* to the Holarctic *Anthobium*-group (viz., *Anthobium, Camioleum, Deliphrum, Mathrilaeum, Olophrum*) suggested by Scheerpeltz (1972) and Newton (1975) mainly on the basis of general habitus does not seem to be supported by more detailed evidence gathered to date. There are several characters for which the members of the *Anthobium*-group share what we believe are derived character states within the Omaliinae, and *Glypholoma* shows what we believe to be primitive character states. These characters appear in the *Anthobium*-group as follows: presence of a sharp post-ocular ridge, absence of the epistomal suture, gular sutures very close together or partly fused, presence of lateral foveae on the pronotum with internal pillars connecting dorsal and ventral surfaces of pronotum, and female genitalia with the proximal gonocoxites fused. We feel that this assemblage of differences constitutes strong evidence against a close relationship between *Glypholoma* and the *Anthobium*-group. Unfortunately any more precise statement concerning the placement and relationships of *Glypholoma* must await future clarification of the evolution and higher classification of the Omaliinae as a whole. In the meantime, tarsal, palpal, and mandibular characters dictate placement of *Glypholoma* in the heterogeneous tribe Anthophagini. If a family-group name is eventually needed for *Glypholoma,* the name Glypholomini Jeannel 1962 is available.

The presence of two of the species of *Glypholoma* (*pustuliferum* and *rotundulum*) is strongly correlated with cool moist temperate forests dominated by *Nothofagus;* the other three species have been collected only within the *Nothofagus* zone of southern South America. The fact that each of the latter species is known only from a single small collection suggests that they may differ significantly from *rotundulum* and *pustuliferum* in their biology or ecological preferences. The disjunct southern temperate distribution of the genus is similar to those of some other isolated and apparently archaic groups of staphylinoids, some of whose ranges include New Zealand as well as southern South America and Australia. The occurrence of *Glypholoma* in New Zealand *Nothofagus* forests would not be wholly unexpected.

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AGGREGATIONS OF *MALLOS* AND *DICTYNA* (ARANEAE, DICTYNIDAE): POPULATION CHARACTERISTICS

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Introduction

Generally web spiders are solitary animals. Usually only a single spider occupies a single web, with the relatively common exception of webs jointly occupied by a male-female pair or females with their young. In most species, occupied webs are usually not connected to other occupied webs by silk lines. However, aggregations of various types and degrees occur in some species (reviewed by Buskirk, 1975; Krafft, 1970; and Shear, 1970). These include cases in which occupied webs are in close proximity (sometimes touching), but occupied by single spiders, as well as cases in which single webs are occupied by groups of spiders of all sex/age classes. The species involved are sometimes referred to as "social spiders" (e.g., Burgess, 1978; Kullmann, 1972). At present relatively little is known about the social adaptations of these spiders. Some of the first things we would like to know about animals that occur in aggregations are the size, composition and spacing characteristics of naturally occurring groups. Data concerning these basic social characteristics will be presented in this paper for several species of dictynid spiders.

The Dictynidae are a group of web-building cribellate spiders, most of which have body lengths less than 5 mm. In the closely related genera *Mallos* and *Dictyna,* there are species with different types of social organization. Most are solitary; at least three are communal, territorial; and at least one is communal, non-territorial. Each individual web of a solitary species consists of a mesh in which prey is captured and a nest within the mesh. Communal, territorial

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species (*M. trivittatus* Banks, *Dictyna calcarata* Banks, *D. albopilosa* Franganillo) live in web complexes. Web complexes consist of variable numbers of web units, each consisting of a nest and a mesh; and web units are connected to each other by strands of silk in the interstitial web. Evidently, web units are treated by the occupants as defended territories (Jackson, 1978a). In the communal, non-territorial species (*M. gregalis* Simon), groups of spiders live in communal webs which consist of surface sheets with holes leading into the interior. The interior contains nests, tunnels and supporting lines connecting the sheet with the substrate beneath (see Burgess, 1976; Diguet, 1909a, 1915). Communal webs are not divided into defended units as in web complexes. More detailed information concerning social organization, web characteristics, and habitats is provided elsewhere (Jackson, 1978a).

METHODS

DATA FROM NATURAL POPULATIONS

For census areas, locations were chosen which seemed to have particularly high densities of spiders. The census areas for *Mallos niveus* O. P. Cambridge were one-dimensional (horizontal lines). All other census areas were rectangular. For *D. calcarata* and Censuses 3–6 for *M. trivittatus,* complete web complexes of relatively small size were used; and the boundaries of the census areas were chosen to closely correspond to the edges of the web complexes. The distance from each spider in the complex to the nearest conspecific in the vicinity but not in the complex was greater than twice the diameter of the complex in each of these census areas. For Census No. 1 and 2 for *M. trivittatus,* each area censused was part of a large web complex.

The corners of each census area were marked with pieces of tape. Each web or web unit was completely searched, a process that destroyed the web unit. The occupants of the units were recorded; and a piece of tape, with a code number, was placed at the location of each occupied nest before it was destroyed. The distance of each of these nests to its nearest neighboring nest was measured.

The exact locations of spiders on the sheet and interstitial webs proved excessively difficult to measure accurately. This was because they were frequently obscured from view by silk and debris; and the process of locating spiders inevitably disturbed them, leading to changes in their positions before they could be recorded. Only the component of the web (nest, mesh, interstitial web) occupied by the spider could be recorded with confidence. When counting the number of spiders per web unit, those in the interstitial web were included in the record of the web unit to which they were in closest proximity.

Spacing and density data were not collected for *D. albopilosa.* The web complexes of this species were particularly difficult to disassemble in the field because they were three-dimensional and located on the leaves, stems and roots in dense growths of herbaceous plants. Those of *D. calcarata* and *M. trivittatus,* in contrast, were two-dimensional and usually built on more accessible flat surfaces.

At San Anton Falls (Morelos, Mexico), 23 occupied web units of *D. albopilosa* were searched, and the occupants were recorded, with no attempt to assess density or spatial relations. In addition to the spiders in the census areas, the occupants of another 48 web units of *D. calcarata* and 152 of *M. trivittatus* were recorded. Each of these was in the general vicinity of the census areas.

Data for *M. trivittatus* were collected in June; those for *M. niveus, D. calcarata,* and *D. albopilosa* were collected in September. These species seem to feed predominantly in the late afternoon and early evening (Jackson, 1977a). Data in this study were collected at mid-day, when the spiders were less active.

LABORATORY STUDIES — *Mallos gregalis*

In the laboratory, *M. gregalis* in large communal webs were maintained on a diet of houseflies (*Musca domestica*), provided at approximately 5-day intervals. Temperature was maintained at approximately 24° C, and the light cycle was approximately 13 L: 11D. These large colonies were begun from fewer than 200 spiders collected by Burgess (see Burgess, 1976) in Guadalajara, Mexico, 3 yr previous. The webs in the laboratory were on plants and other objects, and they were not enclosed.

Two census methods were used. 1. Small discrete communal webs and relatively discrete portions of larger communal webs were completely disassembled in the spring and early summer. All occupants were recorded; and the condition, structure, and size of the webs were recorded. 2. The surface of a large communal web, at least 2 years old, was censused with 30cm transects in the fall. Each transect consisted of a string laid haphazardly onto the web, and all spiders within 1 mm of the string were counted. The web was arbitrarily divided into 3 sections. Two transects were placed onto each section on each census-day; and there were 11 census days, each 2 to 3 days apart. A "census" was defined as the sum of the spiders found on the two transects on a given section on a given census-day.

CENSUS AREAS

Mallos niveus

Three aggregations of *M. niveus* were censused in Guanajaato (Guanajaato, Mexico), each under a different window sill on exterior walls of buildings in the city. The webs were arranged in horizontal straight lines, and the length of the aggregation was defined as the distance between the first web at one end and the last web at the other end (Census Area No. 1, 54 cm; No. 2, 87 cm; No. 3, 273 cm). The distance to the nearest conspecific not in the aggregation was greater than length of the aggregation in each case.

Mallos trivittatus

Census Areas Nos. 1, 2, and 3 were at East Turkey Creek in the Chiracahua Mountains (Arizona, USA). The creek passes through a 1.8 m diameter metal culvert, with an interior surface area of $88 m^2$. Almost the entire interior of the culvert was covered by a single enormous web complex. The bottom of the culvert was covered by water; and in the immediate vicinity of the water, web units were scarce. Subtracting these parts of the culvert, the web complex was conservatively estimated to be $79 m^2$ in area. Census Areas Nos. 1 and 2 were each inside the culvert, within 2 m of opposite entrances and 1.5 m above the bottom of the culvert. Census Area No. 1 was 56 cm × 50 cm; No. 2, 60 cm × 56 cm. Census Area No. 3 was a web complex (54 cm × 42 cm) 30 m from the culvert, on a large boulder (ca. 2 m high) beside the creek. The boulder was overhanging the ground, forming a shallow cave (ca. 1 m from ground to top; 0.5 m from entrance to back). The web complex was on the upper surface of the cave.

Census Area No. 4 (56 cm × 32 cm) and No. 5 (56 cm × 56 cm) were web complexes on rock ledges near Estes Park (Colorado, USA). Each was 1 to 2 m above the ground. Census Area No. 6 was a web complex (124 cm × 34 cm) on the upper surface of a shallow cave (ca. 1 m high and 1 m deep) made by an overhanging rock ledge in Big Thompson Canyon (Colorado, USA).

Dictyna calcarata

Census Area No. 1 (24 cm × 24 cm) and No. 2 (54 cm × 46 cm) were web complexes on the external walls of buildings in Chapala (Jalisco, Mexico).

RESULTS

POPULATION SIZE AND DENSITY

Densities for *M. trivittatus* and *D. calcarata* were relatively similar (Table 1). Since the *M. niveus* aggregations were linear (one-dimensional) it is problematic to compare densities in this species with the densities found in the other species. The webs of *M. niveus* in the census areas were oriented such that the shorter distance across each was vertical. The areas given in Table 1 were obtained by multiplying the length of the aggregations by 3 cm, the mean widths of *M. niveus* webs found on buildings (Jackson, 1978a). *M. gregalis* tends to live in higher densities. The webs censused by Method No. 1 (Table 2) had a mean density of 0.5 ± 0.66 spiders per cm^2 and 0.2 ± 0.14 per cm^3.

Based on many hours spent in the culvert at E. Turkey Creek, it seems that the densities obtained in Census Nos. 1 and 2 for *M. trivittatus* were representative of the large complex in the culvert. Using the mean of the two densities for spiders (14.23 per 1000 cm^2), webs (9.79 per 1000 cm^2), and occupied webs (8.79 per 1000 cm^2) as estimates for the densities for the complex as a whole, this web complex contained 10,200 spiders, 7,700 webs, and 6,500 occupied webs. This was by far the largest web complex of this or any other species in this study.

Web units of *M. trivittatus* tend to be 5 cm × 4 cm; those of *D. calcarata* tend to be 3 cm × 2 cm; and webs of *M. niveus* on walls of buildings tend to be 4 cm × 3 cm (Jackson, 1978a). In the culvert on E. Turkey Creek, the interstitial area between web units tended to be quite small, since the mean for nearest neighbor distance was not much greater than the diameter of web units (Table 1). In all other censused web complexes, web units tended to be 2 to 4 web unit diameters apart; and aggregated *M. niveus* webs tended to be 2 to 4 web diameters apart also.

Table 1. Censuses of web complexes (*M. trivittatus* and *D. calcarata*) and aggregations of individual webs (*M. niveus*) in the natural habitats of the spiders.

	Mallos trivittatus						*Dictyna calcarata*		*Mallos niveus*		
Census	1	2	3	4	5	6	1	2	1	2	3
Area (Cm^2)	2800	3360	2268	1792	3136	4216	576	2484	162	261	273
Number of Spiders	48	38	4	5	23	23	5	13	5	4	18
Number of Web Units or Webs	29	31	4	5	7	13	5	13	7	4	19
Occupancy Rate[1]	93	90	100	100	86	77	100	100	71	100	95
Density (Spiders per 1000 Cm^2)	17.14	11.31	1.76	2.79	7.33	5.46	8.68	5.23	24.70	19.20	23.20
Inter-Nest Distance[2]	6.11	5.43	22.25	12.80	10.50	12.00	7.40	9.15	7.20	4.00	6.39
	±0.68	±0.50	±3.35	±2.58	±2.33	±2.99	±1.12	±1.15	±1.32	±1.15	±0.93

[1] No. of web units (or webs) occupied by dictynids/total No. of web units (webs) × 100.

[2] Mean ± S.D. for distance between each nest and the nearest neighboring nest. Only occupied nests considered.

Some of the larger communal webs of *M. gregalis* in the laboratory had surface areas and volumes estimated to be as large as 1300 cm^2 and 1500 cm^3. If the densities in these large webs were comparable to those in smaller webs, they can be estimated to have contained 300 to 700 spiders. Based on the descriptions of Diguet (1909a, b) and Burgess (1976), 4 m^2 will be used as an approximate estimate for the surface area of larger communal webs on trees in Mexico. If densities in nature are comparable to those in the laboratory then these very large webs may have contained as many as 20,000 spiders.

WEB OCCUPANTS

Solitary species, including *M. niveus,* usually occurred one spider per web (Jackson, 1978a), and this was true of all censused webs in the aggregations of *M. niveus.* However, each occupied web unit of the three communal, territorial species usually contained a set of several spiders. These could be almost any combination of females, males, and immatures of varied sizes (Table 3), except that web units were never shared by two adults of the same sex. In the only instances in which male-male or female-female pairs were seen together in the same web units, aggressive interactions took place, after which one individual departed. In contrast, large numbers of *M. gregalis* belonging to all sex/age classes shared the same communal webs without aggressive behavior or cannibalism.

DISTRIBUTION OF WEB OCCUPANTS

Large proportions of each sex/age class of *M. trivittatus* occupied the nests (Tables 3 and 4); but adult females were especially prone to be inside nests, and there was a preponderance of immatures in the interstitial web. These data were consistent with more casual observations of *M. trivittatus* in other locations and of the other communal, territorial species. During the day, *M. niveus* and other solitary species were most often, but not always, inside nests. All *M. niveus* in censuses were inside nests.

Many hours of casual observation in the laboratory gave the impression that adult males and immatures of *M. gregalis* were more prone to be on the outer surfaces of webs, and females were more prone to be in the interior. (Data related to this will be presented below.)

Table 2. Data from complete disassembly of 19 *M. gregalis* webs or subunits of webs (census Method No. 1, see text). Area and volume are estimates, since borders of webs were irregular. Small immature: ca. 1 mm in body length (color: uniformly brown). Large immature: body length ca. 2 mm (gray markings present on body). Adult females: ca. 3 mm. Adult males: ca. 3 mm. Web class A: 3-D and lacking evidence of deserted areas. B: 3-D and containing conspicuous deserted areas. C: 2-D and lacking conspicuous deserted areas. D: 2-D (but not as flat as C) and containing conspicuous deserted areas. E: 3-D, small discrete web on irregular substrate. A-D: census areas were subunits of large webs, except for some of C that were discrete webs. 3-D: web occupies relatively much space in each of 3 dimensions. 2-D: web confined predominately to 2 dimensions ("flat"). "Deserted" areas: no longer occupied by *M. gregalis,* not substantially adhesive, and covered by fly carcasses and dust. Note: as population size increases, composition of population shifts toward decreasing percentages of females and increasing percentages of immatures. Kendall rank correlation (Sokal and Rohlf, 1969) for increasing percentages of small immatures with increasing population size ($P < 0.001$).

					Sex/Age Class Composition (%) of Population			
Population	Area (cm^2)	Volume (cm^3)	Web Class	Population Size	Adult Female	Adult Male	Large Immature	Small Immature
1	144	144	C	5	60.0	0.0	20.0	20.0
2	144	144	C	7	71.4	0.0	14.2	14.2
3	105	300	C	9	0.0	11.1	44.4	44.4
4	150	300	D	10	90.0	10.0	0.0	0.0
5	144	144	D	10	30.0	0.0	10.0	60.0
6	75	150	B	11	27.3	0.0	27.3	45.4
7	70	150	B	21	19.0	0.0	19.0	61.0
8	70	350	A	23	65.2	17.4	17.4	0.0
9	150	150	B	25	4.0	4.0	8.0	84.0
10	70	350	A	27	48.2	18.5	7.4	25.9
11	144	144	C	31	12.9	0.0	0.0	87.0
12	70	350	E	34	11.7	5.8	32.3	50.0
13	64	320	B	40	27.5	0.0	40.0	32.5
14	150	600	A	47	23.4	6.3	21.3	48.9
15	155	155	D	53	32.1	0.0	20.7	47.2
16	100	300	A	74	17.5	1.3	22.2	55.4
17	400	800	A	82	9.7	2.4	7.3	80.4
18	45	225	A	114	7.0	0.0	12.3	80.4
19	150	600	A	288	9.3	2.0	9.7	78.8

SEX/AGE CLASS RATIOS

Based on the spiders in the two censuses in the culvert at E. Turkey Creek, this large web complex was estimated to have had a population consisting of 27% adult females, 9% adult males, and 64% immatures. The adult sex ratio (Male:Female) was approximately 1:3. Based on the censuses at Chapala, populations of *D. calcarata* in web complexes on buildings were composed of 14% adult females, 5% adult males, and 81% immatures; and the adult sex ratio was 1:3, as for *M. trivittatus.* No males were found in the censuses of *M. niveus.* Generally only small numbers of males of the solitary species were found, and these were predominantly ones in webs with females (Jackson, 1977b).

Based on the 19 censuses of *M. gregalis* by Method No. 1 (disassembly), population composition was 29.8 ± 25.49% adult females, 4.1 ± 5.97% adult males, 17.6 ± 12.17% large immatures, and 48.2 ± 27.41% small immatures. Immatures comprised a greater proportion of the spiders in webs with large population size (Table 2). The average adult sex ratio was approximately 1:7. For the 33 transect censuses (Method No. 2), population composition was 12.3 ± 7.44% adult females, 3.0 ± 3.85% adult males, 38.0 ± 12.96% large immatures, and 46.2 ± 13.11% small immatures (adult sex ratio, ca. 1:4), with a total of 16.8 ± 2.34 spiders occurring in each census. The three sections of the web were comparable.

DISCUSSION

AGGREGATION SIZE AND DENSITY — EVOLUTIONARY CONSIDERATIONS

The occurrence in certain areas of very large populations of some species, especially *M. gregalis* and *M. trivittatus,* and the great densities of spiders within these populations contrast markedly with the majority of *Dictyna* and *Mallos* species. Most species are solitary, with individuals living in relatively widely spaced individual webs on stems and leaves of vegetation (Jackson, 1978a); and although density censuses were not carried out for these, our impression is that an area of 50 to 100 m^2 in a population of a solitary species would usually contain fewer than a dozen individuals. In contrast, the largest web complex of *M. trivittatus* occupied approximately this much space and contained more than 10,000 individuals.

A related comparison can be made by looking at the amount of web area or volume per individual spider for different species. There is a trend toward decreasing web surface per spider as one goes from solitary to communal species. Individual webs of solitary species tend to have a surface area of 35 cm^2 (Jackson, 1978a). Since each web unit in web complexes of communal, territorial species tends to contain 2 or 3 spiders (Table 3), and since web units tend to have a surface area of 4 to 21 cm^2 (Jackson, 1978a), there tends to be 1 to 7 cm^2 of surface area per spider in these species. In the laboratory, in communal webs of *M. gregalis,* there tends to be a surface area of 2.1 cm^2 and a volume of 6.4 cm^3 of web per spider. (Volume was not calculated for other species since their webs tended to be largely 2-dimensional; Jackson, 1978a.)

The influence of prey availability on these trends deserves attention. Diptera of the same approximate size relative to the spider seem to predominate in the diet of species of *Dictyna* and *Mallos*

Table 3. Percentages of web units (in web complexes) occupied by different sex/age class combinations. Data based on nests alone (*M. trivittatus*) given in parentheses. More than one immature sometimes occurred together in same web unit. More than one adult of same sex never occurred together. N: No. of web units sampled, including ones in Table 1 plus others (ones not occupied by dictynids excluded).

	M. trivittatus	*D. calcarata*	*D. albopilosa*
Females[1]	33.33 (34.15)	30.30	39.13
Males[1]	7.58 (4.07)	24.24	21.74
Immatures[1]	84.09 (75.61)	77.24	65.22
Female Only	14.39 (20.33)	7.58	21.74
Male Only	0.76 (1.63)	9.09	8.70
Immatures Only	61.36 (61.79)	56.06	47.83
Female plus Immatures Only	16.67 (13.82)	12.12	8.70
Female plus Male Only	0.76 (0.00)	9.09	8.70
Male plus Immatures Only	4.55 (2.44)	7.58	8.70
Female, Male, and Immatures	1.52 (0.00)	1.52	0.00
No. of Spiders per Web Unit[2]	3.1 ± 4.83 (20)	1.6 ± 0.91 (4)[3]	1.3 ± 0.47 (2)[3]
N	132 (123)	66	23

[1] Regardless of other sex/age classes present.

[2] Mean ± S.D. (maximum).

[3] Larger maxima were seen during more casual observations.

(Jackson, 1977a). Thus large prey populations would seem necessary to support some of the larger aggregations of dictynids. Diguet (1909a, b, 1915) and Burgess (pers. comm.) noted numerous adult Diptera in the vicinity of *M. gregalis* webs in Mexico during the rainy season. Studies are needed to determine whether Diptera populations are larger and/or more predictable in habitats containing communal webs of *M. gregalis* compared to neighboring areas without communal webs. Great numbers of Diptera were noted in the metal culvert in Arizona that contained the enormous web complex of *M. trivittatus.* Another consideration in this case is that flies entering the culvert may be especially vulnerable to capture, since inside the culvert they were almost completely surrounded by web. Great masses of nematocerous flies were active in the vicinity of web complexes of *D. calcarata* in Chapala, emerging from nearby Lake Chapala in the late afternoon and early evening. Diptera were also numerous in the vicinity of web complexes of *D. albopilosa* at San Anton Falls. In general, wherever there were web complexes, there were also numerous Diptera.

However, the question of why some species live in large, dense populations, while others do not, cannot be answered simply on the basis of prey densities in the habitats of different species. Riechert and Tracy (1975) have shown relationships between density within spider populations and prey availability. However, they found prey availability to depend not only on the absolute abundance of prey but also on factors that influence how the spider experiences prey abundance, especially its thermal relations with its environment.

Another consideration is that species of *Dictyna* and *Mallos* with differing aggregating tendencies may occur side-by-side in the same habitats (Jackson, 1978a). For example, *M. niveus* were found in individual webs on the same trees with web complexes of *M. trivittatus* in the Chiracahua Mountains. It would seem that dictynid species that routinely occur in aggregated states (communal, territorial and communal, non-territorial) and those that generally live more widely dispersed (solitary) are somehow adapted to exploit different sets of resources, but we have no clear insights at this time concerning what these different resources might be.

The adaptive advantages and disadvantages for animals related to living in groups have been subjects of considerable interest in recent years (see Wilson, 1975). For a review of ideas concerning spiders,

Table 4. Distribution of sex/age classes of *M. trivittatus* within web complexes. Based on occupied web units. No. of spiders: means ± S.D. Females, Immatures, Males: percentages of the total found for each that were in each part of the web complex. Total: Number of spiders — mean ± S.D. for spiders — per web unit (spiders in interstitial web included with nearest web unit); Females, Immatures, Males — percentage of total number of spiders belonging to each sex/age class.

	Number of Spiders	Females	Males	Immatures
Inside Nest	1.5 ± 1.88	93.33	50.00	52.49
Inside Mesh				
Less than 2 cm from Nest	0.1 ± 0.47	6.67	30.00	4.32
More than 2 cm from Nest	0.1 ± 0.38	0.00	20.00	5.98
Inside Interstitial Web	0.9 ± 2.19	0.00	0.00	37.21
Total	3.1 ± 4.83	12.64	2.81	84.55

see Buskirk (1975) and Lubin (1974). With the dictynids, we need to compare the varied species with respect to the importance of each potential advantage and disadvantage, given the nature of the resources each species exploits.

PHENOLOGY

Most *Dictyna* and *Mallos* probably have an annual life cycle in nature, with adult females and males present during spring, summer and/or fall (Chamberlin and Gertsch, 1958). The mating season for *Mallos* species generally seems to be later than that of *Dictyna* species, although the season for some species may last many months. Since both adult males and adult females were found, evidently each census was carried out during the mating season of the species involved, although not necessarily during the peak of the season for all species. No doubt, if censuses had been undertaken at different times of the year, different ratios of each sex/age class would have been found for each species.

Seasonal changes in the ratios of the different sex/age classes in laboratory populations of *M. gregalis* apparently occur, although data have not been collected. Each sex/age class was found throughout the year, but males were less numerous in winter than in other seasons. The differences in adult sex ratios in the two types of censuses of *M. gregalis* may be a reflection of the tendency, noted during casual observation, for females to predominate in the interior of webs, with males predominating on the exterior. However, another factor that must be considered is that the two types of censuses were made at different times of the year, and differences may be influenced by phenology.

CAUSES OF DISTRIBUTION PATTERNS WITHIN WEBS

In all species, eggs tend to be oviposited in the vicinity of the nests, and the tendency for females to be found in nests is probably at least partly related to this. Also, nests may be optimal resting sites with respect to protection from predators and parasites (Jackson, 1978a). If obtaining space within a nest is accompanied by aggressive behavior, which seems likely in the communal, territorial species, then females may have an advantage related to their larger size. Females in each species have the largest body size of any sex/age class. Compared to males, females may be more sedentary; and a stronger tendency to occupy nests may be related to this. This might also apply to comparison of females with immatures if the immatures are the dispersal phase in the life histories of these species. Also, by virtue of their smaller size, young immatures may be safer from predation on the mesh or interstitial web than females, since they might take refuge under strands of silk, particles of debris, etc., which are too small to be effective for females. As a result, there might be lesser selection pressure against immatures that remain outside nests compared to larger females that remain outside nests.

Since females seem to be prone to be in the interior of webs of *M. gregalis,* we might expect males to spend considerable time searching for and courting females in the interior of webs. Instead, more males seem to be on the exterior surfaces of the webs. In *M. gregalis,* unlike *M. trivittatus* and *D. calcarata,* the presence of females and silk spun by females are not releasers of courtship behavior. Instead, males seem to have an advertising routine, as part of their daily activity pattern, in which they perform behavior referred to as "pluck-walking." Females seem to indicate their receptivity to pluck-walking males by failing to run away (Jackson, 1978b). We do not know the factors that determine female receptivity, but perhaps receptive females are more likely to be on the outer surfaces of webs. For example, females might be unreceptive near the time of oviposition, and oviposition takes place in the interior of the web. Although the difficulty of observing behavior of spiders in the interior of webs should be kept in mind, it is of interest that the majority of observed instances of pluck-walking involved males on the surfaces of webs.

We have no information at this time concerning how new communal webs are formed by *M. gregalis.* One possibility is that new webs are founded by single adult females or by groups of several adult females. In the laboratory web censuses (method 1), the webs with fewer spiders (predominantly adult females) may have been ones that were newly founded. Those with more spiders and a greater proportion of smaller immatures may have been older webs in a period of rapid growth. Further study, especially in the natural habitats of these spiders, is necessary. Information is also lacking on the formation of web complexes by *M.trivittatus* and *D. calcarata.*

CAUSES OF SKEWED SEX RATIOS

The causes of the relative rarity of males in all species investigated are unknown. We do not know the sex ratios at hatching. If maternal investment in progeny of the two sexes is equal, we would expect a 1:1 ratio (Fisher, 1930; but see Hamilton, 1967; Trivers and Willard, 1973). There are a number of factors that might skew the adult ratio in favor of females even if the ratio at hatching is 1:1. Earlier studies (Jackson, 1978b) suggested that adult males of solitary and communal, territorial species are relatively nomadic, expending considerable time and energy wandering about searching for females. As a result, a sizeable proportion of the males in populations of these species might not be found in censuses of webs. Also, the nomadic character of males might subject them to earlier mortality from predation, starvation, and other factors. Shorter male longevity would skew the adult sex ratio in favor of females. However, mortality factors such as predation would seem less important for *M. gregalis* populations in the laboratory; yet the sex ratio was skewed in favor of females here also, suggesting that mortality factors of a more intrinsic nature might be involved. Females of each investigated species oviposited several batches of eggs over a period of time. In contrast to females, males may be adapted to a lifestyle that emphasizes courtship, mating, and searching for females, in conjunction with greater vagility and smaller size, at the expense of maintenance functions that would serve to prolong survival.

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SUMMARY

Three types of social organization and three corresponding types of webs occur in the Dictynidae: solitary (individual webs); communal, territorial (web complexes); communal, non-territorial (communal webs). Solitary (*M. niveus*) and communal, territorial (*M. trivattatus, D. calcarata,* and *D. albopilosa*) species were censused in nature; for *M. gregalis* (communal, non-territorial), free-living populations in communal webs in the laboratory were censused. Web surface area per spider decreases as one goes from solitary (ca. 35 cm^2) to communal, territorial (ca. 10 cm^2) to communal, non-territorial (ca. 2 cm^2) species. Very large populations may occur on single web structures of communal species (estimates of maxima: *M. trivittatus,* 10,000 spiders; *M. gregalis,* 20,000). There is a tendency for adult females to occupy nests and the interior of webs, with males and immatures occupying the exterior and the interstitial areas. Sex ratios (male:female) are skewed in favor of females (*M. gregalis* 1:7; communal, territorial species, 1:3; males of solitary species are infrequently found).

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A SOLITARY WASP THAT PREYS UPON LACEWINGS (HYMENOPTERA: SPHECIDAE; NEUROPTERA: CHRYSOPIDAE)*

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The tendency of solitary wasps to restrict predation to members of specific groups of arthropods is well known. There are several hundred records for diverse species of *Bembix,* for example, which suggest that all Northern Hemisphere species of this genus prey only upon Diptera. This includes 16 of the 19 species occurring north of Mexico; the remaining three have remained unstudied. Two of these, *gillaspyi* Evans and Matthews (1968) and *frommeri* Bohart (1970) were described only recently, while the third, *stenebdoma* Parker (1917) was described long ago but has remained one of the most infrequently encountered members of the genus. Although *stenebdoma* was placed in the *belfragei* species-group by Evans and Matthews (1968), largely on the basis of the partially preserved ocellar lenses, the species fits poorly in that group on most features and in fact is unique in the genus in having the first intercubital vein straight rather than angulated. Evidently this species is also unique in the genus, indeed among all digger wasps, in that the prey consists of lacewings (Chrysopidae).

The use of Neuroptera is not, however, unknown among Bembicini. Evans and Matthews (1973) presented a record of the Australian species *Bembix wilcannia* Evans and Matthews preying upon adult ant lions (Myrmeleontidae), and Alcock (1975) found *Xerostictia longilabris* Gillaspy preying upon adult ant lions as well as flatid buds in southern Arizona. Thus the record of *Bembix stenebdoma* using Chrysopidae seems less unusual than it would have seemed a few years ago. Why this species appears so rare when it has apparently entered a new and unexploited adaptive zone remains a mystery.

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My observations on *B. stenebdoma* involve a single female seen plunging into an open hole in a small draw 1.5 km SW of Bernardo, Socorro Co., New Mexico, at 1000 hours on 2 August 1978. The soil in this area was coarse, stony, and hard, with sparse desert vegetation, but the draw was sandy and bordered by *Croton* plants which were in bloom and attracting many bees and wasps. Despite several hours of intensive collecting in this area by Kevin M. O'Neill and myself, we took no other specimens of *B. stenebdoma.*

This female was captured as she left the nest, and the nest was excavated. Burrow diameter was about 8 mm, and there was no obvious mound of soil at the entrance. The burrow was straight and oblique, 30 cm long, terminating in a single cell at a vertical depth of 20 cm. The cell was horizontal, 10 mm in diameter by 20 mm in length. It contained 10 paralyzed lacewings, all lying on their sides with their heads facing the entrance to the cell. The egg of the wasp had been laid on the side of one of the lacewings deep in the cell. The egg was elongate and curved, measuring 2.2 mm in length; it was

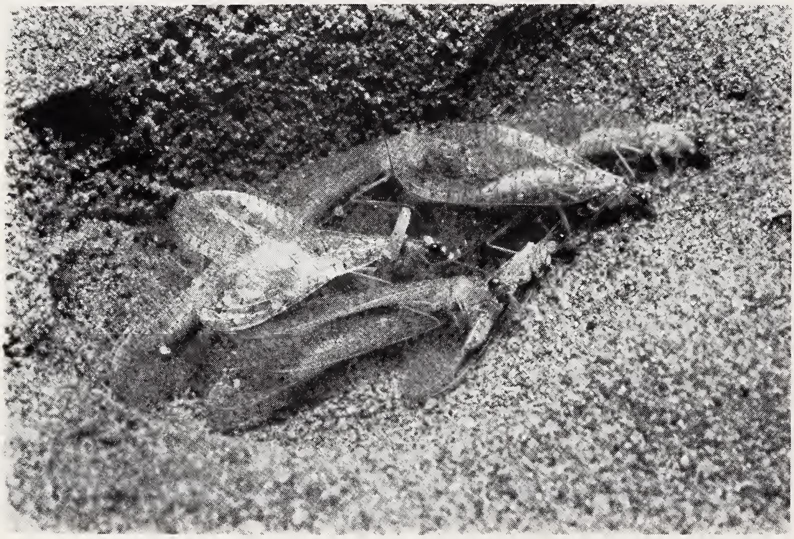

Figure 1. Prey and egg of *Bembix stenebdoma.* The cell contents have here been removed to an artificial cell and the lacewing bearing the egg moved to the top of the pile for purposes of photography.

attached between the middle and hind coxae of the prey and extended over the wing base and well above the dorsum (Fig. 1).

This egg position is similar to that of many *Bembix* which prey upon flies. That there were 10 prey in the cell, with the female still provisioning, indicates that this species mass-provisions its cells. Mass provisioning is uncommon in *Bembix, B. hinei* Parker being the only other North American species for which this has been reported (Evans, 1957).

The lacewings proved to belong to three species: *Eremochrysa tibialis* Banks (2), *E. punctinervis* (McLachlan) (5), and *Chrysoperla comanche* (Banks) (3) (det. Phillip A. Adams). Dr. Adams writes that all three species are common in the Southwest. Although some Chrysopidae release odorous substances from thoracic glands, this is not notably true of members of these genera. It will be of interest to discover if *B. stenebdoma* consistently uses lacewings in other areas and whether predation is restricted to species of *Eremochrysa* and *Chrysoperla.*

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SURVEY OF SOCIAL INSECTS IN THE FOSSIL RECORD*

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Biologists have long been intrigued by the complex social systems of various insects. Despite a voluminous literature dealing with the evolution of these systems, immense gaps remain in our understanding of insect sociality. Several theories have been proposed to explain the evolution of social behavior in certain groups of insects (e.g., Hamilton, 1964), but none consider this problem with respect to geological time. The present paper does so by examining the fossil record for clues not only on the antiquity of sociality, but also on the nature of these early social insects. Included in this survey are those insects recognized as eusocial: the Isoptera, and three superfamilies of the Hymenoptera: Vespoidea, Formicoidea, and Apoidea.

ISOPTERA

The termites are remarkable in two regards: 1) as a group, they are fully eusocial, exhibiting a wide range of behavioral modifications and sophistications, and 2) their record in the geological past, although sparse, is highly indicative of an Early Mesozoic origin. This latter point is of particular significance if one considers sociality among insects as a pinnacle of evolutionary success. Wilson (1971, p. 1) states that "[insect societies] best exemplify the full sweep of ascending levels of organization, from molecule to society." The possibility that termites evolved a social organization as far back in geological time as the Jurassic (roughly 190 million years ago) is of great interest, particularly when attempting to draw parallels with the evolution of sociality in the Hymenoptera, a group phylogenetically very remote from the termites.

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Five of the six families[1] of termites recognized by Emerson (1955) have a fossil record extending at least as far back as the Tertiary. In 1967, *Cretatermes carpenteri* (Hodotermitidae) was found in an Upper Cretaceous deposit in Labrador (Fig. 1), a discovery which immediately placed the origin of the Isoptera no later than the Mesozoic — an extension of 45 million years from previously known specimens. In addition, the advanced phylogenetic position of *Cretatermes* provides evidence for a much earlier origin of the order than has formerly been recognized (Emerson, 1967).

An examination of various fossil localities reveals a widespread termite fauna during the Tertiary Period (Table 1). The Termitidae are found in Miocene deposits of California and Germany; the Rhinotermitidae, Hodotermitidae, and Kalotermitidae are found at various Tertiary deposits throughout the United States and Europe; and the Mastotermitidae have the most widespread Cenozoic distribution of all, having been found at localities in the United States, Europe, South America, and Australia. This latter finding is highly intriguing because the family Mastotermitidae today has but one species, *Mastotermes darwiniensis,* which is restricted to northern Australia.[2] Emerson (1955) postulates that this widespread

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[1] The sixth family is the Serritermitidae — an aberrant taxon known from only one species.

[2] A look at past climatic shifts provides additional insight into the redistribution of the termites, particularly with respect to the Mastotermitidae, now solely restricted to Australia. Reconstructions of paleo-climatic patterns may be made fairly accurately on the basis of floral analyses (Reid and Chandler, 1933). The presence of *Sequoia* stumps in the Florissant Shales of Colorado provides evidence for warmer temperatures during the Oligocene (Emerson, 1969). Tiffney (1977) postulates on the basis of fossil angiosperm assemblages that temperatures in New England during the Oligocene were much more equable than at present — the temperatures ranging from 26° C to 9° C in contrast to today's 21° C to −10° C. Furthermore, extended frosts and hard freezes were unknown. In the more tropical climate of the Oligocene, colony activities were presumably carried out year round in a relatively warm, moist environment, explaining the widespread distribution of the Mastotermitidae during the Lower to Middle Tertiary. By the Late Miocene or Early Pliocene, the earth's climate began shifting towards cooler temperatures with the rising level of the continental land masses and increasingly large polar ice caps. My hypothesis is that, unable to adapt to an increasingly colder climate, and possibly to a concomitant change in predator pressures, the Mastotermitidae began to die out during the Tertiary. And, because at this time the Termitidae were undergoing tremendously successful radiation in Africa and South America, the Mastotermitidae became geographically restricted to northern Australia, represented today by only one relict species, *Mastotermes darwiniensis.*

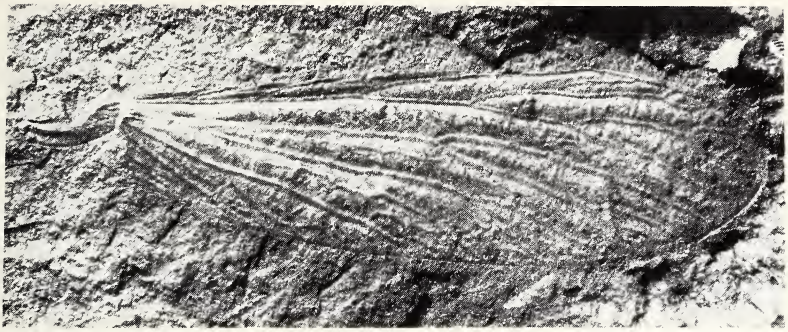

Figure 1. *Cretatermes carpenteri* Emerson from lower part of Upper Cretaceous of Labrador. Note humeral suture at wing base. Original photograph of holotype in Princeton Museum. Length of wing, 7.5 mm.

geographical distribution provides strong evidence to support a Mesozoic origin of the order. He argues (1975) that the breakup of the united land mass Pangaea in the Permian or Lower Triassic must have occurred subsequently to the origin of the Isoptera to explain their distribution in the southern and northern continental land masses and that all five families must have been present in the Late Mesozoic to explain their diversity and distribution by the Tertiary.

In 1971 he looked at a variety of primitive and derived characters of each family and analyzed the geographical distribution of the groups, using plate tectonics to provide the following estimates on the geological origin of the families:

Mastotermitidae — possibly Early Mesozoic.
Hodotermitidae — Triassic, or Early Jurassic before the breakup of southern continents.
Kalotermitidae — mid-Jurassic, or Lower Cretaceous, before the separation of Africa and South America.
Rhinotermitidae — Late Jurassic, Early Cretaceous.
Termitidae — Cretaceous.

Because termites are such poor fliers and do not mate until the adults have cast their wings, he considers water gaps of more than 50 miles capable of preventing termite dispersal.

While I am supportive of the theory that places great importance on the role of a unified land mass in animal dispersal, I do not agree that this can effectively be used to date the origin of the Isoptera.

TABLE 1 ISOPTERA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Hodotermitidae		
**Cretatermes carpenteri* Emerson	Labrador, Canada	Emerson, 1967
EOCENE		
Mastotermitidae		
**Blattotermes wheeleri* Collins	Tennessee, U.S.A.	Emerson, 1965
**Idomastotermes mysticus* Häupt	Geiseltal, Germany	Emerson, 1965
Kalotermitidae		
Neotermes grassei Piton	Menat, France	Emerson, 1969
Hodotermitidae		
Termopsis mallaszi Pongracz	Hungary	Snyder, 1949
OLIGOCENE		
Mastotermitidae		
**Miotermes insignis* (Heer)	Oeningen, Germany	Emerson, 1965
**Miotermes spectabilis* (Heer)	Oeningen, Germany	Emerson, 1965
Mastotermes bournemouthensis von Rosen	England	Emerson, 1965
Mastotermes heeri (Göppert)	Schlesien, Germany	Emerson, 1965
Mastotermes batheri von Rosen	England	Emerson, 1965
Kalotermitidae		
**Prokalotermes hageni* (Scudder)	Florissant, Colorado	Emerson, 1969
**Electrotermes giradi* (Giebel)	Baltic Amber	Emerson, 1969
**Electrotermes affinis* (Hagen)	Baltic Amber	Emerson, 1969
Kalotermes rhenanus Hagen	Rott, Germany	Emerson, 1969
**Eotermes grandaeva* Statz	Rott, Germany	Emerson, 1969
**Proelectrotermes berendti* (Pictet)	Baltic Amber	Emerson, 1969

Hodotermitidae		
Archotermopsis tornquisti von Rosen	Baltic Amber	Snyder, 1949
Termopsis bremii Heer	Baltic Amber	Snyder, 1949
**Parotermes insignis* Scudder	Florissant, Colorado	Snyder, 1949
**Parotermes scudderi* Cockerell	Florissant, Colorado	Cockerell, 1913
**Ulmeriella bauckhorni* Meunier	Rott, Germany	Emerson, 1968
**Ulmeriella cockerelli* Martynov	Siberia, U.S.S.R.	Emerson, 1968
Rhinotermitidae		
**Reticulitermes minimus* (Snyder)	Baltic Amber	Emerson, 1971
Reticulitermes fossarum (Scudder)	Florissant, Colorado	Emerson, 1971
Reticulitermes antiquus (Germar)	Baltic Amber	Emerson, 1971
Reticulitermes creedei Snyder	Creede, Colorado	Emerson, 1971
**Parastylotermes robustus* (Rosen)	Baltic Amber	Emerson, 1971
MIOCENE		
Mastotermitidae		
**Spargotermes costalimai* Emerson	Brazil	Emerson, 1965
Mastotermes vetustus Pongracz	Radoboj, Croatia	Emerson, 1965
Mastotermes minor Pongracz	Radoboj, Croatia	Emerson, 1965
Mastotermes haidingeri (Heer)	Radoboj, Croatia	Emerson, 1965
Mastotermes croaticus von Rosen	Radoboj, Croatia	Emerson, 1965
**Miotermes procerus* (Heer)	Radoboj, Croatia	Emerson, 1965
**Miotermes randeckenensis* von Rosen	Württemberg, Germany	Emerson, 1965
**Pliotermes hungaricus* Pongracz	Radoboj, Croatia	Emerson, 1965
Kalotermitidae		
Cryptotermes ryshkoffi Pierce	Calico, California	Emerson, 1969
Kalotermes swinhoei (Cockerell)	Burma	Emerson, 1969
Kalotermes tristis (Cockerell)	Burma	Emerson, 1969
Kalotermes nigritus Snyder	Chiapas, Mexico	Snyder, 1960

TABLE 1 ISOPTERA IN THE FOSSIL RECORD

Geological Age	Locality	References
CRETACEOUS		
Hodotermitidae		
* *Cretatermes carpenteri* Emerson	Labrador, Canada	Emerson, 1967
EOCENE		
Mastotermitidae		
* *Blattotermes wheeleri* Collins	Tennessee, U.S.A.	Emerson, 1965
* *Idomastotermes mysticus* Haupt	Geiseltal, Germany	Emerson, 1965
Kalotermitidae		
Neotermes grassei Piton	Menat, France	Emerson, 1969
Hodotermitidae		
Termopsis mallaszi Pongracz	Hungary	Snyder, 1949
OLIGOCENE		
Mastotermitidae		
* *Miotermes insignis* (Heer)	Oeningen, Germany	Emerson, 1965
* *Miotermes spectabilis* (Heer)	Oeningen, Germany	Emerson, 1965
Mastotermes bournemouthensis von Rosen	England	Emerson, 1965
Mastotermes heeri (Göppert)	Schlesien, Germany	Emerson, 1965
Mastotermes batheri von Rosen	England	Emerson, 1965
Kalotermitidae		
* *Prokalotermes hageni* (Scudder)	Florissant, Colorado	Emerson, 1969
* *Electrotermes girardi* (Giebel)	Baltic Amber	Emerson, 1969
* *Electrotermes affinis* (Hagen)	Baltic Amber	Emerson, 1969
Kalotermes rhenanus Hagen	Rott, Germany	Emerson, 1969
* *Eotermes grandaeva* Statz	Rott, Germany	Emerson, 1969
* *Proelectrotermes berendti* (Pictet)	Baltic Amber	Emerson, 1969
Hodotermitidae		
Archotermopsis tornquisti von Rosen	Baltic Amber	Snyder, 1949
Termopsis bremii Heer	Baltic Amber	Snyder, 1949
* *Parotermes insignis* Scudder	Florissant, Colorado	Snyder, 1949
* *Parotermes scudderi* Cockerell	Florissant, Colorado	Cockerell, 1913
* *Ulmeriella bauckhorni* Meunier	Rott, Germany	Emerson, 1968
* *Ulmeriella cockerelli* Martynov	Siberia, U.S.S.R.	Emerson, 1968
Rhinotermitidae		
* *Reticulitermes minimus* (Snyder)	Baltic Amber	Emerson, 1971
Reticulitermes fossarum (Scudder)	Florissant, Colorado	Emerson, 1971
Reticulitermes antiquus (Germar)	Baltic Amber	Emerson, 1971
Reticulitermes creedei Snyder	Creede, Colorado	Emerson, 1971
* *Parastylotermes robustus* (Rosen)	Baltic Amber	Emerson, 1971
MIOCENE		
Mastotermitidae		
* *Spargotermes costalimai* Emerson	Brazil	Emerson, 1965
Mastotermes vetustus Pongracz	Radoboj, Croatia	Emerson, 1965
Mastotermes minor Pongracz	Radoboj, Croatia	Emerson, 1965
Mastotermes haidingeri (Heer)	Radoboj, Croatia	Emerson, 1965
Mastotermes croaticus von Rosen	Radoboj, Croatia	Emerson, 1965
* *Miotermes procerus* (Heer)	Radoboj, Croatia	Emerson, 1965
* *Miotermes randeckenensis* von Rosen	Württemberg, Germany	Emerson, 1965
* *Pliotermes hungaricus* Pongracz	Radoboj, Croatia	Emerson, 1965
Kalotermitidae		
Cryptotermes ryshkoffi Pierce	Calico, California	Emerson, 1969
Kalotermes swinhoei (Cockerell)	Burma	Emerson, 1969
Kalotermes tristis (Cockerell)	Burma	Emerson, 1969
Kalotermes nigritus Snyder	Chiapas, Mexico	Snyder, 1960

TABLE 1. (CONCLUDED)

Geological Age	Locality	References
MIOCENE (continued)		
Hodotermitidae		
**Ulmeriella latahensis* Snyder	Latah, Washington	Emerson, 1968
**Ulmeriella martynovi* Zeuner	Biebrich, Germany	Emerson, 1968
Rhinotermitidae		
Heterotermes primaevus Snyder	Chiapas, Mexico	Emerson, 1971
Reticulitermes hartungi (Heer)	Radoboj, Croatia	Emerson, 1971
Reticulitermes laurae Pierce	Calico, California	Emerson, 1971
**Parastylotermes calico* Pierce	Calico, California	Emerson, 1971
**Parastylotermes washingtonensis* (Snyder)	Latah, Washington	Emerson, 1971
Termitidae		
Gnathamitermes magnoculus rousei Pierce	Calico, California	Pierce, 1958
Macrotermes pristinus (Charpentier)	Radoboj, Croatia	Snyder, 1949

*Extinct genera.

Simpson (1952) has made some insightful remarks on the matter. He contests the premise that if a given group of organisms requires a land connection, then disjunctive areas occupied by the group must have been once connected by continuous land. His contention is that there is no group of organisms that cannot be dispersed over water. Given a probability of only one chance in a million that an organism can cross a stretch of water, when geological time is considered the chance that the event will actually take place (over tens of millions of years) becomes significantly greater. It is further argued that successful colonization is dependent on successful invasion and the ability of the intruder to compete with existing species. Chances for survival are much higher when there are numerous, simultaneous arrivals of individuals.

In my opinion, the termites support such reasoning, and this can be argued in several ways. Firstly, termites are relatively light-bodied, winged insects. Studies by Simberloff and Wilson (1969) and Glick (1933) on the repopulation of an island by wind transported insects strongly support the possibility that termites are capable of being carried considerable distances in the upper atmosphere. Furthermore, because termites swarm in such large numbers prior to reproduction, a reasonable possibility exists that they will be dispersed to a new habitat as either a group or at least as a male/female pair. A wind current strong enough to blow one individual into the upper atmosphere should be equally capable of carrying multiple individuals, and, according to windflow, of transporting them in the same directional pathway.

Secondly, termites are ideally suited to dispersal over large bodies of water via floating logs. The more primitive families construct their extensive nesting colonies in wood and logs; as a consequence, it is entirely plausible that a dead tree falling into a body of circulating water could be carried extended distances. Furthermore, this mode of transportation provides the termites with a source of food during their sojourn, and travel *en masse* obviates the problems of reproduction upon arrival. In addition, as Simpson points out, the larger the number of individuals, the more likely it is that they will be successful competitors in the new habitat. I am not presenting this as evidence that the termites did not evolve while the earth's land masses were still contiguous, but am merely pointing out the problems in arguing that land dispersal was essential for termites.

The Isoptera exhibit strong affinities to the Blattodea; evidence linking the two groups to a common ancestor is well marked between the Mastotermitidae, an archaic termite family, and the Cryptocercidae, a family of generalized cockroaches. This theory of common ancestry is supported by several comparative morphological and behavioral studies (Emerson, 1965; McKittrick, 1965; Ahmad, 1950; Cleveland, 1934; Hill, 1925). McKittrick (1965) goes so far as to incorporate both groups into the Dictyoptera, an order which also includes the Mantodea. The gut fauna, female genitalic structures, anal expansion of the hind wing, morphology of the proventriculus, and deposition of eggs in ootheca-like masses are much alike in *Mastotermes* and *Cryptocercus.* Furthermore, both groups inhabit similar habitats. As a consequence, termites have often been referred to as merely social cockroaches. This degree of relatedness becomes immediately interesting in view of the extensive geological record of the cockroaches.

Fossil cockroaches are first found in deposits from the Upper Carboniferous, which makes them among the oldest insects known. Furthermore, they comprise 80 percent of the fossil insect fauna during that period (Carpenter, 1930) — an indication that they have not only existed, but have flourished, for three hundred million years. If the similarities between termites and cockroaches are indeed the result of monophyletic, rather than convergent or parallel evolution, one might speculate on a much earlier origin for the Isoptera than is shown by the fossil record.

McKittrick (1965) admits that the flagellate gut fauna essential for cellulose digestion in both groups may have arisen independently in each; however, she believes that the similarities in two important morphological characters, the female genitalia and the dental belt of the proventriculus, represent primitive characters and are therefore indicative of a common origin for *Mastotermes* and *Cryptocercus.* On the other hand, Tillyard (1926, 1936), Cleveland (1934), Imms (1919), Carpenter (personal communication), among others, believe that the termites were derived from more ancient stock and may have evolved during the Late Paleozoic. Hamilton (1978) supports the view that social termites arose from "roach-like ancestors" in the habitat of dead phloem, and suggests that the invasion of *Cryptocercus* into the same type of habitat was independent of the ancestral termite. The possibility of termite "evolution under bark" seems immensely feasible; not only is isolation (and, hence, inbreeding) possible, but selective pressures leading to dependence on a cellulose diet would also be high. It seems an excellent explanation for the early separation of the termites and cockroaches from a common protorthopteran (protoblattoid) ancestor as long ago as the Late Paleozoic. More definite conclusions on the origin of the Isoptera must wait until termites or termite-like insects have been found in pre-Cretaceous strata.

HYMENOPTERA

The Hymenoptera belong to the major subdivision of the Insecta known as the Endopterygota. There are no clues elucidating the nature or precise age of the earliest endopterygote insects, but the fossil record does provide insight into the history of the group as a whole. Representatives of two endopterygote orders, Neuroptera and Mecoptera, are found as far back as the Early Permian, some 280 million years ago. This occurrence suggests an origin of the Endopterygota approximately 100 million years after the origin of the true insects.[3]

The earliest known Hymenoptera have been found in Triassic beds of Central Asia (Rasnitsyn, 1964) and Australia (Riek, 1955). These fossils establish a minimum age for the order of about 220 million years. All the specimens known from this period belong to the suborder Symphyta, and surprisingly enough belong to the existing family Xyelidae.

A major advance in the evolution of the Hymenoptera occurred with the development of a constriction between the first and second abdominal segments; this presumably had the selective advantage of increasing the flexibility of the abdomen, important for both oviposition and defense. Hymenoptera which possess this adaptation, a diagnostic character of the suborder Apocrita, are first known from Upper Jurassic deposits of Central Asia (Rasnitsyn, 1975, 1977). These specimens have been assigned to the more primitive division of the Apocrita known as the Terebrantia or

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[3] The oldest known insects, found in Upper Carboniferous deposits, comprise 11 orders and include the Apterygota (Thysanura), Paleoptera and Exopterygota. It should be noted that here the use of the term insect does not include the Collembola, Protura or Diplura.

Parasitica; the other division within this suborder is the Aculeata.[4] Members of the latter are characterized by modifications of the ovipositor that have enabled its use not only for oviposition, but also as a transport vessel for defensive and prey-paralyzing compounds. This structure unquestionably plays an important role in colony defense and might provide an explanation for the restriction of eusociality within the Hymenoptera to the Aculeata.

The oldest known aculeate hymenopteron, *Cretavus sibericus,* was discovered in an Upper Cretaceous (Cenomanian) deposit in Siberia in 1957. Although placed by Sharov (1962) in an extinct superfamily Cretavidea, related to the Scolioidea, it has recently been transferred to the existing family Mutillidae by Rasnitsyn (1977, p. 109). Since 1967, species representing 10 families and 19 genera of aculeate Hymenoptera have been found in Upper Cretaceous deposits in Central Asia (Rasnitsyn, 1977) (Table 2). Evans (1966) believes that such diversity by the Late Cretaceous is indicative of an earlier origin and postulates that the group may have evolved during the Jurassic. However, it must be pointed out that the Cretaceous is one of the longer periods in the earth's history, having a duration of roughly 70 million years, and may have been of sufficient length to account for such diversification.

VESPOIDEA

Included in this group are the three families considered to be "true wasps": The Masaridae and Eumenidae, both of which are solitary, and the Vespidae, where one finds behavioral modifications ranging from subsocial to highly advanced eusocial (Richards, 1953, 1971). It is the Vespidae, by virtue of their sociality, with which I am primarily concerned in this paper.

There are many gaps in our record of the early social wasps and of the Vespoidea in general. Most striking, perhaps, about the fossil record of the wasps is their lack of representation (see Table 3). The

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[4] The classification of the Aculeata has recently undergone a major revision by D. J. Brothers (1975), in which the seven previously recognized superfamilies (Bethyloidea, Scolioidea, Pompiloidea, Formicoidea, Vespoidea, Sphecoidea, and Apoidea) are now combined into three: the Bethyloidea, Sphecoidea (subdivided into the Spheciformes and Apiformes), and Vespoidea (subdivided into the Vespiformes and Formiciformes). However, since this revised classification has not been generally accepted in its entirety, I am employing here the more conventional classification (*sensu* Riek, 1970; Richards, 1971).

Table 2. Genera of aculeate Hymenoptera known from Cretaceous deposits (based on Rasnitsyn, 1977, and Evans, 1973). All genera are extinct.

SCOLIOIDEA		
Mutillidae	*Cretavus*	Sharov, 1962; Rasnitsyn, 1977
?SCOLIOIDEA		
Scolioidae	*Oryctopterus*	Rasnitsyn, 1977
Angarosphecidae	*Angarosphex*	Rasnitsyn, 1977
Falsiformicidae	*Falsiformica*	Rasnitsyn, 1977
?SCOLIOIDEA-BETHYLOIDEA		
?Scolebythidae	*Cretabythus*	Evans, 1973
BETHYLOIDEA		
Bethylidae	*Archaepyris*	Evans, 1973
	Celonophamia	Evans, 1973
Cleptidae	*Procleptes*	Evans, 1969
	Hypocleptes	Evans, 1973
	Protamisega	Evans, 1973
Dryinidae	*Cretodryinus*	Rasnitsyn, 1977
POMPILOIDEA		
Pompilidae	*Pompilopterus*	Rasnitsyn, 1977
FORMICOIDEA		
Formicidae	*Sphecomyrma*	Wilson and Brown, 1967
	Cretomyrma	Rasnitsyn, 1977
	Paleomyrmex	Rasnitsyn, 1977
SPHECOIDEA		
Sphecidae	*Lisponema*	Evans, 1969
	Pittoecus	Evans, 1973
?SPHECOIDEA		
?Sphecidae	*Archisphex*	Evans, 1969
	Taimyrisphex	Evans, 1973
VESPOIDEA		
Masaridae	*Curiovespa*	Rasnitsyn, 1975

absence of Vespidae from Baltic Amber (Lower Oligocene) and other fossil resins, in which ants are abundant, is probably due to their relatively large size, which reduces the likelihood of their entrapment in the sticky tree resin. Spradbery (1973, p. 316), attributes their scarcity in sedimentary deposits to "the behavioral characteristics and paper nest structures which do not lend themselves to fossilization." As with any other fossil, the absence of an insect in the paleontological record provides no proof as to its actual occurrence in the past; one can only reconstruct and evaluate paleofaunas on the basis of those organisms that are represented. Therefore, it is conceivable that wasps were present earlier than the record indicates, but that conditions conducive to their preservation were lacking. The following does, however, provide information on the diversity of the group as we know it.

Cretaceous

The earliest record of the Vespoidea extends back to the Upper Cretaceous (Turonian). Two species of vespoid wasp have been found in a deposit of this age in the USSR — both assigned to the genus *Curiovespa* (Rasnitsyn, 1975). Unfortunately, nothing is known about the body structure of these insects but on the basis of their wing venation they are placed in the family Masaridae. The presence of two distinct species in the same deposit suggests that some diversification of the Vespoidea had taken place as early as the Upper Cretaceous, although nothing is known about the morphological character of these early wasps.

Paleocene

No Vespoidea from this period are known.

Eocene

The Eocene beds of Green River have yielded a surprisingly diverse assemblage of aculeates, but most of these belong to the Terebrantia or Sphecoidea; the only vespoid recovered from this deposit, *Didineis solidescens,* is of uncertain systematic position (Evans, 1966, p. 393). Scudder (1890) described this specimen as a sphecid of the subfamily Nyssoninae. However, Evans (1966) examined the type and concluded that it did not belong to the family Sphecidae, but was probably a eumenid, and tentatively assigned it to the genus *Alastor.*

Figure 2. Vespoid wasp from Eocene of British Columbia. Original photograph of specimen in Royal Ontario Museum, Toronto. Length of forewing, 12 mm.

Piton (1940), in a thesis on the Eocene fossil beds of Menat, France, described an assemblage of Vespoidea found in this sedimentary deposit. However, because the six specimens he described are all assigned to extant genera, and do not show the characters essential for such generic designation, Piton's taxonomic determinations are perforce questionable. Particularly dubious is his placement of one specimen in the family Vespidae, genus *Polistes.* Because the morphological features necessary for accurate taxonomic placement are obscured in this fossil, I prefer to place it in Vespoidea *incertae sedis.* The remaining five specimens are assigned to the Eumenidae *incertae sedis.*

Another vespoid species was recently recovered from a Middle Eocene deposit in British Columbia (M. V. H. Wilson, 1977). Although not formally described, the fossil clearly shows the characteristic venation of the vespoid complex (see Fig. 2), but could be either a vespid or a eumenid. Of course, one has no way of stating with certainty that these early vespids were social. Within the Vespidae, divisions into subfamily and tribe are based primarily on behavioral rather than morphological characters. Furthermore, the morphological differences between the castes in any given species are often not obvious in the preserved fossils.

Oligocene

True vespids are first found in the Upper Oligocene shales of Florissant, Colorado and Rott, Germany, two highly productive fossiliferous deposits. These beds and other various localities listed in Table 3 have turned up an assemblage comprised of four genera and 14 species. It is quite remarkable that three of the four genera represented are extant and this supports the possibility that the Vespidae were essentially modern by the Oligocene. Furthermore, the diversification of taxa suggests a much earlier origin for the family than is evidenced by the fossil record.

Miocene

Scarcely any Vespidae are known from the Miocene, although this is most likely due to the overall dearth of deposits from this epoch. One vespid has been described from a deposit in Germany. This is *Polistes kirbyanus* and clearly belongs to the subfamily Polistinae. Other wasps from Miocene deposits have yet to be discovered, but one can assume that the wasp fauna of this age would be barely distinguishable from the wasp fauna of today.

FORMICOIDEA

The following review of the fossil history of the Formicidae provides important information on their dominance, distribution, and supposed habits during the Mesozoic and Cenozoic eras. In contrast to the Vespoidea, ants are the most abundant insects in Tertiary formations. This may be attributed to their foraging behavior on and around trees, which enhances their chances of preservation in amber. A rough total of 20,000 specimens representing some 200 species of ants has been studied (Table 4); this massive amount of work far exceeds the paleontological investigations carried out on any other family of insects. Several comprehensive monographs on the subject have been written, including *The Ants of the Baltic Amber* (Wheeler, 1914), and *The Fossil Ants of North America* (Carpenter, 1930), which are drawn on extensively in the following pages.

Cretaceous

The Cretaceous Period has, without question, provided more information on the early evolution of the ants than any other period, primarily because of the discovery in 1967 of two perfectly preserved worker ants in a New Jersey amber deposit. No doubt exists as to the primitive nature of these Cretaceous ants — both are members of the same species, *Sphecomyrma freyi* Wilson and Brown, and possess a mixture of wasp and ant characters. The petiole is distinctly ant-like, although the mandibles, which are short and bidentate, are very wasp-like (see Fig. 3A). A new subfamily, Sphecomyrminae, was named to accommodate *S. freyi* (Wilson, Carpenter, and Brown, 1967), and is considered ancestral to all known formicid subfamilies (see Taylor, 1978).

Since the discovery of *Sphecomyrma,* several other Cretaceous ants have been found, and these provide strong evidence that the family was widespread during this period. Dlussky (1975) described two new genera and three species, *Cretomyrma arnoldii, C. unicornis,* and *Paleomyrmex zherichini* (from a Late Cretaceous amber deposit in Yantardak, USSR) which he assigned to the Sphecomyrminae. It is of interest that the type of *P. zherichini* is the first winged male ant to be found in a Cretaceous deposit and provides the only indication of wing venation in the Sphecomyrminae (Fig. 3B). The figured specimen of *Cretomyrma unicornis* raises doubts as to its position in the Formicidae for it is a badly mangled, poorly preserved specimen and might be better assigned to Hymenoptera *incertae sedis.*[5] A fifth specimen, apparently a worker, has recently been discovered in the Cretaceous amber of Manitoba, Canada. Although not yet described, it undoubtedly belongs to the subfamily Sphecomyrminae (Wilson, personal communication).

Paleocene

No ants from the Paleocene are known, undoubtedly because so few fossiliferous beds containing insect remains from this epoch

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[5] Dlussky (1975) also described several other "ants" which were found in Upper Cretaceous deposits in the Kzyl-Zhar of Russia. Three genera (3 species) were placed in the subfamily Ponerinae: *Petropone petiolata, Cretopone magna,* and *Archaeopone kzylzharica.* These are all fragmentary specimens, and, as figured by Dlussky, present no characters which would place them unequivocally in the Formicidae. They much more obviously belong in Hymenoptera *incertae sedis,* as does *Dolichomyrma longiceps* from the Upper Cretaceous of Kzyl-Zhar, which Dlussky put into Formicidae *incertae sedis.*

TABLE 3. VESPOIDEA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Masaridae		
*_Curiovespa curiosa_ Rasnitsyn	Kazakh, U.S.S.R.	Rasnitsyn, 1975
*_Curiovespa magna_ Rasnitsyn	Kazakh, U.S.S.R.	Rasnitsyn, 1975
EOCENE		
Eumenidae		
?_Alastor solidescens_ (Scudder)	Green River, Wyoming	Evans, 1966
?_Rhygchium andrei_ Piton	Menat, France	Piton, 1940
?_Odynerus manevali_ Piton	Menat, France	Piton, 1940
?_Ancistrocerus eocenicus_ Piton	Menat, France	Piton, 1940
?_Ancistrocerus berlandi_ Piton	Menat, France	Piton, 1940
?_Eumenes projaponica_ Piton	Menat, France	Piton, 1940
?Vespidae		
?_Polistes vergnei_ Piton	Menat, France	Piton, 1940
OLIGOCENE		
Eumenidae		
Rhynchium sp. Theobald	Cereste, France	Theobald, 1937
Odynerus terryi Cockerell	Florissant, Colorado	Cockerell, 1909a
Odynerus wilmattae Cockerell	Florissant, Colorado	Cockerell, 1914
Odynerus oligopunctatus Theobald	Cereste, France	Theobald, 1937
?_Odynerus praesulptus_ Cockerell	Florissant, Colorado	Cockerell, 1906
Odynerus percantusus Cockerell	Florissant, Colorado	Cockerell, 1914
?_Alastor rottensis_ Statz	Rott, Germany	Statz, 1936
"_Pseudonortania_"† _sepulta_ Timon-David	Camoins, France	Timon-David, 1944

Vespidae		
?**Paleovespa gillettei* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa florissantia* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa scudderi* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa relecta* Cockerell	Florissant, Colorado	Bequaert, 1930
**Paleovespa baltica* Cockerell	Baltic Amber	Cockerell, 1909b
**Paleovespa wilsoni* Cockerell	Florissant, Colorado	Cockerell, 1914
Polistes industrius Theobald	Cereste, France	Theobald, 1937
Polistes signata Statz	Rott, Germany	Statz, 1936
?*Polybia anglica* Cockerell	Isle of Wight, England	Cockerell, 1921a
Polybia oblita Cockerell	Isle of Wight, England	Cockerell, 1921b
Vespa bilineata Statz	Rott, Germany	Statz, 1936
Vespa cordifera Statz	Rott, Germany	Statz, 1936
Vespa nigra Statz	Rott, Germany	Statz, 1936
MIOCENE		
Vespidae		
Polistes kirbyanus Cockerell	Oeningen, Germany	Cockerell, 1914
?*Vespa attavina* Heer	Parschlug, Germany	Heer, 1849
?*Vespa crabroniformis* Heer	Radoboj, Croatia	Heer, 1867

?Of uncertain position within the Vespoidea — clearly Diploptera, but further determination impossible.
†*Pseudonortania* Timon-David is a junior homonym of *Pseudonortania* Soika, 1936.
*Extinct genera.

TABLE 3. VESPOIOEA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Masaridae		
**Curiovespa curiosa* Rasnitsyn	Kazakh, U.S.S.R	Rasnitsyn, 1975
**Curiovespa magna* Rasnitsyn	Kazakh, U.S.S.R	Rasnitsyn, 1975
EOCENE		
Eumenidae		
?*Alastor solidescens* (Scudder)	Green River, Wyoming	Evans, 1966
?*Rhygchium andrei* Piton	Menat, France	Piton, 1940
?*Odynerus manevali* Piton	Menat, France	Piton, 1940
?*Ancistrocerus eocenicus* Piton	Menat, France	Piton, 1940
?*Ancistrocerus berlandi* Piton	Menat, France	Piton, 1940
?*Eumenes projaponica* Piton	Menat, France	Piton, 1940
?Vespidae		
?*Polistes vergnei* Piton	Menat, France	Piton, 1940
OLIGOCENE		
Eumenidae		
Rhynchium sp. Theobald	Cereste, France	Theobald, 1937
Odynerus terryi Cockerell	Florissant, Colorado	Cockerell, 1909a
Odynerus wilmattae Cockerell	Florissant, Colorado	Cockerell, 1914
Odynerus oligopunctatus Theobald	Cereste, France	Theobald, 1937
?*Odynerus praesulptus* Cockerell	Florissant, Colorado	Cockerell, 1906
Odynerus percantusus Cockerell	Florissant, Colorado	Cockerell, 1914
?*Alastor rottensis* Statz	Rott, Germany	Statz, 1936
"*Pseudonortania*"† *sepulta* Timon-Oavid	Camoins, France	Timon-Oavid, 1944
Vespidae		
?**Paleovespa gillettei* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa florissantia* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa scudderi* Cockerell	Florissant, Colorado	Bequaert, 1930
?**Paleovespa relecta* Cockerell	Florissant, Colorado	Bequaert, 1930
**Paleovespa baltica* Cockerell	Baltic Amber	Cockerell, 1909b
**Paleovespa wilsoni* Cockerell	Florissant, Colorado	Cockerell, 1914
Polistes industrius Theobald	Cereste, France	Theobald, 1937
Polistes signata Statz	Rott, Germany	Statz, 1936
?*Polybia anglica* Cockerell	Isle of Wight, England	Cockerell, 1921a
Polybia oblita Cockerell	Isle of Wight, England	Cockerell, 1921b
Vespa bilineata Statz	Rott, Germany	Statz, 1936
Vespa cordifera Statz	Rott, Germany	Statz, 1936
Vespa nigra Statz	Rott, Germany	Statz, 1936
MIOCENE		
Vespidae		
Polistes kirbyanus Cockerell	Oeningen, Germany	Cockerell, 1914
?*Vespa attavina* Heer	Parschlug, Germany	Heer, 1849
?*Vespa crabroniformis* Heer	Radoboj, Croatia	Heer, 1867

?Of uncertain position within the Vespoidea — clearly Oiploptera, but further determination impossible.
†*Pseudonortania* Timon-Oavid is a junior homonym of *Pseudonortania* Soika, 1936.
*Extinct genera.

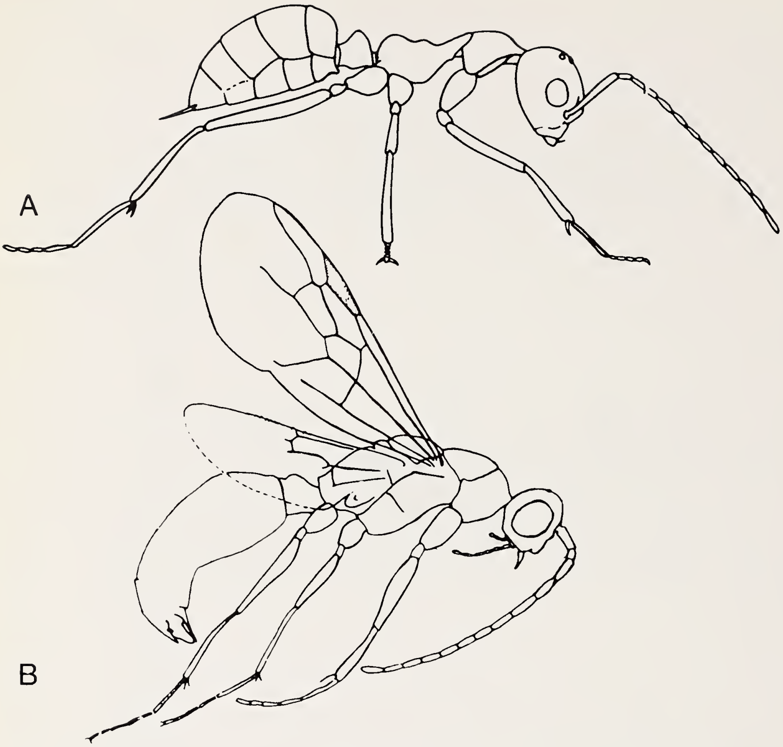

Figure 3A. *Sphecomyrma freyi* Wilson and Brown from the lower part of Upper Cretaceous of New Jersey. Drawing of holotype worker in Museum of Comparative Zoology, modified from Wilson, Carpenter, and Brown (1967). Length of body, 3.5 mm.

Figure 3B. *Paleomyrmex zherichini* Rasnitsyn from the lower part of the Upper Cretaceous of U.S.S.R. Drawing of holotype male in Paleontological Institute, Moscow, from Rasnitsyn, 1977. Length of body, 5.4 mm.

have been discovered. Mention is made by Brues (1936) of a piece of petrified wood containing what he considers ant borings, highly resemblant of borings made by *Camponotus* today. Although there is no clear-cut evidence that these borings represent *Camponotus* activity, or insect activity of any kind, it is conceivable that *Camponotus* was present in New Mexico during the Paleocene; several species have been dscribed from the Florissant Shales, Colorado (Upper Oligocene), and one from the Baltic Amber

(Lower Oligocene). In addition, it must be remembered that the Paleocene did not begin for at least 40 million years after the appearance of *Sphecomyrma freyi.*

Eocene

Very few fossil ants have been found in deposits of this age, and the determinations of many of these ant species are in doubt. Scudder (1877, 1878) described four supposed ants from the Green River formation, and five ants (1877) from the Quesnel Beds in British Columbia. Generic identifications on all of these fossils are to be considered dubious at best, and more likely incorrect (Carpenter, 1930).

In 1920, two species, *Oecophylla bartoniana* and *Formica heteroptera,* were described by Cockerell from an Eocene deposit in Bournemouth, England. Wheeler (1928) considered these ants formicines, but because the descriptions were based on wing fragments, he questioned their generic determinations. Similarly, Cockerell's *Formica eoptera* (1923a) from the Eocene of Texas is of uncertain position at both the generic and subfamily levels. *Archimyrmex rostratus* (Cockerell, 1923b) from the Eocene shales of Colorado is probably a myrmicine (Carpenter, 1930), and is the only Green River ant that can be placed with any certainty in a subfamily. Carpenter (1929) described *Eoponera berryi* from the Wilcox formation of Tennessee, and placed this ant in the subfamily Ponerinae. He suggests that it may be closely allied to the Neotropical genus *Dinoponera.* This is of interest because *Eoponera berryi* is the oldest known ant (Lower Eocene) to be assigned to a living subfamily of Formicidae.

Wilson (personal communication) mentions the recent discovery of three ants in a Middle Eocene amber deposit near Malvern, Arkansas, each belonging to a different subfamily. One belongs to the Dolichoderinae, genus *Iridomyrmex;* one is a formicine closely allied to the genus *Paratrechina,* and considered a relatively primitive, or "typical euformicine"; the last is a new genus of myrmicine, unique by virtue of its inflated postpetiole. These ants have yet to be formally described but they are nevertheless of paramount interest. The presence of these subfamilies in North America in the Eocene is strongly suggestive of their rapid evolution and dispersal during the Paleocene and perhaps during the Cretaceous.

Oligocene

The Baltic Amber is, most certainly, the best studied of all Tertiary insect deposits, and has revealed a great deal about the nature and diversity of Oligocene ants.[6] As of 1928, 11,711 ants (93 species) were examined from this deposit. Of this number, 1461 were studied by Mayr (1868); 690 by André (1895); and 9,560 by Wheeler (1914, 1928).

An examination of the ant fauna reveals wide representation at the subfamily and generic levels. All extant subfamilies of Formicidae are found in the amber with the exception of the Dorylinae and Leptanillinae. The absence of the Dorylinae is probably not due to selective exclusion on the part of the amber, but more likely indicates their absence from that part of the European continent during the Oligocene. Wheeler (1914) speculates that the foraging behavior of doryline ants should readily lead to entrapment in tree resin, but, in all probability, this group was then, as it is now, confined to the tropics. It is not surprising that the Leptanillinae are absent from the Baltic Amber; this is a small subfamily once considered a tribe of the Dorylinae, consisting of one genus and a few species; and although pantropical is hypogaeic and rarely encountered.

The Dolichoderinae and Formicinae together constitute 97 percent of all specimens and evidence indicates that these amber ants were already extraordinarily specialized. Workers of *Iridomyrmex goepperti* were found in a piece of amber (originally in the Königsberg collection) with several aphids. On the basis of this discovery, Wheeler (1914) concludes that Homoptera were attended by ants then much as they are today. The finding of several genera of paussid beetles (e.g., *Arthropterus, Cerapterites* and *Eopaussus*) in the Baltic Amber (Wasmann, 1929) suggests that myrmecophiles were established at this time. Perhaps most remarkable of all was the discovery of two *Lasius schiefferdeckeri* workers — each found with a mite attached to the base of the hind tibia, in precisely the

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[6] Because the Baltic Amber was secondarily deposited in a clay bed of Lower Oligocene age, it is necessarily older than the glauconitic sand ("blue-earth" clay) in which it lies. How much older is uncertain. In some published accounts it is referred to as Eocene. However, since the composition of the Baltic Amber ant fauna is very similar to that of the Florissant Shales and other *bona fide* Oligocene deposits, I am following Zeuner (1939, p. 26) in referring to the amber as Lower Oligocene.

same position on each. This demonstrates almost certainly that by the Lower Oligocene mites had acquired distinct preferences for attachment on specific regions of their host's integument.

Almost as valuable as the Baltic Amber in providing a large and diverse assemblage of fossil ants is the Upper Oligocene deposit in Florissant, Colorado, studied by Carpenter (1930). The ant fauna of this deposit is strikingly similar to that of the Baltic Amber in many respects. It is interesting to note that roughly the same percentage of extant genera is found in both places; in the Florissant Shales this figure is given as 60 percent (Carpenter, 1930), in the Baltic Amber 56 percent (Wheeler, 1914). *Iridomyrmex* is clearly a dominant genus in the Baltic Amber, and although not so common in the Florissant Shales, a closely allied genus, *Protazteca,* comprises more than 25 percent of all specimens (Brown, 1973).

Another similarity between the two deposits is the relative percentages of the various subfamilies. As in the amber, the Dolichoderinae are predominant, comprising 60 percent of the total number of ants. The Formicinae comprise another 25 to 30 percent, and the Myrmicinae in each deposit are represented by five percent or less of the total specimens. This suggests that the ant fauna in the northern hemisphere was essentially homogenous during the Oligocene.

The remaining deposits of Oligocene age from which ants have been described are of relatively minor importance. Most of the specimens are fragmentary and the determinations dubious; nevertheless, a mention of them is certainly necessary. Specimens from Gurnet Bay, Isle of Wight, England, have been studied by Cockerell (1915) and Donisthorpe (1920). Cockerell described eight species of ants from this deposit but, because his generic determinations are based chiefly on highly variable measurements of wing fragments, they are of dubious significance. Donisthorpe examined a total of eight genera and fourteen species belonging to the subfamilies Ponerinae, Dolichoderinae, and Formicinae. Surprising is the large number of *Oecophylla* workers recovered (245); this genus is now restricted to Africa, India, and Australia, and is much more numerous in the Gurnet Bay deposit than in the Baltic Amber or Florissant Shales. This might be due to the difference in latitude between the deposits which would account for a warmer climate at Gurnet Bay later into the Tertiary than at the more northern deposits.

Another Lower Oligocene deposit which has provided beautifully preserved fossil ants is Aix-en-Provence, France. Several species have been described by Theobald (1937), who recognized four subfamilies: Myrmicinae (1 species); Ponerinae (1 species); Dolichoderinae (1 genus, 2 species); and Formicinae (3 genera, 9 species). Also described by Theobald (1937) is an Oligocene collection from Haut-Rhin, France, in which he recognizes the same four subfamilies (16 genera, 34 species). This fauna is very similar to that found in the Baltic Amber; in fact, Theobald has found five species which he considers identical to species in the Baltic Amber. In a deposit in Gard, France, Theobald (1937) describes two species, one a myrmicine, the other a dolichoderine.

Meunier (1917) has described four ant species from an Upper Oligocene deposit in Rott, Germany. These have been assigned to three genera: *Formica, Ponera,* and *Myrmica.* The specimens are well-preserved, as may be seen in Meunier's photographs, but his generic determinations are questionable.

In 1957, two female reproductives of the same species were discovered in an Upper Oligocene deposit in Argentina. The authors described the species as *Ameghinoia piatnitskyi* and placed it in the subfamily Ponerinae (Viana and Haedo-Rossi, 1957). E. O. Wilson (personal communication) is highly sceptical of the placement of *A. piatnitskyi* in the Ponerinae, and thinks that it is very clearly a myrmeciine. This is quite extraordinary because no other fossil ants have been recovered from South America, and more importantly, if Wilson is correct, this is the first indication that the Myrmiciinae were so widespread by the Oligocene.

Miocene

The deposits of Miocene age which have provided the greatest number of ant specimens have been the Oeningen beds in Germany, and the Radoboj formation in Croatia. Approximately 60 species of ants from these places were described by the Swiss myrmecologist Heer (1849, 1856, 1867), but his generic assignments are necessarily questionable in terms of present-day concepts of a formicid genus. Regrettably, the type specimens which are essential to a revision of this fossil fauna are believed to be lost.

A few species were described by Emery (1891) in Sicilian amber, presumed to be Miocene, but these, like the specimens studied by Heer, are of questionable generic position.[7]

Another Miocene amber deposit has been found in Chiapas, Mexico, from which some one hundred ants have been recovered. Unfortunately, the majority of these are fragmentary, or otherwise too poor for determination. The assemblage does, however, suggest that the ant fauna in Mexico during the Miocene was essentially the same as might be found in that region today (Brown, 1973).

Fujiyama (1970) described a single ant from the Chôjabaru formation in Japan (middle Miocene) which he named *Aphaenogaster axila,* thought to be closely allied to the subgenus *Deromyrma.* This is not particularly unusual inasmuch as *Aphaenogaster* is a world-wide genus, and several species are found in Japan today.

Perhaps the most interesting of all Miocene material is an ant colony of *Oecophylla leakeyi* found in Kenya (Wilson and Taylor, 1964). This is the first record of an actual, although fragmented, ant colony and contains a total of 366 specimens: 197 larvae, 105 worker pupae, and at least 64 workers. No Nearctic fossils of *Oecophylla* are known, but the species is well represented in European Tertiary deposits. Wilson and Taylor suggest on the basis of these fossil specimens that *Oecophylla* is a morphologically stable paleotropical genus which has persisted through most of the Tertiary with very little specialization.

APOIDEA

The Apoidea form an interesting complex of social insects. Unlike the other social insect groups that are consistent in their degree of social achievement at the ordinal level (Isoptera), family level (Formicidae), and virtually the subfamily level (Vespinae), the Apoidea present a wide spectrum of social behavior at the generic level. Evidence suggests that eusociality has arisen in the bees at least eight times (Michener, 1962; Wilson, 1971), which may explain this variance. Nevertheless, it is noteworthy that of roughly 20,000 existing species of bees only a small minority are thought to be presocial and eusocial (Wilson, 1971). Why sociality in the Apoidea

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[7] These generic determinations are currently being reviewed by Dr. W. L. Brown, Jr.

TABLE 4. FORMICOIDEA IN THE FOSSIL RECORD.

Geological Age	Locality	References
CRETACEOUS		
Sphecomyrminae		
**Sphecomyrma freyi* Wilson and Brown	New Jersey, U.S.A.	Wilson, Carpenter and Brown, 1967
?**Sphecomyrma* sp.	Manitoba, Canada	Wilson, pers. comm.
**Cretomyrma arnoldii* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
**Cretomyrma unicornis* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
**Paleomyrmex zherichini* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
EOCENE		
Myrmicinae		
**Archimyrmex rostratus* Cockerell	Florissant, Colorado	Carpenter, 1930
Formicinae		
Oecophylla bartoniana Cockerell	Bournemouth, England	Cockerell, 1920
Formica eoptera Cockerell	Texas, U.S.A.	Carpenter, 1930
Formica heteroptera Cockerell	Bournemouth, England	Cockerell, 1920
?*Paratrechina* sp.	Arkansas, U.S.A.	Wilson, pers. comm.
Ponerinae		
**Eoponera berryi* Carpenter	Tennessee, U.S.A.	Carpenter, 1929
Dolichoderinae		
Iridomyrmex sp.	Arkansas, U.S.A.	Wilson, pers. comm.
OLIGOCENE		
Myrmiciinae		
**Ameghinoia piatnitskyi* Viana and Haedo-Rossi	Argentina	Viana and Haedo-Rossi, 1957
Ponerinae		
Brachyponera dubia Theobald	Haut-Rhin, Germany	Theobald, 1937a

**Archiponera wheeleri* Carpenter	Florissant, Colorado	Carpenter, 1930
**Prionomyrmex longiceps* Mayr	Baltic Amber	Wheeler, 1914
**Procerapachys annosus* Wheeler	Baltic Amber	Wheeler, 1914
**Procerapachys favosus* Wheeler	Baltic Amber	Wheeler, 1914
**Bradoponera meieri* Mayr	Baltic Amber	Wheeler, 1914
Ectatomma europaeum Mayr	Baltic Amber	Wheeler, 1914
**Electoponera dubia* Wheeler	Baltic Amber	Wheeler, 1914
Platythyrea primaeva Wheeler	Baltic Amber	Wheeler, 1914
Euponera calcarea Theobald	Haut-Rhin, Germany	Theobald, 1937
Euponera succinea (Mayr)	Baltic Amber	Wheeler, 1914
Euponera crawleyi Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Euponera globiventris Theobald	Haut-Rhin, Germany	Theobald, 1937
Ponera atavia Mayr	Baltic Amber	Wheeler, 1914
Ponera minuta Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Ponera elegantissima Meunier	Rott, Germany	Meunier, 1923
Ponera hypolitha Cockerell	Isle of Wight, England	Cockerell, 1915
Ponera rhenana Meunier	Rott, Germany	Meunier, 1917
?*Ponera gracilicornis* Mayr	Baltic Amber	Wheeler, 1914
**Emplastus emeryi* Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
**Syntaphus wheeleri* Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Pseudomyrmicinae		
Pseudomyrma extincta Carpenter	Florissant, Colorado	Carpenter, 1930
Myrmicinae		
Aphaenogaster mayri Carpenter	Florissant, Colorado	Carpenter, 1930
Aphaenogaster donisthorpei Carpenter	Florissant, Colorado	Carpenter, 1930
Aphaenogaster maculipes Theobald	Haut-Rhin, Germany	Theobald, 1937
Aphaenogaster maculata Theobald	Aix-en-Provence, France	Theobald, 1937
Aphaenogaster sommerfeldti Mayr	Baltic Amber	Wheeler, 1914
Aphaenogaster oligocenica Wheeler	Baltic Amber	Wheeler, 1914

TABLE 4 FORMICOIDEA IN THE FOSSIL RECORD

Geological Age	Locality	References
CRETACEOUS		
Sphecomyrminae		
•*Sphecomyrma freyi* Wilson and Brown	New Jersey, U.S.A	Wilson, Carpenter and Brown, 1967
?•*Sphecomyrma* sp.	Manitoba, Canada	Wilson, pers. comm.
•*Cretomyrma arnoldii* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
•*Cretomyrma unicornis* Dlussky	Taymyr, U.S.S.R	Rasnitsyn, 1975
•*Paleomyrmex zherichini* Dlussky	Taymyr, U.S.S.R.	Rasnitsyn, 1975
EOCENE		
Myrmicinae		
•*Archimyrmex rostratus* Cockerell	Florissant, Colorado	Carpenter, 1930
Formicinae		
Oecophylla bartoniana Cockerell	Bournemouth, England	Cockerell, 1920
Formica eoptera Cockerell	Texas, U.S.A.	Carpenter, 1930
Formica heteroptera Cockerell	Bournemouth, England	Cockerell, 1920
?*Paratrechina* sp.	Arkansas, U.S.A	Wilson, pers comm.
Ponerinae		
•*Eoponera berryi* Carpenter	Tennessee, U.S.A.	Carpenter, 1929
Dolichoderinae		
Iridomyrmex sp.	Arkansas, U.S.A.	Wilson, pers. comm.
OLIGOCENE		
Myrmiciinae		
•*Ameghinoia piatnitskyi* Viana and Haedo-Rossi	Argentina	Viana and Haedo-Rossi, 1957
Ponerinae		
Brachyponera dubia Theobald	Haut-Rhin, Germany	Theobald, 1937a
•*Archiponera wheeleri* Carpenter	Florissant, Colorado	Carpenter, 1930
•*Prionomyrmex longiceps* Mayr	Baltic Amber	Wheeler, 1914
•*Procerapachys annosus* Wheeler	Baltic Amber	Wheeler, 1914
•*Procerapachys favosus* Wheeler	Baltic Amber	Wheeler, 1914
•*Bradoponera meieri* Mayr	Baltic Amber	Wheeler, 1914
Ectatomma europaeum Mayr	Baltic Amber	Wheeler, 1914
•*Electoponera dubia* Wheeler	Baltic Amber	Wheeler, 1914
Platythyrea primaeva Wheeler	Baltic Amber	Wheeler, 1914
Euponera calcarea Theobald	Haut-Rhin, Germany	Theobald, 1937
Euponera succinea (Mayr)	Baltic Amber	Wheeler, 1914
Euponera crawleyi Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Euponera globiventris Theobald	Haut-Rhin, Germany	Theobald, 1937
Ponera atavia Mayr	Baltic Amber	Wheeler, 1914
Ponera minuta Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Ponera elegantissima Meunier	Rott, Germany	Meunier, 1923
Ponera hypolitha Cockerell	Isle of Wight, England	Cockerell, 1915
Ponera rhenana Meunier	Rott, Germany	Meunier, 1917
?*Ponera gracilicornis* Mayr	Baltic Amber	Wheeler, 1914
•*Emplastus emeryi* Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
•*Syntaphus wheeleri* Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Pseudomyrmicinae		
Pseudomyrma extincta Carpenter	Florissant, Colorado	Carpenter, 1930
Myrmicinae		
Aphaenogaster mayri Carpenter	Florissant, Colorado	Carpenter, 1930
Aphaenogaster donisthorpei Carpenter	Florissant, Colorado	Carpenter, 1930
Aphaenogaster maculipes Theobald	Haut-Rhin, Germany	Theobald, 1937
Aphaenogaster maculata Theobald	Aix-en-Provence, France	Theobald, 1937
Aphaenogaster sommerfeldti Mayr	Baltic Amber	Wheeler, 1914
Aphaenogaster oligocenica Wheeler	Baltic Amber	Wheeler, 1914

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Myrmicinae (continued)		
Aphaenogaster mersa Wheeler	Baltic Amber	Wheeler, 1914
Sima klebsi Wheeler	Baltic Amber	Wheeler, 1914
Sima ocellata Mayr	Baltic Amber	Wheeler, 1914
Sima simplex Mayr	Baltic Amber	Wheeler, 1914
Sima angustata Mayr	Baltic Amber	Wheeler, 1914
Sima lacrimarum Mayr	Baltic Amber	Wheeler, 1914
Sima klebsi Theobald	Haut-Rhin, Germany	Theobald, 1937
Sima oligocenica Theobald	Gard, France	Theobald, 1937
Monomorium pilipes Mayr	Baltic Amber	Wheeler, 1914
Monomorium mayrianum Wheeler	Baltic Amber	Wheeler, 1914
Erebomyrma antiqua (Mayr)	Baltic Amber	Wheeler, 1914
Erebomyrma thorali Theobald	Haut-Rhin, Germany	Theobald, 1937
Vollenhovia beyrichi (Mayr)	Baltic Amber	Wheeler, 1914
Vollenhovia prisca (Andre)	Baltic Amber	Wheeler, 1914
Stenamma berendti (Mayr)	Baltic Amber	Wheeler, 1914
**Electromyrmex klebsi* Wheeler	Baltic Amber	Wheeler, 1914
**Agroecomyrmex duisburgi* (Mayr)	Baltic Amber	Wheeler, 1914
Myrmica longispinosa Mayr	Baltic Amber	Wheeler, 1914
Myrmica archaica Meunier	Rott, Germany	Meunier, 1915
**Nothomyrmica rudis* (Mayr)	Baltic Amber	Wheeler, 1914
**Nothomyrmica intermedia* Wheeler	Baltic Amber	Wheeler, 1914
**Nothomyrmica rugosostriata* (Mayr)	Baltic Amber	Wheeler, 1914
**Nothomyrmica petiolata* (Mayr)	Baltic Amber	Wheeler, 1914
Leptothorax gracilis Mayr	Baltic Amber	Wheeler, 1914

Leptothorax glaesarius Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax longaevus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax hystriculus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax placivus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax gurnetensis Cockerell	Isle of Wight, England	Cockerell, 1915
Leucotaphus cockerelli Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
**Stiphromyrmex robustus* (Mayr)	Baltic Amber	Wheeler, 1914
**Parameranoplus primaevus* Wheeler	Baltic Amber	Wheeler, 1914
Stigmomyrmex venustus Mayr	Baltic Amber	Wheeler, 1914
**Enneamerus reticulatus* Mayr	Baltic Amber	Wheeler, 1914
Solenopsis maxima (Förster)	Haut-Rhin, Germany	Theobald, 1937
Solenopsis valida (Förster)	Haut-Rhin, Germany	Theobald, 1937
Solenopsis major Theobald	Haut-Rhin, Germany	Theobald, 1937
Solenopsis superba Förster	Haut-Rhin, Germany	Theobald, 1937
Solenopsis försteri Theobald	Haut-Rhin, Germany	Theobald, 1937
Solenopsis blanda Theobald	Haut-Rhin, Germany	Theobald, 1937
Pheidole tertiaria Carpenter	Florissant, Colorado	Carpenter, 1930
Messor sculpteratus Carpenter	Florissant, Colorado	Carpenter, 1930
Pogonomyrmex fossilis Carpenter	Florissant, Colorado	Carpenter, 1930
Lithomyrmex rugosus Carpenter	Florissant, Colorado	Carpenter, 1930
Lithomyrmex striatus Carpenter	Florissant, Colorado	Carpenter, 1930
**Cephalomyrmex rotundatus* Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderinae		
**Protaneuretus succineus* Wheeler	Baltic Amber	Wheeler, 1914
**Paraneuretus tornquisti* Wheeler	Baltic Amber	Wheeler, 1914
**Paraneuretus longipennis* Wheeler	Baltic Amber	Wheeler, 1914
**Mianeuretus mirabilis* Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus oviformis Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus coquandi Theobald	Haut-Rhin, Germany	Theobald, 1937

TABLE 4 (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Myrmicinae (continued)		
Aphaenogaster mersa Wheeler	Baltic Amber	Wheeler, 1914
Sima klebsi Wheeler	Baltic Amber	Wheeler, 1914
Sima ocellata Mayr	Baltic Amber	Wheeler, 1914
Sima simplex Mayr	Baltic Amber	Wheeler, 1914
Sima angustata Mayr	Baltic Amber	Wheeler, 1914
Sima lacrimarum Mayr	Baltic Amber	Wheeler, 1914
Sima klebsi Theobald	Haut-Rhin, Germany	Theobald, 1937
Sima oligocenica Theobald	Gard, France	Theobald, 1937
Monomorium pilipes Mayr	Baltic Amber	Wheeler, 1914
Monomorium mayrianum Wheeler	Baltic Amber	Wheeler, 1914
Erebomyrma antiqua (Mayr)	Baltic Amber	Wheeler, 1914
Erebomyrma thorali Theobald	Haut-Rhin, Germany	Theobald, 1937
Vollenhovia beyrichi (Mayr)	Baltic Amber	Wheeler, 1914
Vollenhovia prisca (Andre)	Baltic Amber	Wheeler, 1914
Stenamma berendti (Mayr)	Baltic Amber	Wheeler, 1914
•*Electromyrmex klebsi* Wheeler	Baltic Amber	Wheeler, 1914
•*Agroecomyrmex duisburgi* (Mayr)	Baltic Amber	Wheeler, 1914
Myrmica longispinosa Mayr	Baltic Amber	Wheeler, 1914
Myrmica archaica Meunier	Rott, Germany	Meunier, 1915
•*Nothomyrmica rudis* (Mayr)	Baltic Amber	Wheeler, 1914
•*Nothomyrmica intermedia* Wheeler	Baltic Amber	Wheeler, 1914
•*Nothomyrmica rugosostriata* (Mayr)	Baltic Amber	Wheeler, 1914
•*Nothomyrmica petiolata* (Mayr)	Baltic Amber	Wheeler, 1914
Leptothorax gracilis Mayr	Baltic Amber	Wheeler, 1914

Leptothorax glaesarius Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax longaevus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax hystriculus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax placivus Wheeler	Baltic Amber	Wheeler, 1914
Leptothorax gurnetensis Cockerell	Isle of Wight, England	Cockerell, 1915
Leucotaphus cockerelli Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
•*Stiphromyrmex robustus* (Mayr)	Baltic Amber	Wheeler, 1914
•*Parameranoplus primaevus* Wheeler	Baltic Amber	Wheeler, 1914
Stigmomyrmex venustus Mayr	Baltic Amber	Wheeler, 1914
•*Enneamerus reticulatus* Mayr	Baltic Amber	Wheeler, 1914
Solenopsis maxima (Förster)	Haut-Rhin, Germany	Theobald, 1937
Solenopsis valida (Forster)	Haut-Rhin, Germany	Theobald, 1937
Solenopsis major Theobald	Haut-Rhin, Germany	Theobald, 1937
Solenopsis superba Förster	Haut-Rhin, Germany	Theobald, 1937
Solenopsis försteri Theobald	Haut-Rhin, Germany	Theobald, 1937
Solenopsis blanda Theobald	Haut-Rhin, Germany	Theobald, 1937
Pheidole tertiaria Carpenter	Florissant, Colorado	Carpenter, 1930
Messor sculpteratus Carpenter	Florissant, Colorado	Carpenter, 1930
Pogonomyrmex fossilis Carpenter	Florissant, Colorado	Carpenter, 1930
Lithomyrmex rugosus Carpenter	Florissant, Colorado	Carpenter, 1930
Lithomyrmex striatus Carpenter	Florissant, Colorado	Carpenter, 1930
•*Cephalomyrmex rotundatus* Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderinae		
•*Protaneuretus succineus* Wheeler	Baltic Amber	Wheeler, 1914
•*Paraneuretus tornquisti* Wheeler	Baltic Amber	Wheeler, 1914
•*Paraneuretus longipennis* Wheeler	Baltic Amber	Wheeler, 1914
•*Mianeuretus mirabilis* Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus oviformis Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus coquandi Theobald	Haut-Rhin, Germany	Theobald, 1937

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Dolichoderinae (continued)		
Dolichoderus bruneti Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus explicans Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus affectus Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus balticus Theobald	Aix-en-Provence, France	Theobald, 1937
Dolichoderus balticus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus oviformis Theobald	Gard, France	Theobald, 1937
Dolichoderus antiquus Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus rohweri Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus cornutus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus passalomma Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus elegans Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus mesosternalis Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus vexillarius Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus sculpteratus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus tertiarius (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus longipennis Mayr	Baltic Amber	Wheeler, 1914
Dolichoderus britannicus Cockerell	Isle of Wight, England	Cockerell, 1915
Dolichoderus gurnetensis Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Dolichoderus ovigerus Cockerell	Isle of Wight, England	Cockerell, 1915
Dolichoderus vectensis Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Iridomyrmex goepperti Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex goepperti Mayr	Baltic Amber	Wheeler, 1914
Iridomyrmex geinitzi Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex geinitzi (Mayr)	Baltic Amber	Wheeler, 1914

Iridomyrmex breviantennis Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex florissantius Carpenter	Florissant, Colorado	Carpenter, 1930
Iridomyrmex obscurans Carpenter	Florissant, Colorado	Carpenter, 1930
Iridomyrmex constrictus (Mayr)	Baltic Amber	Wheeler, 1914
Iridomyrmex samlandicus Wheeler	Baltic Amber	Wheeler, 1914
Iridomyrmex oblongiceps Wheeler	Baltic Amber	Wheeler, 1914
Protazteca elongata Carpenter	Florissant, Colorado	Carpenter, 1930
Protazteca quadrata Carpenter	Florissant, Colorado	Carpenter, 1930
Protazteca capitata Carpenter	Florissant, Colorado	Carpenter, 1930
Liometopum miocenicum Carpenter	Florissant, Colorado	Carpenter, 1930
Liometopum oligocenicum Wheeler	Baltic Amber	Wheeler, 1914
Liometopum scudderi Carpenter	Florissant, Colorado	Carpenter, 1930
Elaeomyrmex gracilis Carpenter	Florissant, Colorado	Carpenter, 1930
Elaeomyrmex coloradensis Carpenter	Florissant, Colorado	Carpenter, 1930
Asymphylomyrmex balticus Wheeler	Baltic Amber	Wheeler, 1914
Pityomyrmex tornquisti Wheeler	Baltic Amber	Wheeler, 1914
Miomyrmex impactus (Cockerell)	Florissant, Colorado	Carpenter, 1930
Miomyrmex striatus Carpenter	Florissant, Colorado	Carpenter, 1930
Petraeomyrmex minimus Carpenter	Florissant, Colorado	Carpenter, 1930
Formicinae		
Plagiolepis succini André	Baltic Amber	Wheeler, 1914
Plagiolepis klinsmanni Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis kuenowi Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis squamifera Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis singularis Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis solitaria Mayr	Baltic Amber	Wheeler, 1914
**Rhopalomyrmex pygmaeus* Mayr	Baltic Amber	Wheeler, 1914
Dimorphomyrmex theryi Emery	Baltic Amber	Wheeler, 1914, 1929
Dimorphomyrmex mayri Wheeler	Baltic Amber	Wheeler, 1914

TABLE 4 (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Dolichoderinae (continued)		
Dolichoderus bruneti Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus explicans Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus affectus Theobald	Haut-Rhin, Germany	Theobald, 1937
Dolichoderus balticus Theobald	Aix-en-Provence, France	Theobald, 1937
Dolichoderus balticus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus oviformis Theobald	Gard, France	Theobald, 1937
Dolichoderus antiquus Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus rohweri Carpenter	Florissant, Colorado	Carpenter, 1930
Dolichoderus cornutus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus passalomma Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus elegans Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus mesosternalis Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus vexillarius Wheeler	Baltic Amber	Wheeler, 1914
Dolichoderus sculpteratus (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus tertiarius (Mayr)	Baltic Amber	Wheeler, 1914
Dolichoderus longipennis Mayr	Baltic Amber	Wheeler, 1914
Dolichoderus britannicus Cockerell	Isle of Wight, England	Cockerell, 1915
Dolichoderus gurnetensis Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Dolichoderus ovigerus Cockerell	Isle of Wight, England	Cockerell, 1915
Dolichoderus vectensis Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
Iridomyrmex goepperti Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex goepperti Mayr	Baltic Amber	Wheeler, 1914
Iridomyrmex geinitzi Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex geinitzi (Mayr)	Baltic Amber	Wheeler, 1914
Iridomyrmex breviantennis Theobald	Haut-Rhin, Germany	Theobald, 1937
Iridomyrmex florissantius Carpenter	Florissant, Colorado	Carpenter, 1930
Iridomyrmex obscurans Carpenter	Florissant, Colorado	Carpenter, 1930
Iridomyrmex constrictus (Mayr)	Baltic Amber	Wheeler, 1914
Iridomyrmex samlandicus Wheeler	Baltic Amber	Wheeler, 1914
Iridomyrmex oblongiceps Wheeler	Baltic Amber	Wheeler, 1914
Protazteca elongata Carpenter	Florissant, Colorado	Carpenter, 1930
Protazteca quadrata Carpenter	Florissant, Colorado	Carpenter, 1930
Protazteca capitata Carpenter	Florissant, Colorado	Carpenter, 1930
Liometopum miocenicum Carpenter	Florissant, Colorado	Carpenter, 1930
Liometopum oligocenicum Wheeler	Baltic Amber	Wheeler, 1914
Liometopum scudderi Carpenter	Florissant, Colorado	Carpenter, 1930
Elaeomyrmex gracilis Carpenter	Florissant, Colorado	Carpenter, 1930
Elaeomyrmex coloradensis Carpenter	Florissant, Colorado	Carpenter, 1930
Asymphylomyrmex balticus Wheeler	Baltic Amber	Wheeler, 1914
Pityomyrmex tornquisti Wheeler	Baltic Amber	Wheeler, 1914
Miomyrmex impactus (Cockerell)	Florissant, Colorado	Carpenter, 1930
Miomyrmex striatus Carpenter	Florissant, Colorado	Carpenter, 1930
Petraeomyrmex minimus Carpenter	Florissant, Colorado	Carpenter, 1930
Formicinae		
Plagiolepis succini André	Baltic Amber	Wheeler, 1914
Plagiolepis klinsmanni Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis kuenowi Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis squamifera Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis singularis Mayr	Baltic Amber	Wheeler, 1914
Plagiolepis solitaria Mayr	Baltic Amber	Wheeler, 1914
**Rhopalomyrmex pygmaeus* Mayr	Baltic Amber	Wheeler, 1914
Dimorphomyrmex theryi Emery	Baltic Amber	Wheeler, 1914, 1929
Dimorphomyrmex mayri Wheeler	Baltic Amber	Wheeler, 1914

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Formicinae (continued)		
Gesomyrmex annectens Wheeler	Baltic Amber	Wheeler, 1914
Gesomyrmex expectans Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex miegi Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex hoernesi Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex hoernesi Mayr	Baltic Amber	Wheeler, 1929
**Prodimorphomyrmex primigenius* Wheeler	Baltic Amber	Wheeler, 1914
Oecophylla superba Theobald	Haut-Rhin, Germany	Theobald, 1937
Oecophylla brischkei Mayr	Baltic Amber	Wheeler, 1914
Oecophylla brevinodis Wheeler	Baltic Amber	Wheeler, 1914
Oecophylla megarche Cockerell	Isle of Wight, England	Donisthorpe, 1920
Oecophylla atavina Cockerell	Isle of Wight, England	Cockerell, 1915
Oecophylla perdita Cockerell	Isle of Wight, England	Cockerell, 1915
Prenolepis henschei Mayr	Baltic Amber	Wheeler, 1914
Prenolepis pygmaea Mayr	Baltic Amber	Wheeler, 1914
Lasius schiefferdeckeri Mayr	Baltic Amber	Wheeler, 1914
Lasius pumilus Mayr	Baltic Amber	Wheeler, 1914
Lasius epicentrus Theobald	Aix-en-Provence, France	Theobald, 1937
Lasius chambonensis Piton and Theobald	Lac Chambon, France	Piton and Theobald, 1935
Lasius tertiarius Zalessky	Ukraine, U.S.S.R.	Zalessky, 1949
Lasius punctulatus Mayr	Baltic Amber	Wheeler, 1914
Lasius nemorivagus Wheeler	Baltic Amber	Wheeler, 1914
Lasius edentatus Mayr	Baltic Amber	Wheeler, 1914
Tetramorium peritulus (Cockerell)	Florissant, Colorado	Wilson, 1955
Eoformica eocenica Cockerell	Florissant, Colorado	Cockerell, 1921c

Formica flori Mayr	Baltic Amber	Wheeler, 1914
Formica flori Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica horrida Wheeler	Baltic Amber	Wheeler, 1914
Formica phaethusa Wheeler	Baltic Amber	Wheeler, 1914
Formica clymene Wheeler	Baltic Amber	Wheeler, 1914
Formica constricta (Mayr)	Baltic Amber	Wheeler, 1914
Formica strangulata Wheeler	Baltic Amber	Wheeler, 1914
Formica tripartita Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica alsatica Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica serresi Theobald	Aix-en-Provence, France	Theobald, 1937
Formica latinodosa Theobald	Aix-en-Provence, France	Theobald, 1937
Formica oculata Theobald	Aix-en-Provence, France	Theobald, 1937
Formica minutula Theobald	Aix-en-Provence, France	Theobald, 1937
Formica sepulta Theobald	Aix-en-Provence, France	Theobald, 1937
Formica robusta Carpenter	Florissant, Colorado	Carpenter, 1930
Formica cockerelli Carpenter	Florissant, Colorado	Carpenter, 1930
Formica grandis Carpenter	Florissant, Colorado	Carpenter, 1930
Formica masculipennis Piton and Theobald	Auxillac, France	Piton and Theobald, 1935
Formica pitoni Theobald	Lac Chambon, France	Piton and Theobald, 1935
Formica bauckhorni Meunier	Rott, Germany	Meunier, 1917
Formica auxillacensis Piton and Theobald	Auxillac, France	Piton and Theobald, 1935
Glaphyomyrmex oligocenicus Wheeler	Baltic Amber	Wheeler, 1914
Pseudolasius boreus Wheeler	Baltic Amber	Wheeler, 1914
Dryomyrmex fuscipennis Wheeler	Baltic Amber	Wheeler, 1914
Dryomyrmex fuscipennis Theobald	Haut-Rhin, Germany	Theobald, 1937
Dryomyrmex claripennis Wheeler	Baltic Amber	Wheeler, 1914
Glaphyromyrmex oligocenicus Theobald	Haut-Rhin, Germany	Theobald, 1937
Camponotus mengei Mayr	Baltic Amber	Wheeler, 1914
Camponotus mengei Theobald	Haut-Rhin, Germany	Theobald, 1937

TABLE 4. (CONTINUED)

Geological Age	Locality	References
OLIGOCENE Formicinae (continued)		
Gesomyrmex annectens Wheeler	Baltic Amber	Wheeler, 1914
Gesomyrmex expectans Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex miegi Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex hoernesi Theobald	Haut-Rhin, Germany	Theobald, 1937
Gesomyrmex hoernesi Mayr	Baltic Amber	Wheeler, 1929
•*Prodimorphomyrmex primigenius* Wheeler	Baltic Amber	Wheeler, 1914
Oecophylla superba Theobald	Haut-Rhin, Germany	Theobald, 1937
Oecophylla brischkei Mayr	Baltic Amber	Wheeler, 1914
Oecophylla brevinodis Wheeler	Baltic Amber	Wheeler, 1914
Oecophylla megarche Cockerell	Isle of Wight, England	Donisthorpe, 1920
Oecophylla atavina Cockerell	Isle of Wight, England	Cockerell, 1915
Oecophylla perdita Cockerell	Isle of Wight, England	Cockerell, 1915
Prenolepis henschei Mayr	Baltic Amber	Wheeler, 1914
Prenolepis pygmaea Mayr	Baltic Amber	Wheeler, 1914
Lasius schiefferdeckeri Mayr	Baltic Amber	Wheeler, 1914
Lasius pumilus Mayr	Baltic Amber	Wheeler, 1914
Lasius epicentrus Theobald	Aix-en-Provence, France	Theobald, 1937
Lasius chambonensis Piton and Theobald	Lac Chambon, France	Piton and Theobald, 1935
Lasius tertiarius Zalessky	Ukraine, U.S.S.R.	Zalessky, 1949
Lasius punctulatus Mayr	Baltic Amber	Wheeler, 1914
Lasius nemorivagus Wheeler	Baltic Amber	Wheeler, 1914
Lasius edentatus Mayr	Baltic Amber	Wheeler, 1914
Tetramorium peritulus (Cockerell)	Florissant, Colorado	Wilson, 1955
Eoformica eocenica Cockerell	Florissant, Colorado	Cockerell, 1921c
Formica flori Mayr	Baltic Amber	Wheeler, 1914
Formica flori Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica horrida Wheeler	Baltic Amber	Wheeler, 1914
Formica phaethusa Wheeler	Baltic Amber	Wheeler, 1914
Formica clymene Wheeler	Baltic Amber	Wheeler, 1914
Formica constricta (Mayr)	Baltic Amber	Wheeler, 1914
Formica strangulata Wheeler	Baltic Amber	Wheeler, 1914
Formica tripartita Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica alsatica Theobald	Haut-Rhin, Germany	Theobald, 1937
Formica serresi Theobald	Aix-en-Provence, France	Theobald, 1937
Formica latinodosa Theobald	Aix-en-Provence, France	Theobald, 1937
Formica oculata Theobald	Aix-en-Provence, France	Theobald, 1937
Formica minutula Theobald	Aix-en-Provence, France	Theobald, 1937
Formica sepulta Theobald	Aix-en-Provence, France	Theobald, 1937
Formica robusta Carpenter	Florissant, Colorado	Carpenter, 1930
Formica cockerelli Carpenter	Florissant, Colorado	Carpenter, 1930
Formica grandis Carpenter	Florissant, Colorado	Carpenter, 1930
Formica masculipennis Piton and Theobald	Auxillac, France	Piton and Theobald, 1935
Formica pitoni Theobald	Lac Chambon, France	Piton and Theobald, 1935
Formica bauckhorni Meunier	Rott, Germany	Meunier, 1917
Formica auxillacensis Piton and Theobald	Auxillac, France	Piton and Theobald, 1935
Glaphyomyrmex oligocenicus Wheeler	Baltic Amber	Wheeler, 1914
Pseudolasius boreus Wheeler	Baltic Amber	Wheeler, 1914
Dryomyrmex fuscipennis Wheeler	Baltic Amber	Wheeler, 1914
Dryomyrmex fuscipennis Theobald	Haut-Rhin, Germany	Theobald, 1937
Dryomyrmex claripennis Wheeler	Baltic Amber	Wheeler, 1914
Glaphyromyrmex oligocenicus Theobald	Haut-Rhin, Germany	Theobald, 1937
Camponotus mengei Mayr	Baltic Amber	Wheeler, 1914
Camponotus mengei Theobald	Haut-Rhin, Germany	Theobald, 1937

TABLE 4. (CONCLUDED)

Geological Age	Locality	References
OLIGOCENE Formicinae (continued)		
Camponotus vehemens Förster	Haut-Rhin, Germany	Theobald, 1937
Camponotus longiventris Theobald	Aix-en-Provence, France	Theobald, 1937
Camponotus saussurei Theobald	Aix-en-Provence, France	Theobald, 1937
Camponotus penninervis Theobald	Aix-en-Provence, France	Theobald, 1937
Camponotus fuscipennis Carpenter	Florissant, Colorado	Carpenter, 1930
Camponotus microcephalus Carpenter	Florissant, Colorado	Carpenter, 1930
Camponotus petrifactus Carpenter	Florissant, Colorado	Carpenter, 1930
Camponotus brodiei Donisthorpe	Isle of Wight, England	Donisthorpe, 1920
MIOCENE		
Ponerinae		
Ponera umbra Popov	Caucasus, U.S.S.R.	Popov, 1933
Myrmicinae		
Aphaenogaster axila Fujiyama	Chôjabaru, Japan	Fujiyama, 1970
Formicinae		
Camponotus obesus Piton	Joursac, France	Piton and Theobald, 1935
Camponotus tokunagai Naora	China	Naora, 1933
**Pseudocamponotus elkoanus* Carpenter	Elko, Nevada	Carpenter, 1930
Solenopsis longaevus Heer	Radoboj, Croatia	Poncracz, 1928
Formica cantalica Piton	Joursac, France	Piton and Theobald, 1935
Lasius crispus Piton	Joursac, France	Piton and Theobald, 1935
Lasius martynovi Popov	Caucasus, U.S.S.R.	Popov, 1933
Oecophylla leakeyi Wilson and Taylor	Kenya	Wilson and Taylor, 1964

*Extinct genera.

is so highly polyphyletic remains unanswered, and is a problem unlikely to be resolved by the geological past.

However, the fossil record does provide intriguing information on the evolution of the bees and indicates that their sociality may well have been established prior to the Oligocene. The following survey of the fossil Apoidea is indicative of the diversity of bees which have been found (Table 5). Those species which were described by early 19th century entomologists (Latreille, Heer, Heyden, etc.) are excluded from this coverage because these were uniformly assigned to modern genera.[8] Cockerell (1909) claims that most of these species actually belonged to quite different and extinct genera.

Oligocene

The earliest bees in the fossil record are found in the Baltic Amber, of Lower Oligocene age. The bees in this deposit are well-diversified (Zeuner and Manning, 1976), and the most prevalent apoid genus in the amber, *Electrapis,* is thought to have been social. Cockerell (1909) based this conclusion on the occurrence of many specimens of *Electrapis meliponoides* crowded together in a small piece of amber, a suggestive but certainly not conclusive deduction. Zeuner (1944, 1951), however, believed *Electrapis* to be social based on its pollen collecting apparatus. The extent to which social behavior was developed in this genus nevertheless remains a matter of conjecture. *Electrapis* is considered by some to be directly ancestral to the highly eusocial *Apis,* although Kelner-Pillault (1974) disagrees with this relationship. She suggests that *Electrapis* is actually a long extinct genus which possessed many primitive characters and represents an evolutionary side-line of the Apoidea. Both hypotheses are highly conjectural.

The presence of long-tongued bees such as *Electrapis* suggests that the Baltic Amber bees were rather specialized. Tongue structure is assumed to have evolved in response to various morphological changes (i.e., longer corollas) which took place during the evolution of the angiosperms (Michener, 1974). Short-tongued bees such as the colletids are considered the more primitive members of the Apoidea and are representative of bee radiation that occurred at a time when most of the angiosperms had shallow flowers (Michener, 1974).

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[8] For a listing of these specimens, see Zeuner and Manning (1976).

In Late Oligocene deposits, the Apoidea are extremely well represented. Six major families of bees are known from this epoch: Halictidae, Andrenidae, Melittidae, Megachilidae, Anthophoridae, and Apidae. A total of 29 genera are represented, many of which are extant. Several specimens belonging to *Chalcobombus* and *Bombus* are described from deposits in both Europe and North America suggesting widespread radiation of this specialized group of bees by the Early Oligocene. In the Late Oligocene, bees very similar to *Apis mellifera* are found. Manning (1952) feels that some species from the Rott Shales possess almost all the necessary characters for placement in the genus *Apis* (Fig. 4). Moreover, in the Dominican Amber of Oligocene-Miocene age, several *Trigona* workers are found, providing convincing proof that social behavior was well established at this time (Michener, 1974).

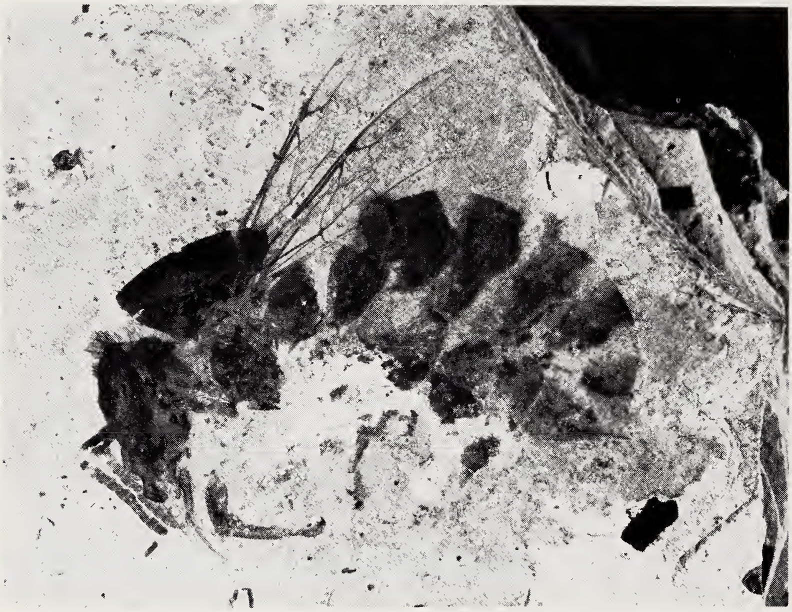

Figure 4. *Apis henshawi* Cockerell from Upper Oligocene of Rott, Germany. Original photograph of holotype in Museum of Comparative Zoology. Length of body, 15 mm.

Miocene

By the Miocene, the bee fauna is essentially modern. In Chiapas Amber from Mexico, bees have been discovered that are so similar to an existing Neotropical species that they have been assigned to the same subgenus, *Trigona* (*Nogueirapis*), and are scarcely different at the specific level (Wille, 1959). Fujiyama (1970) mentions the discovery of a fossil bee in a Japanese Miocene deposit and states that, “There is no room for doubt that this is a species of honeybee.”

A review of the fossil record reveals the following about the evolution of the bees. 1) We know that the Early Oligocene fauna is a mixture of primitive and advanced genera, although it appears to be dominated by fairly advanced species. By the end of this epoch, the fauna is modern in overall character. 2) We know that sociality had clearly arisen by the end of the Oligocene, and possibly much earlier. And 3) by the Miocene, the bees were virtually indistinguishable from the bees of today. Six families of bees are represented in the Oligocene: including the phylogenetically advanced Apidae with six genera and 22 species. Such diversity of relatively advanced bees is indicative of either a much longer history of the group than is evidenced by the fossil record, or a fairly short history characterized by the rapid speciation and explosive radiation of the group.

The bees are clearly derived from the spheciform wasps, although nothing is known about the nature of this sphecid ancestor (Wilson, 1971; Michener, 1974). In 1964, just prior to his death, F. J. Manning was investigating a sphecid from the Jurassic beds of Lerida Province, Spain, which “he thought might be (or be closely related to) the ancestor of the bees” (Zeuner and Manning, 1976, p. 155). This would be an astounding find if true, and it is unfortunate that nothing more is known — either about the specimen or about Manning’s reasons for thinking it ancestral to the bees.

The distinction between the Sphecoidea and the Apoidea is sufficiently subtle as to make determinations of fossil compressions extremely difficult. The presence of plumose hairs and enlarged basitarsi, characters which are important apoid features, rarely survive preservation unless the insect is preserved in amber.

The origin of the bees remains a subject of much speculation. It is believed that “insect-plant interactions played a key role in the origin of the angiosperm flower and component structures” (Hickey and Doyle, 1977, p. 92). Conversely, angiosperms have been instrumental to the evolutionary success of the Apoidea. On the basis of the evolutionary dependence of the two groups, can anything be said about their relationship in geological time? Two possibilities present themselves: 1) the angiosperms evolved first and were initially wind pollinated[9] or pollinated by arthropods other than Hymenoptera (e.g., Coleoptera, Diptera, Thysanoptera, possibly spiders); and 2) the first bees evolved from sphecid wasps prior to the origin of the angiosperms by adapting themselves to feeding on pteridosperm pollen or reproductive organs.

A closer look at these possibilities is warranted. Coleoptera and Diptera are found in the fossil record at least by the Triassic. This supports the argument that they could have served as vectors for dispersal of angiosperm pollen. The question arises, if these insects were capable of performing essential roles as pollinators, why didn't angiosperms arise earlier in the Mesozoic than the Cretaceous? Regal (1977) suggests that the limiting factor to angiosperm dispersal was the presence of seed-carrying birds and mammals. He argues that this method of seed dispersal, acting in conjunction with insect pollination, provided the selective advantages behind the subsequent primary radiation of the angiosperms. This is a sound argument, but says little about the insects which may have been pollinating these early plants. It would seem that successful dispersal of flowering plants is dependent on efficiency at two levels — pollination and seed dispersal. The explosive radiation of the angiosperms during the Cretaceous indicates that the more specialized insect pollinators, the bees, may have been present in order to explain this success.

This might support the possibility that pollen collecting bees had already evolved by the time the first angiosperms appeared. According to Wilson (1971, p. 75), the "Apoidea can be loosely characterized as sphecoid wasps that have specialized in collecting pollen instead of insect prey as larval food." The possibility, however speculative, exists that bees evolved in response to the food source presented by the pteridosperms but subsequently abandoned this resource when the angiosperms appeared. Certainly one way of accounting for the explosive radiation of the angiosperms would be

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[9] Stebbins (1970, p. 323) suggests that the earliest angiosperms were not wind pollinated.

TABLE 5. APOIDEA IN THE FOSSIL RECORD.[10]

Geological Age	Locality
EOCENE	
?Apidae	
Probombus hirsutus Piton	Menat, France
OLIGOCENE	
Halictidae	
**Cyrtapis anomalis* Cockerell	Florissant, Colorado
Halictus ruissatelensis Timon-David	Marseille, France
Halictus florissantellus Cockerell	Florissant, Colorado
Halictus miocenicus Cockerell	Florissant, Colorado
Halictus scudderiellus Cockerell	Florissant, Colorado
Andrenidae	
Andrena wrisleyi Salt	Baltic Amber
Andrena clavula Cockerell	Florissant, Colorado
Andrena grandipes Cockerell	Florissant, Colorado
Andrena hypolitha Cockerell	Florissant, Colorado
Andrena lagopus Latreille	Florissant, Colorado
Andrena percontusa Cockerell	Florissant, Colorado
Andrena sepulta Cockerell	Florissant, Colorado
**Lithandrena saxorum* Cockerell	Florissant, Colorado
**Pelandrena reducta* Cockerell	Florissant, Colorado
**Libellulapis antiquorum* Cockrell	Florissant, Colorado
**Libellulapis wilmattae* Cockerell	Florissant, Colorado
Melittidae	
**Ctenoplectrella dentata* Salt	Baltic Amber
**Ctenoplectrella viridiceps* Cockerell	Baltic Amber
**Ctenoplectrella splendens* Kelner-Pillault	Baltic Amber
**Glyptapis fuscula* Cockerell	Baltic Amber
**Glyptapis mirabilis* Cockerell	Baltic Amber
**Glyptapis neglecta* Salt	Baltic Amber
**Glyptapis reducta* Cockerell	Baltic Amber
**Glyptapis reticulata* Cockerell	Baltic Amber
Melitta willardi Cockerell	Baltic Amber
Megachilidae	
Anthidium mortuum (Meunier)	Rott, Germany
Anthidium exhumatum Cockerell	Florissant, Colorado
Anthidium scudderi Cockerell	Florissant, Colorado
**Dianthidium tertiarium* Cockerell	Florissant, Colorado
**Lithanthidium pertriste* Cockerell	Florissant, Colorado
Heriades bowditchi Cockerell	Florissant, Colorado
Heriades halictinus Cockerell	Florissant, Colorado
Heriades laminarum Cockerell	Florissant, Colorado
Heriades mersatus Cockerell	Florissant, Colorado

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[10] See Zeuner and Manning (1976) for reference citations.

TABLE 5. (CONTINUED)

Geological Age	Locality
OLIGOCENE Megachilidae (continued)	
Heriades mildredae Cockerell	Florissant, Colorado
Heriades priscus Cockerell	Florissant, Colorado
Heriades saxosus Cockerell	Florissant, Colorado
Megachile praedicta Cockerell	Florissant, Colorado
Osmia carbonum Heyden	Rott, Germany
Anthophoridae	
Ceratina disrupta Cockerell	Florissant, Colorado
Xylocopa friesei Statz	Rott, Germany
Tetralonia berlandi Theobald	Gard, France
Anthophora melfordi Cockerell	Florissant, Colorado
**Anthophorites gaudryi* Oustalet	Corent, France
**Protomelecta brevipennis* Cockerell	Florissant, Colorado
Apidae	
**Chalcobombus hirsutus* Cockerell	Baltic Amber
**Chalcobombus humilis* Cockerell	Baltic Amber
**Chalcobombus martialis* Cockerell	Baltic Amber
Bombus florissantensis (Cockerell)	Florissant, Colorado
**Sophrobombus fatalis* Cockerell	Baltic Amber
Trigona dominicana Wille and Chandler	Dominican Amber
Trigona eocenica Kelner-Pillault	Baltic Amber
**Electrapis apoides* Manning	Baltic Amber
**Electrapis meliponoides* (Buttel-Reepen)	Baltic Amber
**Electrapis indecisus* (Cockerell)	Baltic Amber
**Electrapis tristellus* (Cockerell)	Baltic Amber
**Electrapis palmnickenensis* (Roussy)	Baltic Amber
**Electrapis minuta* Kelner-Pillault	Baltic Amber
**Electrapis bombusoides*	Baltic Amber
Electrapis proava (Menge)	Baltic Amber
Electrapis tornquisti Cockerell	Baltic Amber
Apis cuenoti Theobald	Cereste, France
Apis henshawi Cockerell	Rott, Germany
Apis henshawi dormitans (Cockerell)	Rott, Germany
Apis henshawi kaschkei (Statz)	Rott, Germany
Apis aquitanensis de Rilly	Aix-en-Provence, France

TABLE 5. (CONCLUDED)

Geological Age	Locality
MIOCENE	
Halictidae	
Halictus schemppi (Armbruster)	Randeck, Germany
Andrenidae	
Andrena primaeva Cockerell	Oeningen, Germany
Megachilidae	
Lithurge adamitica (Heer)	Oeningen, Germany
Megachile amaguensis Cockerell	Siberia, U.S.S.R.
Osmia antiqua Heer	Oeningen, Germany
Osmia nigra Zeuner and Manning	Oeningen, Germany
Anthophoridae	
Xylocarpa jurinei (Heer)	Oeningen, Germany
Xylocopa hydrobiae Zeuner	Biebrich, Germany
Xylocopa senilis Heer	Oeningen, Germany
**Anthophorites thoracica* Heer	Radoboj, Croatia
**Anthophorites longaeva* Heer	Radoboj, Croatia
**Anthophorites mellona* Heer	Oeningen, Germany
**Anthophorites titania* Heer	Oeningen, Germany
**Anthophorites tonsa* Heer	Oeningen, Germany
**Anthophorites veterana* Heer	Oeningen, Germany
Apidae	
Bombus abavus Heer	Oeningen, Germany
Bombus proavus Cockerell	Latah, Washington
Trigona succini (Tosi)	Sicilian Amber
Trigona sicula (Tosi)	Sicilian Amber
Trigona silacea Wille	Chiapas, Mexico
Trigona devicta Kerr and Maule	Burma Amber
Apis armbrusteri armbrusteri Zeuner	Württemburg, Germany
Apis armbrusteri scharmanni (Armbruster)	Württemburg, Germany
Apis armbrusteri scheeri (Armbruster)	Württemburg, Germany
Apis armbrusteri scheuthlei (Armbruster)	Württemburg, Germany
Apis catanensis avolii Roussi	Sicilian Amber
Apis melisuga (Handlirsch)	Italy

*Extinct genera.

the explanation that the insect pollinators so important to their success were pre-adapted as pollination vectors. It is interesting to note at this point that bees have been observed foraging on conifer pollen in areas where other food resources are scarce. Ray Angelo (personal communication, May, 1978) reports observing *Colletes* sp. foraging in high numbers on *Juniperus virginiana* pollen cones. This is noteworthy in two respects: 1) this conifer is the only readily available pollen source in the particular habitat where observations took place (Concord, Mass.), and 2) the bees foraging on the tree are members of the primitive bee family Colletidae. This suggests that they are generalized enough to have retained the ability to forage on gymnosperm pollen. Nevertheless, the hypothesis that bees evolved before the advent of the angiosperms is highly speculative, and remains a difficult theory to prove. The possibility of a pre-angiosperm origin for the bees implies that the Apoidea, and possibly sociality in the Apoidea, may be older than indicated by the fossil record. An inherent problem, of course, is whether or not these early bees would be recognizable as such, or would be mistaken for sphecid wasps. The discovery of additional Cretaceous amber might well provide valuable insight into this problem.

SUMMARY

Wheeler writes in his 1928 book, "from the lowest to the highest forms in the series, all animals are at some time in their lives immersed in some society." It is the elaboration or evolution of these habits that leads to the eusocial behavior found in the Isoptera and certain groups of the Hymenoptera. The preceding account has examined insect sociality from a paleontological perspective in the hope that it will provide insight into the antiquity of this behavioral phenomenon. In addition, it has provided information on certain aspects of the evolution of the four major groups of social insects.

The Isoptera are highly eusocial at the ordinal level and evidence suggests an ancient origin for the group. The oldest fossil termite known is from a Late Cretaceous deposit in Canada. The presence of a distinct humeral suture at the wing base indicates that social behavior was developed in the Isoptera at this time. It is furthermore presumed that the termites arose in the early Mesozoic or possibly earlier, and from "protoblattoid" or blattoid stock. The hypogaeic lifestyle of most termites is not conducive to their

preservation as fossils and this may explain their absence in pre-Cretaceous deposits.

The first Hymenoptera appear in the Triassic and belong to the primitive family Xyelidae (Symphyta). Social Hymenoptera are not, however, found in the fossil record until the Upper Cretaceous. The ant species discovered in deposits of this age are more primitive than any now existing and have been of paramount importance in our understanding of ant phylogeny. By the mid-Tertiary, the ant fauna was extremely diverse; by the Miocene, the genera were essentially modern, and geographic distribution of the ants was apparently similar to that of today.

The Vespoidea although not very numerous in fossil deposits, have been found as far back as the Late Cretaceous, represented by one specimen assignable to the Masaridae. The presence of several vespoids in Eocene deposits strongly supports the possibility that social wasps evolved during the Late Cretaceous or Early Paleocene.

Apoidea extend into the fossil record only as far as the Oligocene, although it is speculated that they may have evolved much earlier. This is suggested by the fact that the bee fauna was essentially modern by the end of the Oligocene and also because the interdependence of angiosperms and bees suggests a co-evolutionary relationship beginning sometime in the Cretaceous.

Any discussion of sociality in the geological past must necessarily involve a certain amount of speculation. Morphological characters play an essential role in the analysis of an insect's social status, an example of this being the presence of the humeral suture in *Cretatermes*. In those social insect groups possessing very little morphological variation between castes, recognition of such social distinctions in the fossils is virtually impossible. It is generally assumed that extinct species belonging to extant genera possessed a similar type of social behavior in the past as is exhibited by the group today. To speculate further about the social habits of fossil insects is simply not possible. The mechanisms behind the evolution of eusociality in the insects remain unknown, yet the success of this form of social behavior is unquestioned. Only the recovery of additional material will provide evidence to further elucidate our understanding of the paleontological record of these insects.

As the record now stands, it is possible to state with a fair degree of certainty that insect sociality had evolved by the middle of the Cretaceous and perhaps much earlier.

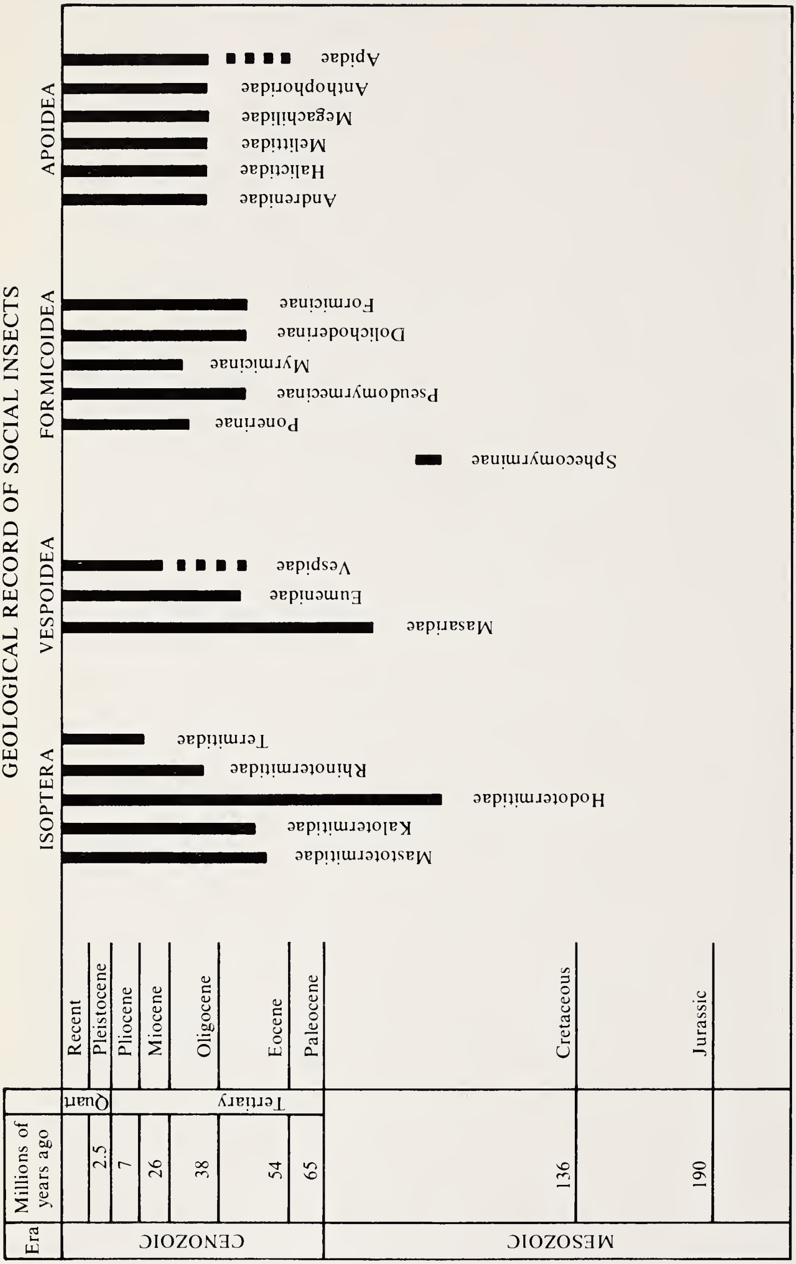

Figure 5. Geological time scale showing the distribution of twenty social insect families found in the fossil record. Dotted lines represent age extensions based on specimens of questionable taxonomic assignment.

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PARENTAL CARE IN *GUAYAQUILA COMPRESSA* WALKER (HOMOPTERA: MEMBRACIDAE)*

By T. K. Wood

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Introduction

Egg guarding or parental care is common in the Heteroptera. In the Hemipteran families studied (Bequaert 1925, Eberhard 1975, Melber and Schmidt 1975, 1977), most females desert their offspring before they reach maturity. Typically, parental investment in offspring is provided by females, but in the families Reduviidae (Ralston 1977) and Belostomatidae (Smith 1976), they are replaced by males. In the Homoptera, only females in the Membracidae (Hinton 1976, Wood 1974, 1976a, b, 1977a) and closely related families (Brown 1975) provide parental care of offspring. My studies (unpublished) and those by Hinton (1977) indicate female parental care is common in this family, particularly in the new world tropics.

My studies of 3 membracid species provide evidence for 2 major types of parental care in the family. In the 1st type, exemplified by *Umbonia crassicornis* Amyot and Serville and *Platycotis vittata* F., females remain on eggs until hatch and make a series of feeding slits for nymphs in the branch of the host plant. First instars move off the egg mass and aggregate along these slits with the female positioned below. Parent females actively maintain aggregated nymphs and defend them from potential predators such as adult coccinelids. Successful maturation in the field depends on both nymphs and the parent female remaining together on the same branch until offspring become adults (Wood 1974, 1976a, b).

Entylia bactriana Germar exemplifies the 2nd type of parental investment where the role of the parent female is reduced to the protection of eggs and the 1st two instars. Presumably, reduction of female investment is brought by mutualistic ant associations in this species. Although females are capable of protecting eggs and 1st to 2nd instar offspring, protection is enhanced if ants are in attendance. When females desert 1st to 2nd instars, nymphal maturbation in the field depends on protection provided by ants (Wood 1977a).

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Haviland's (1925) observations suggested females of *Guayaquila compressa* Walker may protect eggs. Although detailed observations were not reported, she clearly indicates females relocate offspring and that nymphs readily disperse when disturbed. Such reports require detailed confirmation before attempting a systematic analysis of the types of parental investment within Membracoidea.

METHODS

The study site was a lowland wet forest at Finca, LaSelva, a field station of the Organization for Tropical Studies in the province of Heredia in Costa Rica. *G. compressa* was always found in successional or edge areas along the forest on the following host plants: *Alchornea* sp., *Pterocarpus officinalis, Theobroma cacao, Euphorbiaceae* and an unidentified vine. Branches or leaves with insects were marked and observations were made daily for 2 to 16 days. Observations of 17 different females on eggs or with nymphs were made during 2 separate trips in August 1976 and 1977. Extensive attempts to increase numbers were made, but individuals tended to be on isolated trees some distance from each other.

RESULTS

Females on egg masses — Eggs are deposited by females in masses surrounded or embedded in a sticky, white matrix on top of plant tissue (Figs. 1 and 2). Two egg masses contained 78 and 88 eggs. Ovipositional sites varied; 6 females placed eggs on the underside of mature leaves on top of the main midrib, while 4 others placed egg masses on branches 6 to 12 inches from the apical meristem. Females sat on egg masses and usually faced the leaf petiole or the apex of the branch. In 1 egg mass, eggs hatched 12 days after deposition, while 9 others were observed for 7 to 10 days before eggs hatched. All egg masses which hatched had females present, while 1 egg mass where the female was removed failed to hatch. A portion of this egg mass without a female was damaged (as if eaten by a predator) the following day and developed mold growth during the subsequent 6 days of observation. This egg mass, deposited within 3 days of an egg mass which hatched, was followed long enough that if there were viable eggs, they should have hatched.

Figure 1. Photograph of female *G. compressa* on egg mass deposited on plant tissue on the underside of leaf (×7).

Females on eggs are sensitive to disturbances and will fly off egg masses. In several cases, touching the branch or leaves caused flight, while other females had to be repeatedly poked with a pencil before taking flight. Six females were disturbed to the point of flight in 12 separate trials. Some of these females simply dropped from the egg mass, but most flew off, landing on plants 5 to 15 feet away or made a circular flight back to the host. In all 12 trials, these 6 females found their way back to egg masses. In 5 trials, females returned within a 24-hour period, while in the remaining 7 trials they returned within 5 to 80 min. Females which could be observed often moved to several plants before locating the tree with the egg mass. Once on the host, they walked up and down branches until finding an egg mass. As they approached egg masses, females appeared to make fewer movements away from the egg mass, suggesting some ability to orient to cues associated with the egg mass (chemical or visual).

Parent female — offspring interaction — First instars associated with 5 parent females averaged 51.8 (range 37 to 60) individuals with nymphs forming tight clusters occupying 2 to 5 linear cm of plant surface. Egg hatch observed for 3 egg masses on the underside of the leaf midrib was completed within a 24-hour period. In 1 egg mass, 15 nymphs after egg hatch lined up along the leaf midrib between egg mass and leaf petiole facing the female next to the egg mass. When the leaf was turned over, all nymphs moved toward the female and clustered together under the egg mass until the leaf was returned to its normal position. During the subsequent 24 hrs, the remaining eggs hatched and all 60 nymphs with the parent female had moved 1 foot from the depleted egg mass on the leaf to the main woody branch. The behavior of nymphs and females on 2 other leaves was similar. One group moved 27 inches to another large branch within 24 hrs of egg hatch. Females which deposited eggs on branches moved with their nymphs away from the old egg mass to the apex of the branch, where they became associated with new leaves.

Relocation movements of parent females and nymphs is not only restricted to the 24 hr period after egg hatch. Four aggregations during a 4 to 7-day observation period relocated naturally 1 to 2 times. Relocation is not simply a matter of moving to an adjacent leaf or new shoot, but involves distances up to 3 feet in a 24-hr period. For example, one female and apparently all her offspring were observed to move down a main branch to a fork, then up the 2nd branch to the tip of a lateral twig.

The escape response of parent females and nymphs is different from other treehoppers. Six marked females and their offspring on isolated plants were disturbed by either moving the branch or probing the female with a pencil. Each of 5 females was tested 2 to 5 times and 1 female was tested once for a total of 18 trials. Only 1 trial for a female was done each day, but some females were tested on consecutive days. The amount of "violence" necessary to provoke flight by the female varied from trial to trial. My approaching the branch or touching it was sometimes effective, while in others, females had to be pushed with a pencil 5 to 30 times before taking flight. Distances females flew varied from 1 to 15 feet. Females relocated nymphs in 9 trials within 24 hrs; in 2 trials in 1.5 to 4.5 hrs, but in 7 trials, they returned within 50 min. (range of 12 to 50 min.). No one female consistently returned faster than others. Females sometimes simply dropped down into the tree, flew off making a

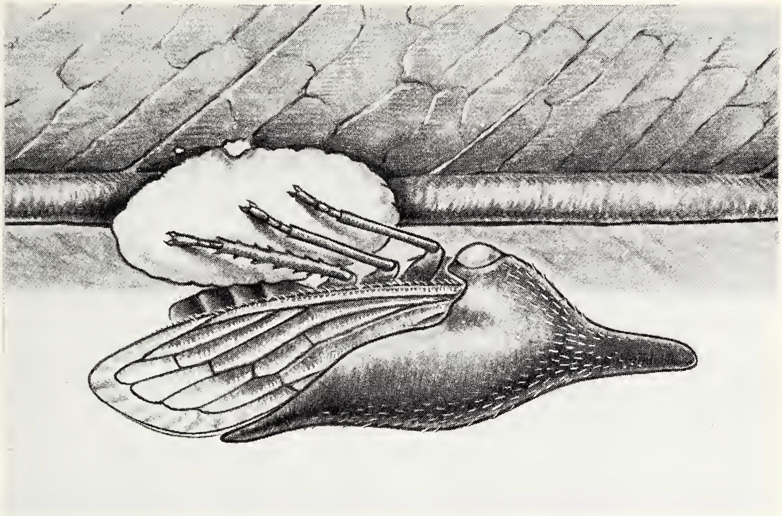

Figure 2. Female of *G. compressa* on egg mass [Original drawing by Sarah Landry].

circular flight back, or flew to adjacent trees with a series of short flights back to the host. One undisturbed female was observed to desert and relocate offspring, but whether this was triggered by a predator could not be determined.

Nymphs dispersed almost immediately in 12 of 18 trials after the female was disturbed. Nymphs moved distances of up to several feet and often reaggregated on new branches. In one trial, when the female was probed once, she fanned her wings which produced an audible clicking while nymphs dispersed up and down the branch. This female did not fly off until all nymphs had dispersed. Careful hand removal of 2 other females triggered immediate nymphal dispersal and reaggregation within a 40-min period. When the female was removed from 3 aggregations, nymphs remained together for 3 days.

When an injured or crushed nymph was presented, both siblings and female responded. In 1 case, as 7 of 56 1st instars moved past the female, she responded by a rapid twisting motion and followed the nymphs for 6 inches. When the female started to move, the remaining nymphs dispersed within a minute and walked past her. Lead nymphs stopped at a petiole 12 inches from the original site. After nymphs dispersed from the petiole, the female followed them up the branch, but then returned to the original site where 2 nymphs remained. After a total of 10 minutes, all nymphs were on 9 leaves on 3 different shoots. During the next 8 minutes, the female walked back and forth at the original site before moving to the main branch. Nymphs were still on several leaves but several groups were increasing to the point where 1 leaf had 29 of the 56 nymphs. In the next 70 minutes, the female repeatedly twisted laterally or walked up and down the branch and nymphs continued to consolidate into larger groups. Three groups were formed, one at the tip of shoot, one at its base, and one on the next shoot up the branch. The female after this period positioned herself below the group of nymphs at the base of the shoot. These nymphs then moved to the tip of the shoot, followed by the female. Within 2 min, all but 2 nymphs from the shoot above joined the aggregation. This aggregation then remained in the same place for 24 hours.

Single females on eggs or with offspring were typically the only conspecifics on most host plants. However, 1 host plant about 6 feet high had 2 females with offspring which were observed daily for 9 consecutive days. Initially, the eggs of 1 female had just hatched and nymphs had lined up along the midrib of a mature leaf, while the 2nd female with 50 1st instars was located on the same trunk, but 12 inches below the leaf with the 1st female. During the next 24 hr, nymphs with the 2nd female moved 2 feet up the trunk to new leaves on the apical shoot. The 1st female and her 60 nymphs moved off the leaf to the trunk while 10 nymphs remained on the leaf petiole. On the 3rd day of observation, both females and their broods had merged together on the terminal growth tip where they remained for the next 5 days. On 2 separate days during this 5-day period, leaves were touched with a pencil, triggering immediate movement of several nymphs down the petiole toward the females. One or both females responded to these nymphs by lateral twisting, back and forth walking, or walking backwards. In both trials, some nymphs went past females, but others which followed were stopped by tapping movements made by a female's prothoracic legs. In neither trial was there massive dispersal and within 5 min., all nymphs had reaggregated at the original site.

On the 8th day of observation, both females were probed with a pencil until they flew off and nymphs immediately dispersed from the petiole to the main trunk of the plant. Within 23 min., all nymphs had moved down the plant 2½ feet and reaggregated along the midrib of 3 mature leaves. Consolidation into 1 aggregation took place during the next 17 minutes without the presence of either parent female. Both females made a series of short flights back to the host and at the end of 1 hr, one female had located nymphs while the other was rapidly walking up and down branches off the main trunk. This last female, during a 6-min. period, walked to 5 different branches within 12 in. of nymphs. After 24 hrs, both females were with nymphs, but had relocated 18 inches away from the previous observation.

Adult aggregations — One aggregation of 34 teneral adults was observed for 10 days before dispersal. I could not determine if the parent female was present since coloration of teneral adults was similar to that of other parent females. The number of adults decreased during the first 5 days to 28, then to 15 during the next 4 days, with all individuals gone on the 10th day of observation. In the first 5 days, 2 females deposited eggs, one on the same host, the other on a host 15 feet away. I failed to locate other females on eggs in the surrounding area during a 7-day period after complete dispersal.

This adult aggregation was more sensitive to disturbance than females on eggs or with nymphs. On the first day of observation, all adults were together on the petiole of the leaf. When I accidentally moved the tree trunk, there was an explosive, almost synchronous dispersal with 3 individuals observed 10 feet away. In the following 60 min., individuals moved back to the host and began to form 2 aggregations near the original site. Once on the host, individuals walked up and down branches or flew short distances until coming to the one of the 2 groups where they stopped. At the end of 1 hr, 30 insects were in the 2 groups. In the next 48 hrs, 1 aggregation attracted all but 5 insects from the other. When this aggregation was disturbed again, dispersal occurred with all 28 adults back together at a new site on the same plant within 24 hrs. Without further disruptions, this aggregation remained in the same place for 3 days.

DISCUSSION

Female parental investment is well developed in the subfamily Membracinae (classification of Dietz 1975), particularly the tribes Hoplophorionini (*U. crassicornis* and *P. vittata*) and Aconophorini (*G. compressa*). Although the behavior of *G. compressa* is similar in most respects to species in the Hoplophorionini, certain aspects of nymphal behavior are similar to *E. bactriana* in the subfamily Smiliinae (tribe: Polyglyptini).

Placement of eggs by female *G. compressa* on top of plant tissue and held together by an accessory secretion is typical of the Aconophorini (Hinton 1977), while in the Hoplophorionini or Polyglyptini, eggs are inserted into plant tissue. Although all females sit on egg masses, the insertion of eggs into, as opposed to on top of, plant tissue may offer more protection from desiccation, parasites or egg predators due to less exposed egg surface area. Female *G. compressa* as with some Pentatomids with similar ovipositional habits, may not be able to protect peripheral eggs from parasites (Eberhard 1975).

Female *G. compressa* on egg masses are extremely sensitive to disturbances while females of *U. crassicornis* and *P. vittata* usually do not desert egg masses, even when given more violent treatment. Physically displaced females of the latter 2 species can relocate egg masses (Wood 1976b, Wood in preparation), but female *U. crassicornis* do not recognize individual egg masses (Wood in preparation). Whether individual female *P. vittata* or *E. bactriana* recognize their own egg masses has not been tested. Female *G. compressa* return to egg masses, but this may be an artifact of this species' patchy distribution and low population densities. A dislodged female, which flew 10 or so feet, may encounter an egg mass which has a high probability of being her own through random flights or walking, but whether females recognize their own egg masses must wait until choice tests can be made. Activity which results in egg mass relocation by female *G. compressa* is adaptive since females appear to be necessary in preventing mold growth, protection from egg parasites or predators, and maintaining offspring aggregations.

Protective or defensive adaptations of female *U. crassicornis* on eggs are cryptic coloration and lack of movement, but also involve the shape and hardness of the pronotum (Wood 1975, 1977a). Although mature female *P. vittata* are not physically protected by the pronotum, their cryptic coloration and lack of movement make them difficult to find on woody branches of the host plant (Wood 1976b). The pronotum of female *G. compressa* is similar in shape and hardness to that of mature *P. vittata,* but the black females provide contrast to the green leaf background. Thus, rapid female dispersal producing a startle response in a predator such as an arboreal anole would be a viable alternative for an otherwise unprotected female.

Herding of offspring by parent females within a host plant is unique to *G. compressa.* Female *U. crassicornis* and *P. vittata* remain with their offspring on the woody branches where eggs were deposited until nymphs reach maturity. Eggs of *E. bactriana* are deposited in leaves on herbaceous plants but nymphs move from these leaves and reaggregate on new ones after being deserted by females (Wood 1977a). Herding in *G. compressa* may permit enhanced exploitation of the host plant by reducing localized feeding damage.

Alarm or escape behavior actively involves both female *G. compressa* and offspring, differing significantly from that of *U. crassicornis* or *P. vittata.* Alarm displays by females of the latter species are produced in response to injured nymphs or predators, but nymphs do not disperse from the feeding site, nor are they deserted by parent females (Wood 1976a, b). *E. bactriana* females place themselves between predator and offspring. Nymphs remain with females initially, but upon prolonged exposure to alarm pheromones or injured females, nymphs disperse from the leaf. Escape behavior of nymphs is also modified by the behavior of various ant species which provide predator protection (Wood 1977a). Thus, the startle response produced by female *G. compressa* provides time to permit nymphal dispersal. Dispersed nymphs reaggregate with or without parent females and maintain an effective nymphal escape response if the parent female is captured or dies from other causes.

Females in a number of membracid species deposit eggs close to each other on a branch even when there appears to be an abundance of oviposition space, suggesting cooperative brood care (Wood, unpublished). *G. compressa* provides the first evidence to suggest an hypothesis for the adaptive nature of this cooperation. Normal herding behavior on a small host plant means 2 aggregations have a high probability of contacting each other. Even if the females were not related, it could be adaptive to merge aggregations to increase the effectiveness of the startle response since 2 females dispersing together or slightly out of phase may provide more time for nymphal dispersal. Even if 1 female is captured, the remaining female can facilitate reaggregation and maintenance of the aggregation. The interaction of 2 or more females may also facilitate normal maintenance of nymphal aggregations, promoting increased feeding efficiency and maturation.

Adult *G. compressa* maintain stable aggregates as do *U. crassicornis* and *P. vittata.* In both of the Hoplophorionini species, aggregations are stable for 15 to 20 or more days. During this period, individuals within the aggregation become progressively more sensitive to disturbances. Individual teneral adult *U. crassicornis* are unpalatable to *Anolis* lizards, but in addition, employ both an individual and collective cataleptic behavior to reduce predation (Wood 1975, 1977b). Older aggregations disperse explosively about the time of sexual maturity, but do not appear to reaggregate. The explosive dispersal and subsequent reaggregation of adult *G. compressa* is an extension of nymphal behavior and appears to be an effective response to predators such as anoles which are often seen walking or sunning themselves on branches similar to those where treehoppers are found.

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The illustration on the front cover of this issue of Psyche is a reproduction of the published figure of the minute diapriid, *Solenopsia americana* (1.3 mm. long), described by C. T. Brues in Psyche (1936, vol. 43, p. 17). The insect was taken in the nest of an ant, *Paratrechina parvula,* in eastern Tennessee.

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GEOGRAPHICAL DISTRIBUTION AND BIOLOGICAL OBSERVATIONS OF *CYPHODERRIS* (ORTHOPTERA: HAGLIDAE) WITH A DESCRIPTION OF A NEW SPECIES

BY GLENN K. MORRIS[1] AND DARRYL T. GWYNNE[2]

INTRODUCTION

With the exception of *Prophalangopsis obscura* (F. Walker) from India, *Cyphoderris* are sole survivors of a primitive orthopteran family, the Haglidae, abundant in the Triassic and ancestral to modern Ensifera (Zeuner, 1939; Ander, 1939; Ragge, 1955; Sharov, 1968).

There are presently two recognized species of *Cyphoderris: C. monstrosa* Uhler and *C. buckelli* Hebard. Their most dramatic distinguishing feature is the presence in *C. monstrosa,* and the absence in *C. buckelli,* of a prominent ventrally-directed sternal process, shaped like the claw of a hammer and located on the IXth sternum (Hebard, 1934). Specimens of both species have been extensively collected from mountainous areas of the North American northwest.

When Uhler established *Cyphoderris* in 1864 he had before him two adult male specimens. He published body measurements for both of these and there is a substantial size difference e.g. body length 22 mm for one specimen and only 16 mm for the other. These specimens are in the Museum of Comparative Zoology, Harvard University and we have examined them. The larger has a prominent

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sternal process and is *C. monstrosa* of present usage; the smaller specimen lacks the process and is *C. buckelli* of Hebard. It is the *C. buckelli* specimen which bears a red 'Type 792' label. Uhler's description concentrates on the larger specimen. Thus *monstrosa* is said to have a "pointed keel-like elevation, projected backwards upon the segment, grooved and emarginated at tip", i.e. a sternal process. He does not indicate that such a structure is absent from the other specimen.

Caudell (1904) described a variety of *C. monstrosa* which he called *Cyphoderris monstrosa piperi.* His types, which we have seen, are a male and a female from Mt. Rainier, Washington, housed in the U.S. National Museum. The male has a sternal process identical with that of Uhler's larger specimen and the female has Ander's organs (see below).

In 1922 Fulton collected a series of males in Oregon about 30 mi. southwest of Crater Lake (Fulton, 1930). He compared these with specimens furnished him by E. R. Buckell from southern British Columbia and found that Buckell's specimens lacked a genitalic process. Drawings were sent to Nathan Banks and to Caudell who compared them with the types of *monstrosa* and *piperi.*

It might now have become apparent that Uhler's types differed in their genitalia and that only the larger was of the same species as *piperi.* Since the published description applied substantially to the larger specimen one would then have expected it to be designated as *monstrosa.* But for some reason *piperi* was given specific status by Fulton and applied to the taxon with the sternal process while Uhler's name was conferred upon the smaller of Uhler's two species. Probably it was at this point that the red type label was appended at Harvard.

Hebard (1934), responding to Uhler's published description, recognized *piperi* as a synonym of *monstrosa* and gave the name *buckelli* to the species without the sternal process. It is clear that he did not examine Uhler's types and was unaware that one of these was his new species. Uhler did not designate a holotype and so in accordance with Article 74 of the code and in the interest of taxonomic stability, we here designate as lectotype the larger of the two specimens in his type series, that possessing the sternal process. This ensures that application of the name *monstrosa* continues in conformity with present custom.

A third species of *Cyphoderris, C. strepitans,* is described here. Its distribution lies southeast of both *monstrosa* and *buckelli* (Figure 5), populations of *strepitans* being originally considered as southern range extensions of *monstrosa* (Alexander, 1935; Willey and Willey, 1963). *C. strepitans* appears to be most similar in morphology and calling song to *buckelli* but is readily distinguished from the latter species by the structure of the male terminalia.

We have made use of the following abbreviations: ROM/ Royal Ontario Museum, Toronto, Canada; UMMZ/ University of Michigan, Museum of Zoology, Ann Arbor; ANSP/ Academy of Natural Sciences, Philadelphia; CNC/ Canadian National Collection, Ottawa, Canada; MCZ/ Museum of Comparative Zoology, Harvard University; USNM/ National Museum of Natural History, Smithsonian, Washington, D.C.

Cyphoderris strepitans new species
Figures 1 and 2

The specific name refers to the calling song: *strepitans* (Latin) 'making a great noise'.

SYNONOMY:

Cyphoderris monstrosus, Thomas (not Uhler), 1876. Proc. Davenp. Acad. Nat. Sci. I, p. 263. Wind River, Wyo.

Cyphoderris monstrosa, Hebard (in part not Uhler), 1934. Trans. Am. ent. Soc. 59, p. 374. Pearl, Col.

Cyphoderris monstrosa, G. Alexander (not Uhler) 1935. Ent. News 46, p. 30. Park Range (Pearl) Col.; *ibid* 1941. Univ. Col. Studies 1, p. 136.

Cyphoderris monstrosa, Willey & Willey (not Uhler) 1963. Ent. News 74, p. 200. Los Pinos Pass, Col.

Cyphoderris monstrosa, Evans (not Uhler) 1970. Bull. Mus. Comp. Zool. Harv. 140, p. 484. Jackson Hole, Wyo.

HOLOTYPE. Adult o. Park Range 24.7 mi. west of Cowdrey via Pearl, nr Big Creek Lakes, Jackson Co., Col., U.S.A.; 19 June 1976; Coll. G. K. Morris & D. T. Gwynne (Deposited ROM).

DESCRIPTION OF MALE TYPE. Body length (fastigium to paraprocts in dorsal view) 18.6 mm; pronotum mid-line length 7.2 mm; caudal pronotum width 7.8 mm; maximum exposed tegminal length in dorsal view 8.2 mm; length in lateral view of left metathoracic femur 8.3 mm.

Figure 1. Adult male *C. strepitans.*

Figure 2. Adult female *C. strepitans* (both antennae broken).

ALLOTYPE. Adult o. Los Pinos Pass, Saguache Co., Col., U.S.A.; 17 June 1977; Coll. D. T. Gwynne (Deposited ROM).

DESCRIPTION OF FEMALE ALLOTYPE. Body length (fastigium to extremity of epiproct in dorsal view) 21.5 mm; pronotum mid-line length 5.9 mm; caudal pronotum width 5.4 mm; length of ovipositor 2.0 mm; length in lateral view of left metathoracic femur 9.6 mm.

DIAGNOSIS. Adult males of *strepitans* are similar in size and coloration to *buckelli,* but readily distinguished by the presence of the sternal process (Figures 3 & 4). Males of both *strepitans* and *buckelli* are generally smaller than males of *monstrosa.* In life they usually lack the vivid pink coloration of *monstrosa*'s venter, their venters being instead cream white. The styli of the IXth sternum are strongly depressed in *monstrosa;* viewed from above each stylus is sublanceolate and broadest at its base; they are inserted on the lamellate dorsal projection of the IXth sternum at a distance slightly greater than the stylus length. By contrast the styli of *strepitans* are distally dilated and broadly rounded (mitten-like), gently arcuate and tapering slightly to the base; they are inserted close together immediately adjacent to the mid-line with less than one stylus length between their bases.

The sternal process of *monstrosa,* viewed in lateral outline, follows a broadly concave arc beyond the base of the styli to where it turns abruptly downward; in *strepitans* this arc is shorter and much shallower. From the end of the arc the process of *monstrosa* is more strongly reflexed than in *strepitans* and is often bent sharply forward at its extremity.

We are unable at present to distinguish between females of *buckelli* and *strepitans* but both of these species may be separated from *monstrosa* by their lack of the 'stridulatory' organs of Ander (1938). In *C. monstrosa* these structures are located dorsolaterally at the junction of abdomen and thorax (Ander, 1938; Kevan, 1954; Dumortier, 1963). Each organ consists of a row of robust posteriorly-directed recurved teeth on the slightly swollen posterolateral edge of the metanotum. The teeth contact a patch of transverse ridges on the first abdominal tergite during telescoping of the abdominal segment. Ander's organs are present in both sexes and are readily seen in later stadia of immatures. While *buckelli* sometimes possesses weak thoracic teeth, it never exhibits the ridged

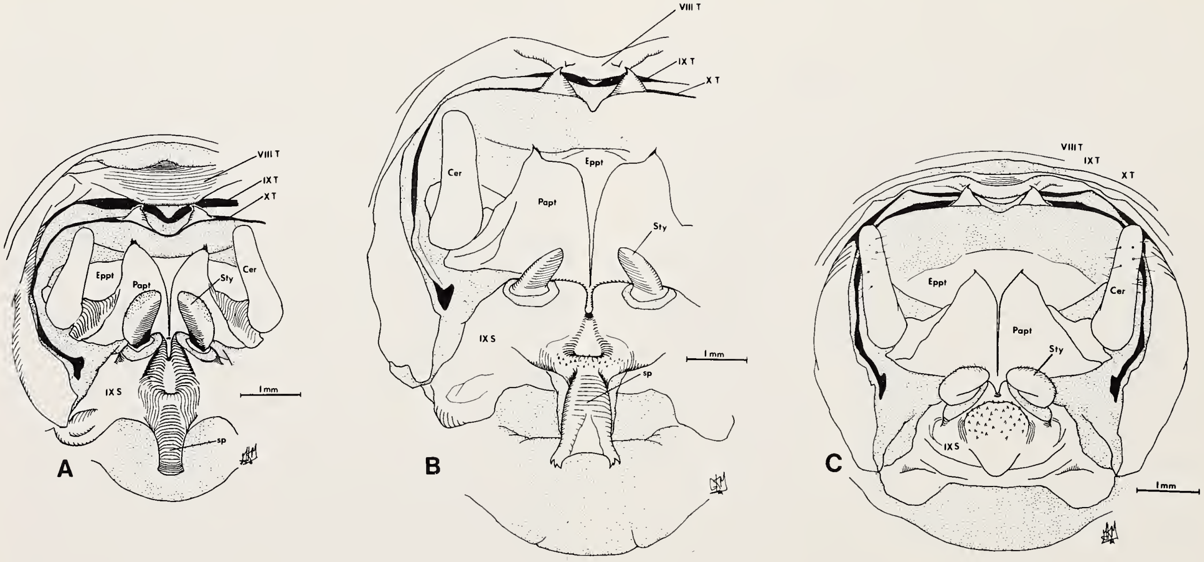

Figure 3. Posterior views of terminalia, A) *C. strepitans,* B) *C. monstrosa,* and C) *C. buckelli.* Symbols: VIIIT, 8th tergum; IXT, 9th tergum; XT, 10th tergum; Cer, cercus; Eppt, epiproct; Papt, paraproct; Sty, stylus; IXS, 9th sternum; sp, sternal process.

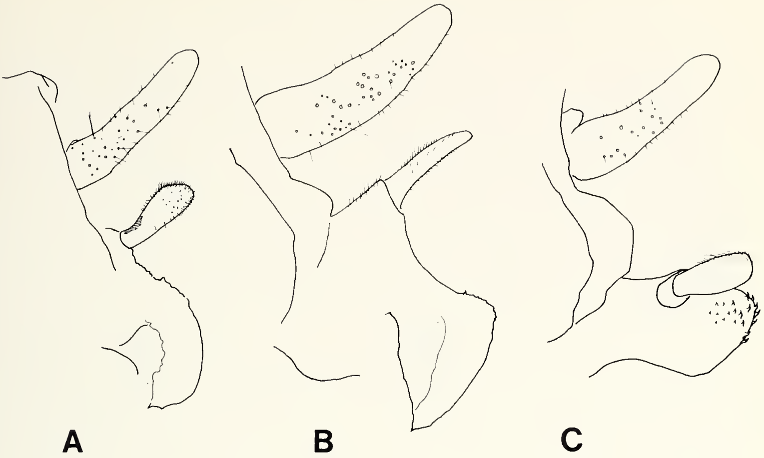

Figure 4. Lateral view of IXth sternum, A) *C. strepitans,* B) *C. monstrosa,* and C) *C. buckelli.*

patch. No stridulatory function has been established for these structures.

Paratypes. 9 adult ♂♂, same data as holotype (ROM, MCZ, & UMMZ); 1 adult ♀, same data as holotype (ROM); 4 adult ♂♂, Cowdrey, 8.8 mi. west on road to Pearl, 4 June 1978 (G. K. Morris & D. T. Gwynne) (ROM & Colorado State Univ., Ft. Collins); 1 adult ♂, Park Range nr Pearl, Col., 17 Aug. 1932 (G. Alexander) (ANSP); 1 adult ♂, Pearl, Col., 17 Aug. 1932 (G. Alexander) (Museum of University of Colorado, Boulder, Col.); 7 adult ♂♂, Los Pinos Pass, Col., 17 June 1977 (D. T. Gwynne) (USNM & CNC); 1 imm. ♂, Los Pinos Pass, Col., 17 June 1977 (D. T. Gwynne) (ROM); 1 adult ♂, Dunraven Pass, Yellowstone Nat. Pk, Wyo., 25 June 1930 (E. C. Van Dyke) (UMMZ); 1 adult ♀, Jackson Hole Res. Stn, Grand Teton Nat. Pk, Wyo., Aug. 1967 (H. E. & M. A. Evans) (USNM); 1 imm. ♂, Jackson Hole Res. Stn, Grand Teton Nat. Pk, Wyo. (H. E. & M. A. Evans) (USNM); 1 adult ♀, Stratton Exp. Watershed, nr Saratoga, Wyo. (J. M. Schmid) (USNM).

Key to *Cyphoderris* Species (Males only)

1. Subgenital plate (IXth sternum) with prominent ventrally-directed process (Figures 4a, b) 2
   Sternal process absent (Figure 4c) ..... *C. buckelli* Hebard
2. IXth sternum strongly produced posteriorly; sternal process with an angularly forward-bent tip, often appearing terminally cleft and toothed; styli of IXth sternum depressed, sublanceolate (Figure 3b); Ander's organ ridge-patch present and thoracic teeth robust; fastigium often weakly rugose .... *C. monstrosa* Uhler
   Posterior of sternal process not angular but rounded, never terminally cleft and toothed (Figure 3a); Ander's organ absent or if present, only as weak thoracic teeth; styli of IXth sternum mitten-like; fastigium smooth ... *C. strepitans* new species

GEOGRAPHICAL DISTRIBUTION

C. strepitans, as presently known, is confined to the mountains of Colorado and Wyoming (Figure 5). Its distribution is disjunct from that of *buckelli* and *monstrosa.* The broad valley of the Snake River isolates it on the northwest from the most southerly populations of Idaho *monstrosa;* if overlap occurs it must be north of Yellowstone in southern Montana.

C. monstrosa is found from the Canadian Rockies in the southwest corner of Alberta, west through southern British Columbia. It reaches much farther north than *buckelli,* to Quesnel and to Smithers B.C. (This latter record exceeds the northern extent of our map and could not be plotted; Smithers is about 700 miles north of the Canada/U.S. border.) A western arm of *monstrosa* extends down the Cascades, reaching almost to northern California. A less documented eastern arm crosses western Montana to a cluster of localities in the Salmon River Mts of central Idaho.

C. buckelli has a more restricted range. It lies between these arms, overlapping broadly with *monstrosa* in southern B.C. and extending south through northern Idaho. There are interesting isolated records from Columbia Falls, Montana and from near Seneca in east central Oregon. Though their distributions overlap substantially we have not found *monstrosa* and *buckelli* together at the demic level.

Figure 5. Geographical distribution of *Cyphoderris*.

However Buckell (1924) states that both species have been seen at Nicola, B.C. "in large numbers during late May feeding together upon flowers of *Amelanchier* . . .".

We have examined about 300 specimens of *monstrosa* and 200 of *buckelli.* In addition to the type, allotype and paratypes of *strepitans,* we have seen 20 or so alcoholic specimens supplied by Dr. R. Willey of the Univ. of Chicago. Dr. Willey's material is from Los Pinos Pass, Col., a locality which he discovered in 1962 (Willey & Willey, 1963).

All plotted localities are based upon actual examination of specimens excepting Wind River, Wyo. This record is taken from Thomas (1876) on the strength of his illustration of an adult male. Though the drawing is small the shape of the sternal process is apparent and marks the specimen as *strepitans.* A listing of localities is given below for each species.

C. strepitans: WYOMING: Dunraven Pass, Yellowstone N. Pk; Jackson Hole, Grand Teton N. Pk.; Wind River, Fremont Co.; Stratton Exp. Watershed, nr Saratoga, Carbon Co. COLORADO: Park Range, nr Big Creek Lks, Jackson Co.; Cowdrey, 8.8 mi. west, Jackson Co.; Los Pinos Pass, Saguache Co.

C. monstrosa: BRITISH COLUMBIA: Smithers; Quesnel; Chilcotin nr Williams Lk; Lac La Hache; Clinton; Lillooet; Whistler Mt., Garibaldi Prov. Pk; Salmon Arm; Field, Yoho N. Pk; Glacier N. Pk; Monck Prov. Pk; Merritt; Lumby; Peachland; Fish Lk, nr Summerland; Manning Prov. Pk; Hedley. ALBERTA: Jasper N. Pk; Mt. Eisenhower Cpgrd, Banff N. Pk; Sulphur Mt., Banff N. Pk; Bragg Creek, w. of Calgary; Barrier Lk, Kananaskis Valley; Kananaskis Lks, Kananaskis Valley. MONTANA: Belton, Flathead Co.; 2 mi. s. Elliston, Powell Co. IDAHO: McCall, Valley Co.; Challis, Custer Co.; Beach Cr., nr Bull Trout Lk, Custer Co.; Red Fish Lk, Custer Co.; Centerville, Boise Co.; 22 mi. ne. Idaho City, n. fork Boise R., Boise Co.; Camas Co.; Arco, Butte Co. WASHINGTON: Lk. Wenatchee St. Pk, Chelan Co.; Entiat R. Trail, Chelan Co.; 2 mi. se. Easton, Kittitas Co.; Stampede, King Co.; Paradise Valley, Mt. Rainier N. Pk.; Berkeley Park, Mt. Rainier N. Pk; Gooseprairie, Yakima Co.; Trout Lk Cpgrd, Klickitat Co. OREGON: Mt. Hood, Hood R. Co.; Hat Point, Wallowa Co.; Middle Sister, Lane Co. & Deschutes Co.; McKenzie Pass, Lane Co. & Deschutes Co.; Salt Creek Falls, Lane Co.; Waldo Lk, Lane Co.; Lost Lk, Willamette Nat. For., Linn Co.; North Santiam R., Linn Co.; Pinehurst, Jackson Co.; Union Creek, Jackson Co.; Crater Lk N. Pk, Klamath Co.; Douglas Co.; Olallie Lk, Marion Co.; Mt. Jefferson, Jefferson Co.

C. buckelli: BRITISH COLUMBIA: Chilcotin; Paul Lk Prov. Pk; Squilax; Salmon Arm; Nicola Lk; 2 mi. s. Merritt; Aspen Grove; Vernon; Lumby; Kelowna, nr airport; 3 mi. se. Rutland; Okanagan Falls; Rock Creek; Yahk; Ainsworth; Rosebery Prov. Pk; Cranbrook; Boswell, Kootenay Lk. IDAHO: Reeder Bay, Priest Lk, Bonner Co.; Sandpoint, Bonner Co.; 10 mi. s. Coeur d'Alene, Kootenai Co.; Moscow Mt., Latah Co.; Moscow, Latah Co.; Kamiah, Lewis Co. WASHINGTON: Newport, Pend Oreille Co.; Palouse, Whitman Co.; Pullman, Whitman Co. MONTANA: Columbia Falls, Flathead Co. OREGON: 3 mi. e. Seneca, Grant Co.

HABITAT AND FEEDING BEHAVIOR

The distribution of *Cyphoderris* corresponds roughly with the Cordilleran forest province (Gleason & Cronquist, 1964). In southern British Columbia *C. buckelli* occurs in the Dry Forest biotic area (Cowan & Guiguet, 1965) characterized by yellow pine (*Pinus ponderosa*) and at higher elevations, by interior Douglas fir (*Pseudotsuga menziesii*). *Amelanchier* (serviceberry), *Balsamorhiza* (arrow-leaf balsam-root) and *Berberis* (tall Oregon grape) are common understory plants in this association. In spring the nymphs and adult females of *C. buckelli* feed upon the flowers of these plants; night collecting at blooms is a good way to obtain specimens.

C. buckelli is also found in the Columbia Forest biotic area, the so-called interior wet belt of British Columbia. In 1977 we located large populations adjacent to Kootenay Lake near Boswell and at Rosebery on Slocan Lake.

C. monstrosa does occur in Dry Forest e.g. at Monck Prov. Park in southern British Columbia, but it is typically encountered in Subalpine Forest. Lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*) are characteristic of the Sub-alpine biotic area. In the Kananaskis Valley of southern Alberta we observed nymphs and adults to feed upon staminate cones of lodgepole pine (this before the cones reach a 'loose pollen' stage). Consumption was established by identifying cone bracts in the feces of field-caught specimens. Also caged insects were given cones and in most cases overnight they ate large portions.

It is presumably to feed upon staminate cones that *C. monstrosa* nymphs and adult females are observed at dusk climbing high into the trees. A useful method of collection is to search tree trunks with a flashlight just after sunset. The insects are always discovered oriented head upward. More often than not they occur in groups of 2 to 4 on the same trunk, which suggests that they may aggregate during their daytime stay in the leaf litter of the forest floor.

David Lightfoot of Oregon State University has studied *C. monstrosa* at Three Sisters in the central Oregon Cascades. He found this species abundant there in drier, more open stands of lodgepole pine and mountain hemlock (*Tsuga mertensiana*) above 5000′ elevation. In contrast to our observations of ascent as the evening progresses Lightfoot notes that the singers begin high in the trees (about 6 m) and gradually occupy lower and lower perches until singing at ground level.

C. strepitans is found in both subalpine forest and high altitude sagebrush prarie. The holotypic site near Big Creek Lakes is an open forest of subalpine fir (*Abies concolor*) and lodgepole pine at an altitude of 8800′. At Los Pinos Pass, Colorado, *strepitans* is found in aspen woods adjacent to open areas of prairie. The mature aspen (*Populus tremuloides*) has an understory of subalpine fir and englemann spruce (altitude 10,200′). Two predominant ground cover plants at both sites are kinnikinik (*Arctostaphylos* spp.) and a shrubby juniper (*Juniperus communis*). In the high altitude (8400′) sagebrush (*Artemesia tridentata*) prairie of North Park, Colorado, the density of singing males appeared to be much greater than in the nearby pine forest of the holotypic site to the east. *C. strepitans* is also very numerous in the sagebrush areas (altitude 6700′) of Grand Teton National Park, Wyoming. In late June, 1978, aggregations of singing males were easily heard while we drove along park roads at night. Thus, *C. strepitans* may be considered a predominantly sagebrush species although occurring in open forest habitats in the vicinity of sagebrush prairie.

ACOUSTIC BEHAVIOR

Males of all three species produce a succession of short musical trills, beginning in late evening and continuing well past midnight if weather permits. *C. buckelli* invariably sing near the ground from low shrubs (knee-height), the bases of tree trunks or on the forest floor itself. The same is true of *C. strepitans.* Only *C. monstrosa* climb high into the trees as the night's signalling progresses. At Monck Park singing heights in excess of 5 m were common and an hour after sunset collection without climbing trees becomes impossible.

The calling songs are generated by tegminal stridulation. As in Gryllidae the tegmina are morphological mirror-images, both left and right bearing a functional file and scraper. Unlike gryllids however, which maintain a characteristic 'right above' forewing overlap, the overlap of a *Cyphoderris* male may change during his lifetime and both files take part in his stridulation.

Certain Tettigoniidae also have mirror-image tegmina and two functional files: *Megatympanon speculatum* Piza (Listroscelinae) (Riek, 1976), *Neduba macneilli* Rentz & Birchim, *Neduba sierranus* Rehn & Hebard (Decticinae) (Morris et al., 1975). Most tettigoniids have structurally distinct left and right forewings and overlap them 'left above'. In the *Neduba* species some individuals show left above, some right above. Unlike *Cyphoderris* they appear to maintain their particular overlap as individuals through life. Both overlaps were represented by Riek's two (pinned) specimens of *M. speculatum.*

Spooner (1973) analysed the calling song of *C. monstrosa* and describes it as a trill of grylloid (sinusoidal) pulses at a carrier frequency of 13 kHz. He noted substantial variation in the intensity and frequency of pulses and suggested that these changes "reflect irregular switching of tegmina from top to bottom position". He refers to this habit as "switch-wing singing" and regards it as occurring several to many times in the course of a single trill.

Overlap at rest (i.e. between singing bouts) is very infrequently changed in *C. buckelli.* The overlap of 16 individually-caged males was monitored by examining them once a day during almost 2 weeks. Of 141 checks, only 4 reversals from the immediately previous overlap were observed; the incidence of resting overlap reversal was less than 3%. Thirteen of these males never showed an overlap reversal.

Four *C. monstrosa* males checked over 5 days, gave similar results: two were never found with reversed overlap (checked respectively 5 and 6 times), one was reversed once in 5 checks and one twice in 6 checks. If *Cyphoderris* alter overlap several times within a single trill, it is strange that individuals end up so consistently at the same overlap with which they began.

We recorded the calling song of a *C. monstrosa* specimen (Figure 6, 75–6) before and after damaging with a scalpel, several teeth in the central region of his right tegmen file. In oscillograms of post-mutilation recorded song, his use of the damaged file (i.e. right above overlap) was apparent as a drastic mid-pulse drop in amplitude. In one oscillogram, a portion of which makes up Figure 6 (second trace from bottom), 20 pulses in succession were 'right above'.

Switch-wing singing as suggested by distinctive pulse envelopes within the same trill was only evident in our records on one occasion. A male of *C. monstrosa* had been released in the immediate vicinity (i.e. within antennal range) of a mature female on the observer's hand. He began to sing while walking about on the hand and directing his attention toward the female. His song was recorded and on analysis found to be a trill in which every other pulse was identical in envelope and distinctly different from the intervening pulse i.e. there were two pulse types occurring in alternation without break in the sequence of the trill (Figure 6, bottom trace). This was apparently a courtship song.

It is clear that pulse envelopes are highly variable in the genus, though usually quite consistent for a particular recording session of a particular individual. Switch-wing stridulation is probably not an everyday feature of *C. monstrosa* calling song but it may occur under special circumstances such as courtship.

Oscillograms of normal calling songs are given in Figure 6. The pulses of *C. strepitans* and *C. buckelli* are apparently indistinguishable. They are usually wedge-shaped: each begins with a steep rise to maximum amplitude, then falls steadily to the pulse's end. The pulses of *C. monstrosa* also have a steep onset but are usually of longer duration. They are drawn out in an uneven envelope near their maximum amplitude before dropping away to silence.

Carrier frequency spectra of all three species are highly similar. Specimens were analysed 'live' (i.e. without tape-recording) by directing the output of a Bruel & Kjaer sound level meter (2204) fitted with a ¼″ microphone (4135) into a Tektronix 3L5 spectrum analyser. This system will detect ultrasonic frequencies up to 100 kHz. No substantial sound energy exists in the ultrasonic range for any of the *Cyphoderris* species. The sinusoidal nature of the waveform is apparent in the narrowness of the dominant frequency

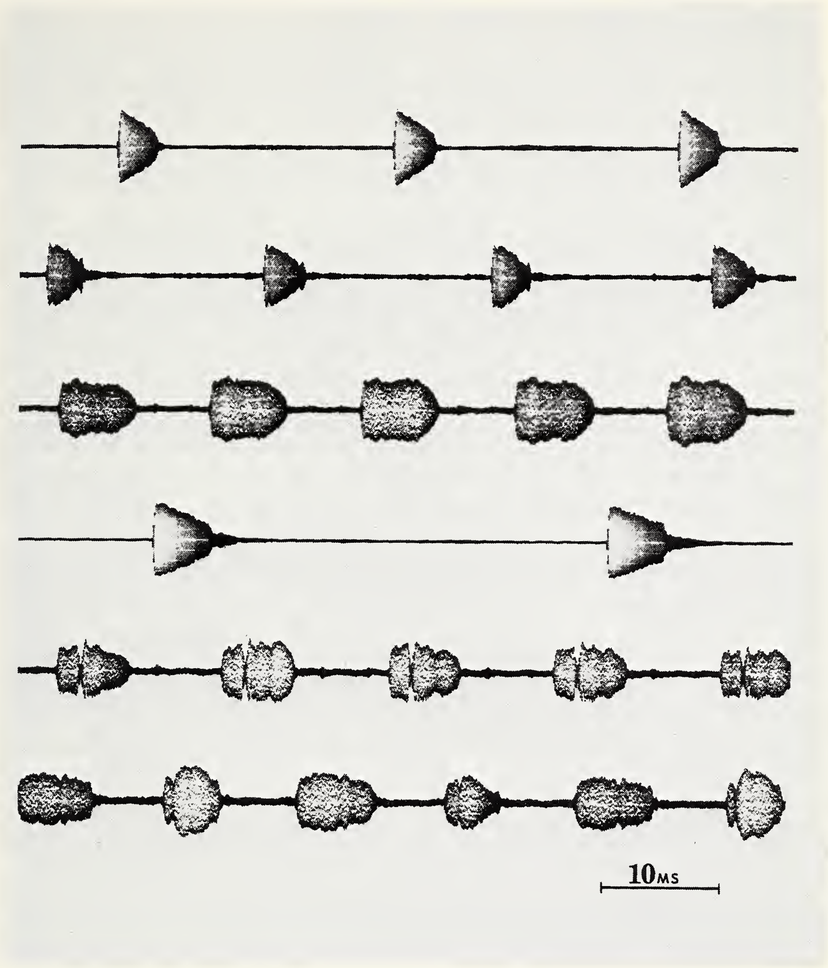

Figure 6. Oscillograms of *Cyphoderris* calling song. From top trace downward: *C. strepitans* 76–8, 17.8° C; *C. buckelli* 76–14, 25.0° C; *C. monstrosa* 75–6, 24.5° C, intact file; *C. monstrosa* 76–2, 8.7° C, field-recorded, Monck Prov. Pk B.C.; *C. monstrosa* 75–6, 24.0° C, file teeth of right forewing damaged; *C. monstrosa* 75–10, 23.1° C, male recorded singing in immediate presence of female.

peak, suggesting the operation of a sharply-tuned (high Q) tegminal resonator (Sales & Pye, 1974).

In the figured *C. strepitans* male (Figure 7), the dominant peak centers on 12.7 kHz and there are very weak second and third harmonics near 25 and 38 respectively. The *C. buckelli* specimen has its principal peak near 13.3 kHz and a lesser peak occupies the range 28–30 kHz. Like Spooner (1973) we obtained 13 kHz as the dominant carrier frequency of *C. monstrosa.*

Sound level measurements were obtained with the ¼″ microphone and the 2204 meter, the latter on 'linear, fast' setting. At 5 cm dorsal aspect, the sound level of *C. strepitans* (76–7) was between 100.5 and 101.0 dB. A specimen of *C. buckelli* (76–3) was 102 ± 2 dB at 6.5 cm dorsal.

Pulse rate varies linearly with temperature (Figure 8) as in other acoustic Ensifera (Walker 1962, 1975). Both field and laboratory recordings of calling song contributed to the regression lines. One *C. monstrosa* plotted point is from Spooner (1973) (S in Figure 8); 5

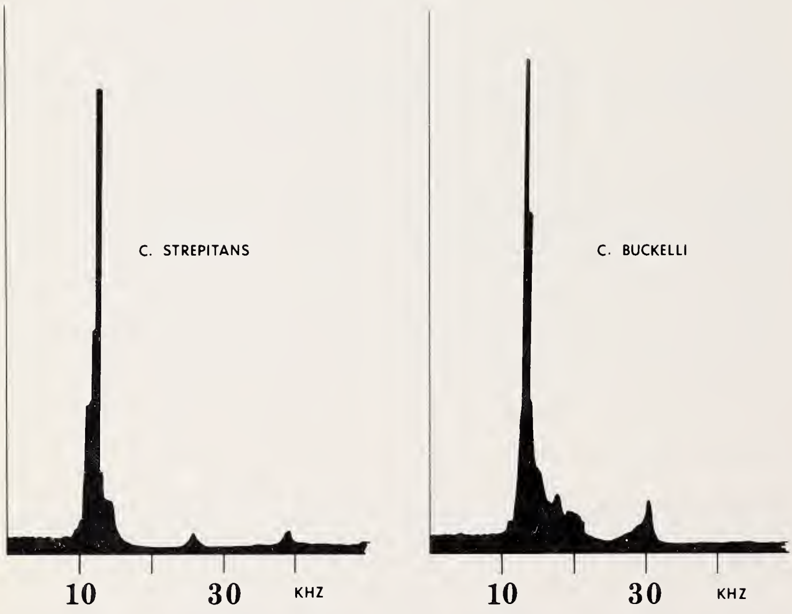

Figure 7. Calling song frequency spectrograms traced from photographs.

different males provide the other 6 points. *C. buckelli*'s regression is based on 12 different individuals, 3 at two different temperatures each. Each of the 13 *C. strepitans* pulse rates derives from a different individual; all those at temperatures of 8° C and below are field recordings. Pulse rates were calculated from an oscilloscope display in which a single beam sweep embraced 3–13 pulses. Successive, single-sweep samples (3–6), were averaged to obtain each plotted value. The coefficients of determination indicate a very good fit to the calculated regression lines. Although the *C. monstrosa* regression line is different from the *strepitans* and *buckelli* lines the slopes and Y intercepts of the latter two species are not significantly different.

C. strepitans males stridulate at very low temperatures. Previous reports cite minimal singing temperatures for acoustic Orthoptera of about 7° C [e.g. Fulton (1925) for the tree cricket *Oecanthus fultoni* (under the name of *O. niveus*) and Frings and Frings (1957) for the katydid *Neoconocephalus ensiger*]. On May 17, 1977, at the holotypic site, one of us (D.T.G.) heard three of four males singing from branches and logs near the ground when the air temperature at waist level was −0.5° C. On June 4 and 5, 1978, tape recordings were made of males singing at temperatures as low as 2° C (see Figure 8). Following the recording the thermometer bulb was placed close to the singing male's perch. There is a suggestion in the plotted rates in Figure 8 of a departure from linearity at very low temperatures.

In conclusion, the song of *C. monstrosa* differs from the other two species in both the shape of the pulse amplitude envelope and in pulse rate, both these parameters being useful diagnostic features. *C. buckelli* and *C. strepitans,* however, have virtually identical calling songs: song intensities, carrier frequencies, and pulse amplitude envelopes provide no basis for human discrimination; the pulse rates, especially, are indistinguishable at any given temperature.

It is interesting to note that Alexander (1969) has questioned the traditional interpretation that reproductive isolating mechanisms evolved to prevent "mating mistakes" between species. He suggested (citing evidence from acoustical insects) that species differences have most likely arisen as a result of the different selection pressures operating on populations while they are in allopatry. He reasoned that if this is so, among other things, we should rarely find identical pair forming signals among allopatric or allochronic species. *C. strepitans* and *C. buckelli* are allopatric (Figure 5) and by the above

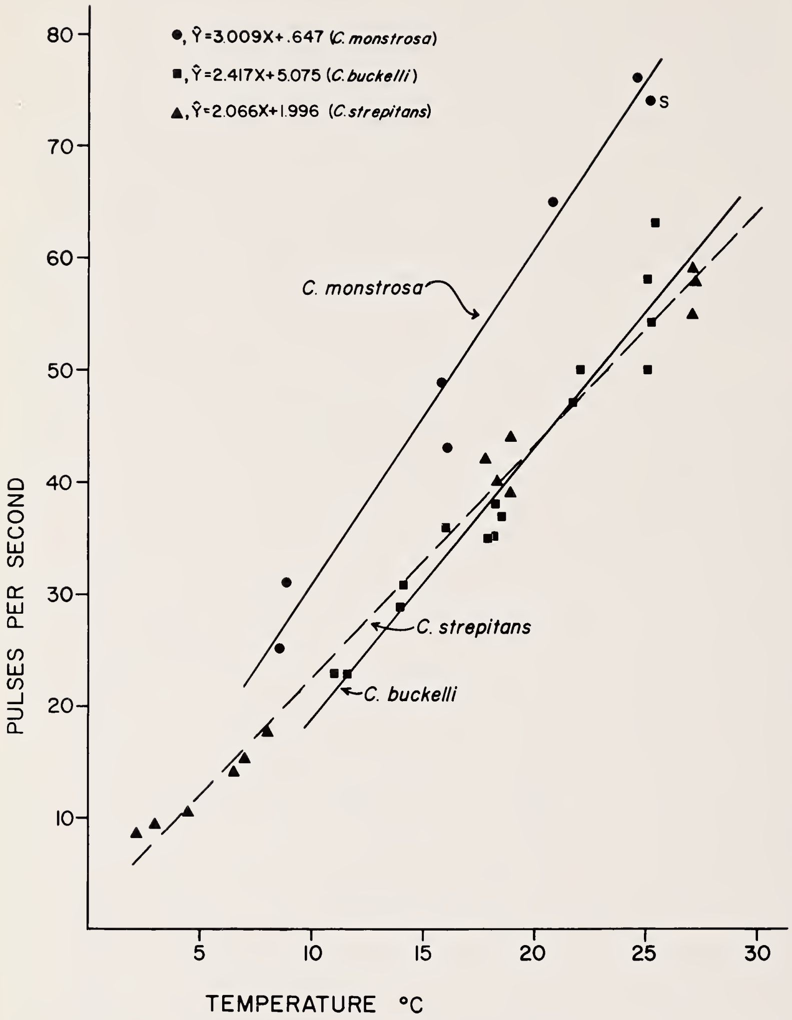

Figure 8. Relation of pulse rate and temperature in *Cyphoderris* calling song (S is from Spooner, 1973).

reasoning their songs should have diverged yet this is not the case. Any difference between these two species (including the above mentioned habitat differences) apparently have not affected their pair forming signals.

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DESCRIPTION OF THE ERGATOID QUEEN OF *POGONOMYRMEX MAYRI* WITH NOTES ON THE WORKER AND MALE (HYM., FORMICIDAE)*

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Introduction

During a recent stay in Santa Marta on the north coast of Colombia, I had the opportunity to study *Pogonomyrmex mayri,* the sole member of the subgenus *Forelomyrmex,* whose entire range is the desert and dry deciduous forest below 200 m. on the northwestern, western, and possibly southern skirts of the Sierra Nevada de Santa Marta.

This ant was described by Forel (1899: 61–62, footnote) from worker(s) and male(s) he collected. Neither he nor subsequent entomologists, including P. J. Darlington, found females. The reason females were unknown became clear as I worked in the area and later began to look at the biology of *P. mayri* more closely. Though I collected males from vegetation nearly year around (3 Sept. to 30 June), no winged females were seen in two years. Furthermore, only after thoroughly excavating 10 nests were any females found at all, one in each of 2 nests dug by my coworker, María del Carmen Hincapié, and her assistant. Both were ergatoid nest queens.

This paper presents a formal description of those queens, notes on the worker and male supplementing Forel's original description, and a discussion of the taxonomic status of *Pogonomyrmex mayri.* Notes on the biology of *P. mayri* will be reported later.

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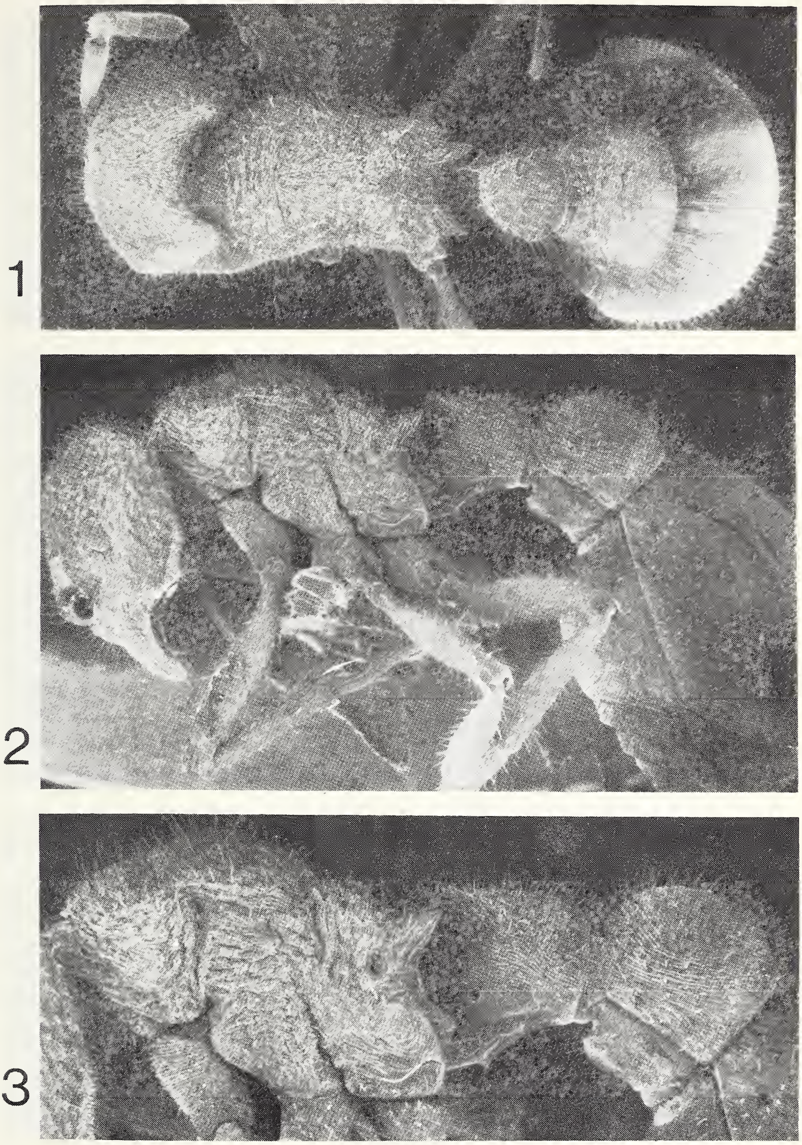
QUEEN

(Figs. 1–4, Table 1)

Two specimens (Museum of Comparative Zoology at Harvard University) taken by María del Carmen Hincapié from nests in soil behind the beach at Bahía Gairaca, about 20 km. by road east of Santa Marta, Colombia, in Parque Nacional Tayrona, on 2 different days, April 22, 1978 (#780422–6) and April 26, 1978 (#780426–9). The following description is based primarily on the first specimen, with occasional remarks on the second if they differ in some way. For each measurement, that of the first specimen is followed by that of the second.

Mandibles subtriangular; basal and masticatory borders meet at obtuse angle; outer border gently convex, slightly flattened midlength; masticatory border with 5 teeth increasing in size apically, the second tooth with a denticle on its distal edge (second specimen with denticle reduced on one mandible, absent on the other). Palpal formula 3,3 as determined from undissected specimens; neither palp reaching posterior margin of buccal cavity. Labrum with rounded lobes on either side of a sharp median emargination. Head (fig. 4) about as wide as long; in full face dorsal view occiput broadly V-shaped, with distinct occipital lobes; sides of head gently convex on temples to small bulge behind the eye, then indented to flat cheeks. Middle of clypeus weakly convex overall, both transversely and longitudinally; sculpture stops a weak median carina short of reaching apron; apron narrow, leading edge convex with median tooth bracketed by low rounded lobes; lateral arms form low narrowly rounded ridges in front of antennal fossae. Frontal triangle reduced to a narrow, deep Y-shaped sulcus separating clypeus from posterior ¾ of frontal lobes. Frontal lobes short, well separated; carinae convex. Eyes small, convex, ringed by a round-bottom sculptured groove.

Antennae 12-merous. Scape short and rather thick, not reaching vertex of head; bent at a nearly right angle within basal ¼ of length and largely flat beyond (extensor surface viewed from side). First 2 segments of flagellum longer than wide, L 0.21, 0.20; 0.18, 0.18; segments 3–7 wider than long; segments 8–11 about as long as wide. Apical segment much longer than any other, L 0.34, 0.37; apex narrowly rounded. Last 4 segments constitute a weakly defined



Figs. 1–3. Queen of *Pogonomyrmex mayri.* Fig. 1, dorsal view. Fig. 2, lateral view. Fig. 3, lateral view of trunk and waist (waviness of some hairs is an artifact of charging).

antennal club. Width of flagellar segments increases uniformly from first (0.13, 0.12) to last (0.18, 0.20).

Trunk in full dorsal view (fig. 1) with complete, fine, immobile, promesonotal suture; mesonotum bisected at about 2/3 of length by a faint shallow sulcus (probable remnant of scutoscutellar suture) which drops out at lateral margins; metanotum reduced to a sharp groove between mesonotum and propodeum. Propodeal spines robust, acute, their bases widely separated by a broad concavity. Propodeal spiracles prominent; their orifices circular, facing posterolaterad.

From the side (figs. 2, 3) dorsal profile convex; mesonotum set off by grooves, its outline higher and more convex than pronotum and propodeum. Distinct sutures separate pronotum and mesonotum from mesopleura; metapleura delimited by weak sulci scarcely distinguishable from the sculpture, expecially in areas anterior to the spiracle. Metapleural gland bulla well developed. Inferior propodeal plates broad, blunt. Dorsal face of propodeum curves broadly into declivous face.

Petiole robust (figs. 1–3), with broadly conical anterior peduncle and weakly differentiated posterior peduncle. Venter seen from below with 3 longitudinal ridges running from short acute tooth to posterior peduncle. Node in side view with flat anterior face (except for 2 low undulations) joining anterior peduncle at about a 135° angle, meeting dorsal face of node at an acute angle; dorsal face flat, broadly curving into short posterior face. Outline of node from above ovoid, slightly wider than long, widest just caudad of midlength. Anterior edge sharp (with low upturned burr in second specimen), gradually softening to broadly rounded along sides.

Postpetiole large, inflated; connection with gaster broad. In lateral view, dorsum strongly and evenly convex; venter much shorter than dorsum, profile undulate, anterior lip broadly rounded. From directly above (not as in fig. 1) node subtrapezoidal; posterior edge a broad convex arc somewhat flattened mesad, posterior corners broadly rounded, sides flat, tapered to corners of weakly concave anterior edge.

Gaster greatly enlarged, subglobose, heavily sclerotized, slightly longer than wide and slightly wider than deep; widest at midlength. Sclerites not fused, but rigidly articulated. Measured from side along axis, first tergum covers 90% of length of gaster; first sternum 53%.

Legs neither long and slender nor very robust. Femur lengths front to back 1.48, 1.50; 1.45, 1.45; 1.64, 1.65 mm., not incrassate (W/L 18, 18; 17, 18; 16, 16%). Hind tibia length 1.33, 1.48 mm. Middle and hind tarsi each with one short simple apical spur. Hind metatarsus 1.16, 1.29 mm.; tarsal claws simple.

Most of body with fine dense punctulate striae overlain by a coarse broken wavy sculpture (figs. 1–4): clypeus, top, sides and back of head, trunk (except those areas listed below), petiolar node and postpetiole. In other places the overlying sculpture is much reduced or absent, leaving largely flat surfaces of fine, punctulate striae: gula (some weakly undulate sculpture present), anterior face of pronotum, prosternum, forecoxae, dorsomedial surfaces of metapleural gland bullae, declivous face of propodeum (striae coarser, less dense), most of first gastric segment (striae weaken caudad). Striation much reduced, leaving predominately fine, densely punctate surfaces on: antennae (striae present but finer than elsewhere and not predominate), legs except first coxae, and end of first and most of succeeding segments of gaster (narrow coriaceous margins on each). Mandibles finely longtitudinally striate, without punctures. Inner surface of mandibles, peduncle and venter of petiole smooth and shining; the latter with scattered punctures. Striation more or less longitudinal on mandibles, antennae, clypeus, dorsum and sides of head, mesonotum, sides of trunk (though much confused in parts), coxae, anterior face and sides of petiolar node, sides and venter of postpetiole, and gaster. Striation essentially transverse on gula (bisected by median longitudinal ridge), pronotum, basal and declivous faces of propodeum (striae converge on apices of spines from all sides), dorsal surface of petiolar node, anterior and dorsal faces of postpetiole (transversely arcuate).

Whole body, except peduncle of petiole, covered with short, stiff, erect, acute golden hairs, interspersed with shorter, more flexuous recurved hairs. Apron of clypeus with longer flexuous hairs; hair on mandibles more decumbent. No psammophore of any sort. Color uniformly dark ferruginous brown, except for brown to yellow apical antennomere.

WORKER
(Figs. 6–8)

The worker is most strikingly different from the queen in its jet black color, its larger head, and smaller waist and gaster. It appears

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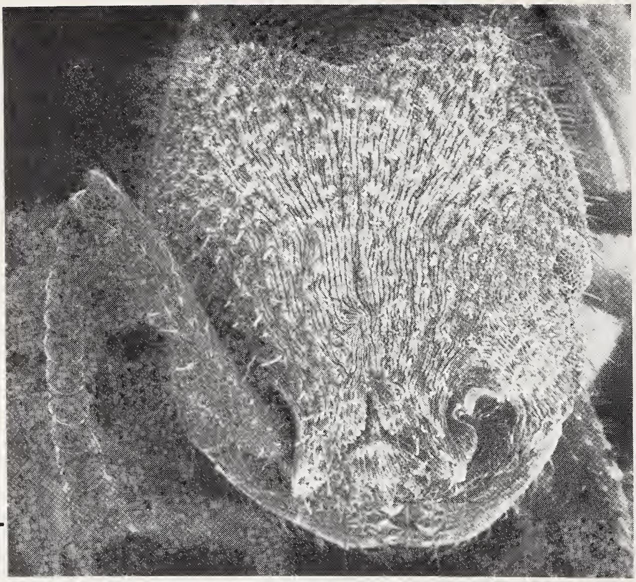

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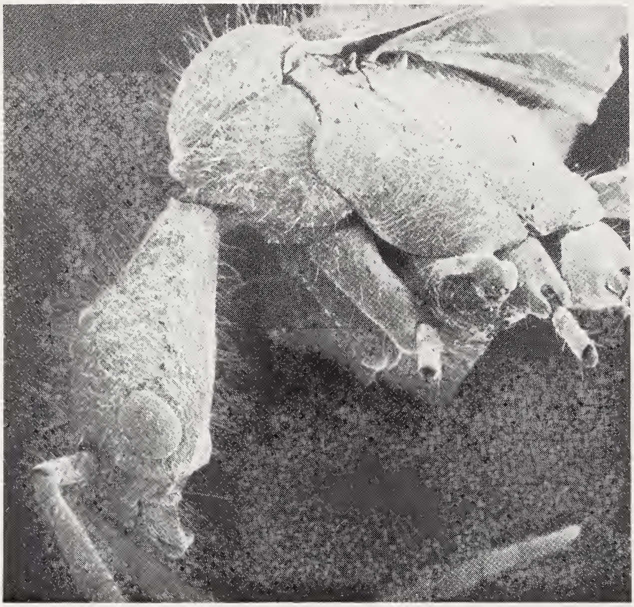
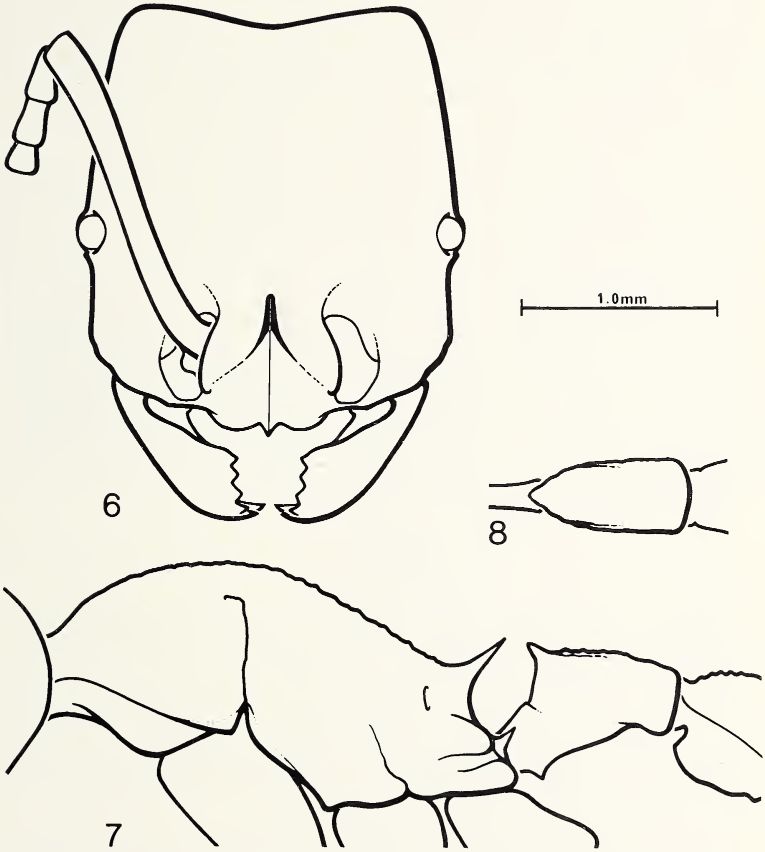


Figs. 4–5. Fig. 4, Head of queen of *P. mayri*, nearly full dorsal view. Fig. 5, side of head and trunk of *P. mayri* male.

as if there is a longitudinal gradient of allometric growth in the queen such that the anterior half grows slower than, and the posterior half faster than in the worker. A detailed description of how the worker differs from the queen follows (see also table 1).

Head much larger, more elongate (fig. 6). Mandibles longer, with 6 distinct teeth and a low basal angle. Papal formula 4, 3. Median carina complete to marginal tooth, but low; seen best from postero-dorsal view. Eye smaller relative to size of head. Trunk more completely fused; profile evenly convex, with poorly differentiated



Figs. 6–8. Worker of *P. mayri*. Fig. 6, head in full dorsal view. Fig. 7, trunk and petiole in lateral view. Fig. 8, dorsal view of petiole.

neck and declivous propodeal face (fig. 7). Propodeal spiracle not prominent; orifice oval, facing caudad. Superior propodeal spines longer, spiniform; their bases narrowly separated. Inferior propodeal plates short, spiniform. Petiole (figs. 7, 8) low, narrow; anterior peduncle very slender in dorsal view, dorsoventrally cuneiform; no posterior peduncle; venter with 2 longitudinal ridges. Anterior ridge of petiolar node drawn out into an acute, dorsoventrally flattened, somewhat upturned tooth; sides of node seen from above parallel, flat in anterior half, weakly convex in posterior half. Postpetiole smaller than in female, especially in width and height; more conical in dorsal view. Gaster much smaller in all dimensions. Legs longer, more slender; middle and hind tibial spurs finely pectinate. Sculpture on dorsum of trunk not broken by sutures; transverse striae on anterior pronotum become longitudinal on mesonotum, then transverse again on propodeum. Striation on first tergum of gaster fades at about midlength; much of caudal half smooth and shining. Color uniformly dull black in mature workers; callows dark ferruginous brown. Petiole, postpetiole and gaster less densely hairy than in female; color of erect hairs can vary from black to golden on any one individual.

The sting apparatus of the worker is most like those of *P.* (*Ephebomyrmex*) *naegeli* and *P.* (*E.*) *imberbiculus* (Kugler, 1978): anterior apodeme of spiracular plate wide and of uniform width along entire length of plate; lancets with 2 distinct barbs and no dorsal ridge; triangular plate without dorsal and medial tubercles; other parts as shown in Kugler (1978) figs. 18, 19, 21, 22, and 26.

MALE
(Fig. 5)

Measurements (ranges from 5 individuals, including the largest and smallest available from 7 collections) TL 7.29–8.10; HL 1.56-1.74; HW just behind eyes 1.10–1.25 (CI 70–73); eye L 0.31–0.34; scape L 0.34–0.42; combined L of 2nd and 3rd flagellar segments 0.81–0.90; ML 0.12–0.19; WL 2.17–2.40; front wing L 4.00–4.10; hind femur L 1.86–2.00; petiole L 0.80–0.94; postpetiole L 0.72-0.93; gaster L 1.74–2.10.

Head remarkably elongate and flattened behind (fig. 5). Clypeus rather long, broadly convex in both dimensions, middle subsiding evenly to sides; free margin broadly arcuate except for slight median flattening or emargination, which possesses in some specimens a very small acute or rounded tooth that is a continuation of a weak median carina running the length of the clypeus. Frontal triangle triangular, with a broad, shallow, V-shaped impression. Frontal carinae reduced to rims encircling the sockets of the antennae. Palpal formula 4, 3. Scape much shorter than combined length of

Table 1. Measurements and indices of *Pogonomyrmex mayri* females and workers. Data for the first female specimen are listed first, followed by those of the second. Worker data are ranges from 6 individuals selected to include the largest and smallest available from 7 collections. Measurements are expressed in millimeters; indices in percentages, and both follow the standard definitions (see Brown, 1953: 11–14; 1975: 3–4). Head width was measured just behind the eyes. Postpetiolar and gaster measurements were taken separately, and from dorsal view.

TABLE 1

Measurements	*Queens*	*Workers*
TL	8.21, 8.49	7.85–9.04
HL	1.57, 1.58	2.00–2.24
HW	1.45, 1.52	1.73–1.96
ML	0.25, 0.27	0.26–0.35
Eye L	0.25, 0.25	0.26–0.30
Scape L	1.12, 1.20	1.67–1.82
WL	2.02, 2.00	2.20–2.54
Petiole L	0.90, 0.90	0.90–1.00
Petiole W	0.72, 0.68	0.36–0.43
Postpetiole L	0.94, 0.94	0.68–0.80
Postpetiole W	1.25, 1.20	0.59–0.70
Gaster L	2.53, 2.80	1.80–2.24
Gaster W	2.18, 2.14	1.38–1.67
Fore femur L	1.48, 1.50	2.00–2.20
Fore femur W	0.27, 0.27	0.30–0.35
Hind femur L	1.64, 1.65	2.32–2.62
Hind femur W	0.27, 0.26	0.30–0.34
Indices		
CI	92, 96	85–88
MI	16, 17	13–16
SI	73, 77	90–96
Scape W/L	15, 13	11–12
Fore femur W/L	18, 18	15–16
Hind femur W/L	16, 16	12–13
Petiole W/L	80, 75	39–54
Postpetiole W/L	133, 128	79–88
Gaster W/L	108, 107	70–78

second and third flagellar segments. Scape and flagellum fairly densely covered with short erect hairs; segments 2–12 of flagellum also very densely endowed with fine appressed pilosity.

Trunk uniquely shaped and proportioned, as if the propodeum has grown forward, compressing the mesoscutum and pronotum, and rotating the neck and head to a more ventral position (fig. 5). Pronotum very constricted mesad. Mesonotum very short (mesoscutal L/WL 20–23%);[1] seen from the side evenly and rather strongly convex, from above nearly equilaterally triangular; with 2 short black lines that indicate underlying apophyses of the notauli. Middle of scutellum and metanotum raised into a prominent subcircular bulge. Propodeum elongate (propodeal L/WL 49–52%),[1] dorsal face curving insensibly into declivous face; unarmed. Petiole long, cylindrical, nodeless. Legs long and slender (hind femur L/WL 83–86%); front coxae long, compressed front to back (fig. 5).

Wings evenly covered with fine hairs. Venation of fore wing variable. Of 154 wings (77 individuals) from 7 collections, the most common venation had a small closed discoidal cell with subequal sides, a hexagonal cubital cell with a narrow opening to the costal cell and sinuate lower edge (Rs), radial cell open distad, and veins Rs and M unjoined by a cross vein beyond the discoidal cell (121 wings). In 11 wings the discoidal cell was open distad, but otherwise the same. In 20 wings the discoidal cell was closed, but a cross vein (r-m) connected the Rs and M veins, creating a second cubital cell. That cross vein joined the Rs well proximad of the end of the first cubital cell, except in one wing where it was almost even with the end of the cell. Two wings had both open discoidal cells and the r-m cross vein. Wings of different venation commonly appear on the same individual.

Hypopygium in ventral view subtriangular; apex broadly rounded, proximal corners square with slender truncate lateral projections, middle of base with a long slender truncate anterior process. Gonostyli (=parameres) of genital capsule tapered in side view, but with apices broadly rounded; setae occur only around apices. Digitus long, slender, blunt, strongly down-curved; not reaching to apex of gonostylus. Cuspis short, pollicate when seen from the side.

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[1] Mesoscutal and propodeal lengths measured from lateral view by taking their maximum length along lines parallel with Weber's length.

Aedeagus fairly slender, with serrate ventral margin; serrations decrease in size to apex. Apex narrow, blunt; half smooth, half finely serrate. Inner dorsal margins of gonocoxites form a long narrow, gently convex V.

Sculpture like that of worker and female, with the following exceptions: Striation on head largely transversely arcuate caudad of antennae, clypeus without coarse undulations. Trunk and petiole without overlying broken wavy sculpture; all but pronotum longitudinally striate. Striation on postpetiole gives way to purely punctate sculpture in caudal half. Gaster, first and second antennomeres, and legs smooth and shining, except for weakly striate fore coxae.

DISCUSSION

Pogonomyrmex mayri clearly belongs to the genus *Pogonomyrmex* as presently constituted; and is most closely related to members of the subgenus *Ephebomyrmex.* It is most like *Ephebomyrmex* in 15 of the 22 characteristics used by Cole (1968) to distinguish males and workers of the subgenera *Ephebomyrmex* and *Pogonomyrmex,* the sting apparatus most resembles that of the *Ephebomyrmex* species I have examined (Kugler, 1978), and some of its most unusual characters, such as the elongate head of the male, the Y-shaped frontal triangle of the queen and worker, and the circumocular groove, may be seen as the extreme development of characteristics of *Ephebomyrmex* species. Nevertheless, it *is* remarkably different from any known *Pogonomyrmex,* with a number of novel characters, and consequently has been placed in its own subgenus (*Forelomyrmex* Wheeler) since its description. The following shows how other *Pogonomyrmex* species compare with *mayri*'s most distinctive features.[2]

The clypeus in most *Pogonomyrmex* has a concave leading edge except in *angustus, darlingtoni, odoratus, schmitti* and *townsendi* (all *Ephebomyrmex*), none of which has a median tooth. The frontal triangle is usually broadly triangulate, but is somewhat elongate, laterally compressed, and except for a median carina, depressed

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[2] Except where indicated, based on the MCZ collection containing 51 of the estimated 67 presently standing species, subspecies and varieties of the subgenera *Ephebomyrmex* and *Pogonomyrmex.*

below the level of the clypeus only in *darlingtoni, saucius* and *schmitti.* In none of these, however, is the front so narrow as in *mayri,* nor is it at all Y-shaped. The back of the head in full dorsal view is broadly and shallowly concave in most *Ephebomyrmex* species, but is only excavated to such a degree that it has definite occipital lobes in the majors of some subgenus *Pogonomyrmex* species, *e.g., badius.* The cephalic index approaches that of *mayri* only in *cunicularius* (84), an undetermined species near *cunicularius*[3] (84, 87), *odoratus* (85–87), and *angustus* (86–89). Only in the latter is the occiput at all concave. In some species the sculpture is flattened at the edge of the eye, but only in *darlingtoni* does it become at all impressed, and then it is shallow, only weakly defined, and limited to the dorsal half of the eye. All species examined have much larger eyes, relative to the size of the head, than *mayri.* The petiolar node in most *Pogonomyrmex* species is well rounded on top, sides and apex, and has a distinct posterior peduncle. A few species have a broad subacute to acute apex, but only in the sp. near *cunicularius* does the node even superficially resemble that of *mayri.* On closer examination, it also is quite distinct. Sculpture in the subgenus *Ephebomyrmex* tends to be "coarsely rugo-reticulate" (Cole 1968: 35), but no species examined has the overlying broken, undulate pattern of *mayri.*

Ergatogyny has occasionally been reported in *Pogonomyrmex,* but most specimens are only occasional aberrations in species with normal queens, *e.g., comanche, maricopa, subnitidus, californicus* (Cole 1968: 175), and *pima* (MCZ). Only one female has been reported for *cunicularius,* and it is ergatoid (Santschi, 1931), but the description indicates nothing more remarkable about it than a more or less distinct scutellum. Ergatogyny seems to be the rule in *laticeps.* Kusnezov (1951: 273–275) describes the range of ergatoid forms, but makes no mention of enlarged waists or gasters, or of reduced heads. Those characters are evidently unique to *mayri.*

The bizarre form of the *P. mayri* male is also apparently unequalled in this genus (Cole, 1968; Creighton, 1952; Gallardo, 1932; Kusnezov, 1949, 1951). Some males of *Aphaenogaster* species have elongate heads constricted behind. In the other *Pogonomyrmex*

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[3] Two specimens collected by W. L. Brown in Argentina: Catamarca, Cat. (airport), 4 Feb. 1967; Prov. Tucuman, Km 1333, Rte. 9, N. of Tapia, 25 Jan. 1967, bosque chaqueño.

species I was able to examine directly, the head is at best only slightly longer than wide in some species (CI range of 4 *Ephebomyrmex* species 89–97). The mesoscutum is long (mesoscutal L/WL 33–50%), propodeum short (propodeal L/WL 26–37%) and the petiole has a distinct node. The legs are shorter than in *mayri* (hind femur L/WL 61–76%), and the front wing usually has a r-m crossvein that joins the Rs at or distal to the end of the first cubital cell (see Cole, 1968: 25–26, plate 1 fig. 1). If the r-m vein is absent, the first cuboidal cell is open.

Pogonomyrmex mayri may in fact deserve full generic status, but for the present it seems prudent not to create a monotypic genus before *Pogonomyrmex* is completely revised. The most recent revisions (Kusnezov, 1951; Cole, 1968) have been regional in scope and thus inadequate to address the question of whether the subgenera *Pogonomyrmex* and *Ephebomyrmex* are really two distinct genera. Should such a split occur, *mayri* would no doubt be placed in the separate genus *Forelomyrmex*.

ACKNOWLEDGEMENTS

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NOTES ON *BRYOTHINUSA* WITH DESCRIPTION OF THE LARVA OF *B. CATALINAE* CASEY (COLEOPTERA: STAPHYLINIDAE)*

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A number of insects are restricted to special marine habitats along the California seashore. At least one of these habitats is intertidal in the sense that its fauna is regularly submerged by the tides. This is the fauna of the reefs. Several species of staphylinids are known from this region. Members of the staphylinid genera *Liparocephalus, Amblopusa* and *Diaulota* are found on the rocky shores of northern California; while in southern California only members of the genera *Diaulota* and *Bryothinusa* are known. Several studies have dealt with these insects including Chamberlain and Ferris (1929) and Moore (1956a, 1956b). Larvae of some of the species have been described. The larva of *Bryothinusa catalinae* Casey is described and illustrated for the first time in this paper.

Bryothinusa catalinae (Fig. 1), the type species of the genus, was described by Casey in 1904. Sawada (1955, 1971) described four species from Japan under the name *Halaesthenus.* Several species were described from the harbor at Hong Kong by Moore and Legner (1971) and Moore, Legner and Chan (1973). Finally, another species was made known by Moore and Legner (1975) from the Gulf of California, bringing the total number of known species to eleven. All but one of these is restricted to an intertidal habitat; the exception being *B. fluenta* Moore et al. which was found by Tai-Din Chan in a strictly fresh water habitat in a stream emptying into Hong Kong harbor.

Bryothinusa catalinae is not common in collections probably because of its restricted habitat. Derham Giuliani collected ten adult specimens of this species incidental to other work in October, 1976, near White Point, San Pedro, California, and presented the specimens to us. We made two trips to the area in November and December, 1977, where we found both adults and larvae fairly common. This special habitat may be described as follows:

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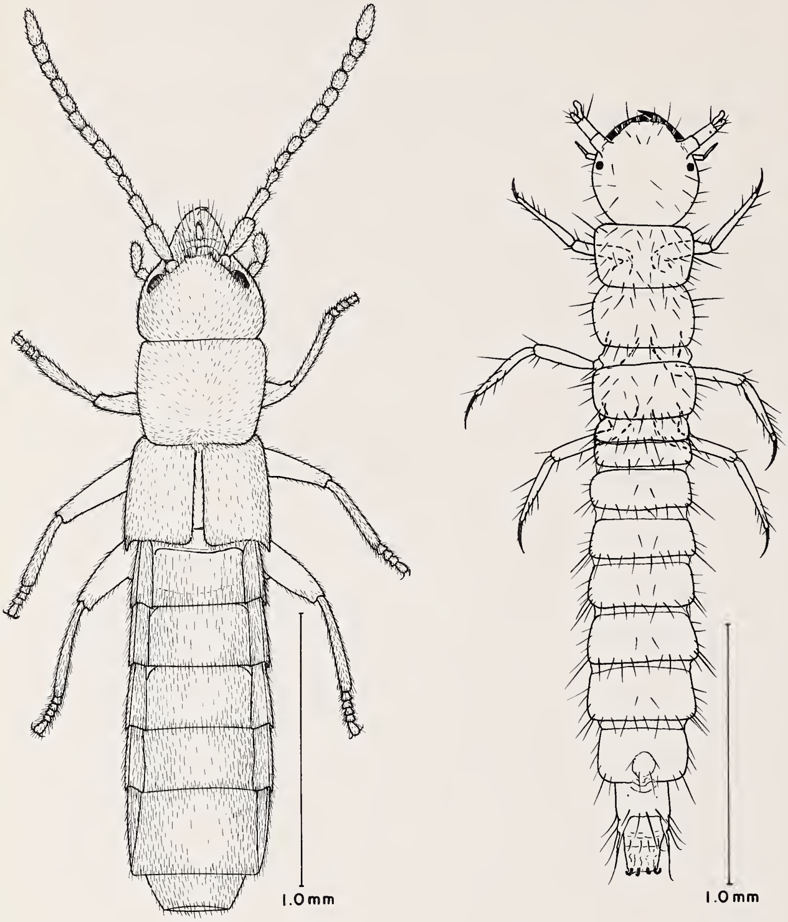


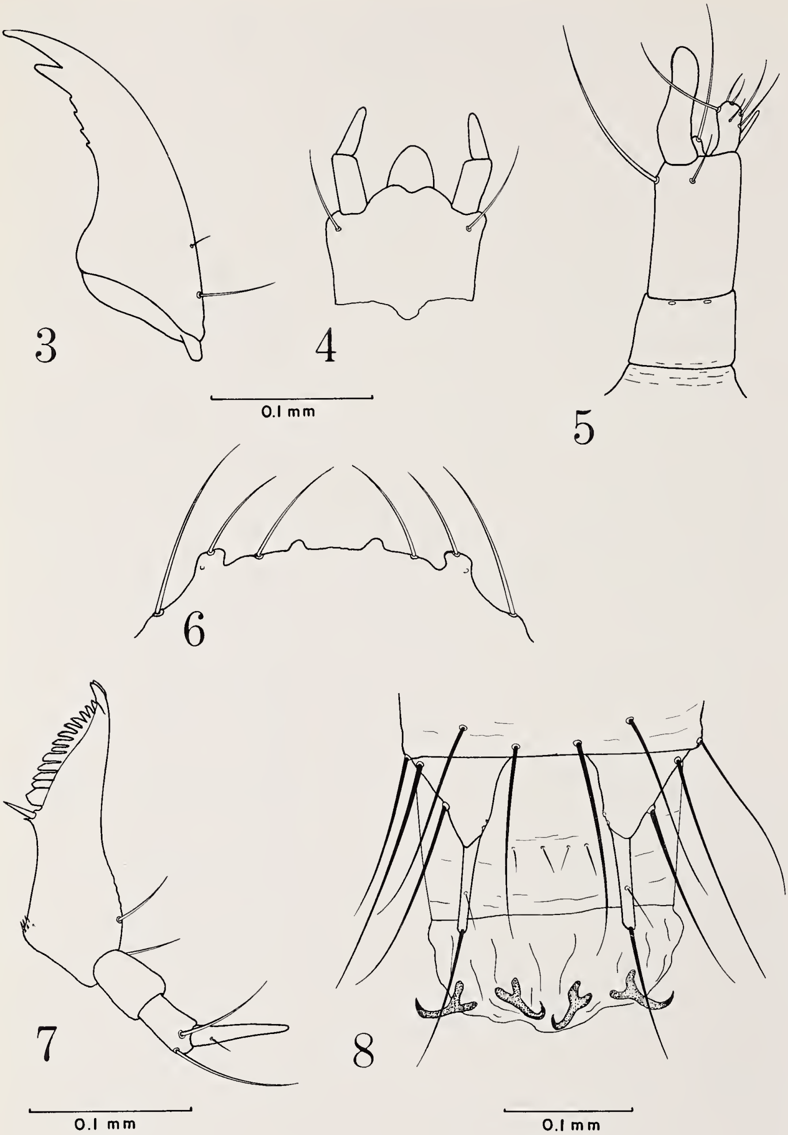
Figures 1–2. *Bryothinusa catalinae* Casey. Fig. 1, Habitus of imago; California, Los Angeles Co., White Point, Dec. 6, 1977, R. E. Orth. Fig. 2, Habitus of larva; same locality data as imago.

White Point City Park, San Pedro, Los Angeles, California (Fig. 9, photograph), occupies approximately a mile of a narrow strip of cliff and rocky beach along the Pacific Ocean just a few miles north of Point Firmin. Access to the beach is by a steep road down the cliff which joins a road along the beach. The beach area consists of four rocky embayments between five short points. The second embayment from the south is somewhat protected from the open ocean by a 6 foot to 10 foot high ledge along the seaward side of which is the ruin of a concrete wall. Between the concrete wall and the road at the base of the cliff is a shallow reef which is exposed at low-water and under water at high tide. The area is largely a field of boulders two or three feet across with smaller stones and gravel in sand. The staphylinids and their larvae were found beneath and on the stones in an association with dense worm tubes, chitons, limpets, small abalones, flat worms, small crabs and brittle stars. They were most readily collected by a flotation method in which stones were agitated in a bucket of seawater. The insects floated to the surface where they were lifted with a camel's hair brush and transferred to a vial of alcohol. Collecting in the intertidal zone is best done in the fall and winter when low tides occur during daylight.

The larva of *Bryothinusa catalinae* Casey
(Fig. 2)

Color. Semitransparent-white except the apices of the mouthparts and the larger setae which are nebulously brown, and black eye-spots on the head.

Head round, widest just behind the eye-spots, neck absent. Ocelli apparently absent. With an ovoid heavily pigmented eye spot on each side near the base of the antenna. Clypeal margin (Fig. 6) with four small teeth. Antenna three-segmented (Fig. 5); first segment wider than long; second segment about as wide as first, almost twice as long as wide, apex with two articulated processes, each about one-third as wide as apex of second segment; one process an "acorn-like seta", bears no seta on its surface, is almost twice as long as the other and is somewhat sinuate; the other process which is the actual third antennal segment, bears several ordinary setae and is about twice as long as wide. Maxilla (Fig. 7) with the stipes longer than the palpus, outer half of inner margin with closely placed short teeth. Maxillary palpus three-segmented; first segment about as long as



Figures 3–8 Larva of *Bryothinusa catalinae* Casey. Fig. 3, left mandible; Fig. 4, labium; Fig. 5, right antenna; Fig. 6, anterior margin of clypeus; Fig. 7, right maxilla; Fig. 8, urogomphi and pseudopod.

wide; second segment somewhat narrower and almost as long as first; third segment narrower and longer than second, tapered to bluntly pointed apex. Mandible (Fig. 3) curved, pointed, with a large internal apical tooth followed by four blunt denticles in the apical half. Ligula (Fig. 4) rounded at apex, about as long as wide, about as long as first segment of labial palpus. Labial palpus (Fig. 4) two-segmented, segments longer than wide, second segment a little narrower than first, tapered to bluntly pointed apex. Gular sutures most approximate in the middle, widely divergent ahead and behind.

Thorax.—Pronotum almost twice as wide as long, apical margin straight, sides gently arcuate, base straight, angles narrowly rounded, with a few scattered setae. Mesonotum and metanotum very similar to pronotum.

Abdomen with the first six segments nearly parallel sided, seventh segment narrower than sixth, eighth segment narrower than seventh. First six segments with two discal setae, a row of about eight setae along the basal margin and scattered setae at the sides. Eighth segment with distinct raised opercula for an osmeterium, the area

Figure 9. Low tide at White Point City Park, Los Angeles County, California, habitat of *Brythinusa catalinae* Casey.

not pigmented. Urogomphus (Fig. 8) two-segmented, first segment broadly triangular, second segment slender, nearly cylindrical, about as long as the first segment. Membrane of apex of pseudopod (Fig. 8) with four small dark hooks, each with a bifid base.

Length 3.0 mm.

Material examined. Two specimens 9 November 1977 and three specimens 6 December 1977, White Point, San Pedro, Los Angeles, California, associated with numerous adults under stones in coarse sand and gravel on the seashore at about the 1 or 2 foot tide level collected by R. E. Orth. In company with these specimens were adults of *Diaulota harteri* Moore, the only other staphylinid genus known from this habitat.

Notes. The larvae of *Bryothinusa* can be distinguished from those of *Diaulota,* the only other staphylinid genus known from this habitat in southern California, by the presence of four small chitinized pigmented hooks with a bifid base imbedded in the apical membrane of the pseudopod. Specimens of larvae examined by us associated with adults of *B. sawadai* Moore et al., *B. Hongkongensis* Moore et al., *B. sinensis* Moore et al. and *B. chani* Moore and Legner all have pseudopodal hooks. Similar pseudopodal hooks have been reported in the larvae of *Alianta incana* Erickson by Paulian (1941). Paulian's illustrations indicate they may be present in other genera.

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GROOMING BEHAVIOR IN DIPLURA (INSECTA: APTERYGOTA)

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Insect grooming studies are adding an important new dimension to knowledge of comparative behavior and evolution. Recent advances include an overview of a few selected movements of insects and myriopods (Jander, 1966), studies of the functional morphology of grooming structures (Hlavac, 1975), extensive reports about individual orders (Coleoptera: Valentine, 1973; Hymenoptera: Farish, 1972), quantitative studies at species levels (Chironomidae: Stoffer, in preparation; *Drosophila:* Lipps, 1973), and many less inclusive works. All such studies have difficulties which include the inability to know when an observed sequence is complete, the enormous number of potential taxa, the problem of generalizing about families and orders from small samples of individuals or species, and the absence of data from primitive or odd groups which may be critical for interpreting evolutionary sequences. The first three difficulties can be partially solved by increasing sample sizes and combining observations; however, the fourth can be solved only by availability. Grooming in the apterygote order Diplura is a good example because we can find only incomplete reports on one species. Recently, we have studied ten live specimens representing two families and three species; the data obtained provide an important picture of grooming behavior in one of the most primitive surviving orders of insects. Our observations greatly extend the limited discussion of grooming in the European japygid *Dipljapyx humberti* (Grassi, 1886) reported by Pagés (1951, 1967). Data on *Dipljapyx* are incorporated here, but have not been verified by us.

Initially we asked two questions: The first concerned whether a very primitive insect would enable us to observe a primitive grooming repertory; what we actually observed were primitive insects with grooming behavior beautifully tuned to a special and restricted environment. The second question concerned the effects

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of endognathous mouthparts on grooming. The invaginated, noncondylar mandibles and maxillae of Diplura might reduce their effectiveness in oral cleaning, and result in an increased importance of leg rubbing movements. In fact, leg rubbing was seldom observed. The rarity of rubbing has two possible explanations: either endognathy does not significantly modify grooming or else most leg rubbing movements have not yet evolved in Diplura.

MATERIAL EXAMINED

Campodeidae (seven specimens and seven hours of recorded observations plus about five additional hours of non recorded observation which add no new data) Ohio, Franklin Co., Columbus, Upper Arlington, 20 September, 1975, B. D. Valentine family, in soil in back yard (1 specimen). Same data except 5 November, 1977, in soil under boards and logs in back yard (6 specimens). Many additional specimens were seen and collected by breaking up clods of dirt in a garden.

Japygidae (three specimens and nine hours of recorded observation plus about four more hours which duplicate previous data). Alabama, Butler Co., 2 mi. N.W. McKenzie on U.S. rte. 31, 7 December, 1975, B. D. Valentine, R. L. Stoffer, A. J. Penniman, in rich humus under leaf litter (1 specimen). Ohio, Franklin Co., Columbus, 23 October, 1977, M. J. Glorioso, under large flat rock at base of overgrown hill (1 specimen). Same data except 24 October, 1977 (1 specimen).

The campodeids key to the genus *Campodea* subgenus *Campodea* Westwood, 1842, in Paclt (1957). Silvestri (1933a) and Paclt (1957) list two species of this subgenus occurring east of the Mississippi River, *Campodea* (*C.*) *fragilis* Meinert, 1865, and *Campodea* (*C.*) *plusiochaeta* Silvestri, 1912. Both are illustrated and described by Silvestri (1912). Our specimens more closely match *C. plusiochaeta* because the cercal setae are fairly long on all segments, as opposed to the long basal and shorter distal cercal setae of *C. fragilis,* and because there are bifurcate antennal setae, as opposed to the serrate or plumose setae of *C. fragilis.* Nevertheless, the determination is not firm and the specimens should be listed as *Campodea* (*Campodea*) ? *plusiochaeta* Silvestri, 1912. The Ohio japygids key in Paclt (1957) to the genus *Metajapyx* Silvestri, 1933. Using Smith and Bolton (1964) they key to *Metajapyx subterraneus* (Packard, 1874) which is recorded from Ohio, Pennsylvania, Kentucky, Virginia, and District of Columbia. It is the only species recorded from Ohio; our Franklin County specimens constitute a new northern-most record in the state, and are one of the very few American records of the genus in glaciated territory. The Alabama japygid keys (in Paclt, 1957, and Smith and Bolton, 1964) directly to *Metajapyx steevesi* Smith and Bolton, 1964, known from Mississippi, Alabama, Georgia, South Carolina, North Carolina, Tennessee, and Virginia. Our record is especially noteworthy because it marks the southernmost limits of both the species and the genus in North America.

RESULTS

CLEANING. Involves grooming with the mouthparts.

Antenna Clean. Passage of the antenna through the mouth is accomplished in two major modes: *unassisted* and *assisted.* In *unassisted,* which is the usual mode in Diplura, the antenna deflects into the mouth due to its intrinsic musculature, and the legs are not involved. In *Campodea* this movement is vertical to the substrate, the antenna is curled ventrally under the head and is chewed by the mouthparts; in japygids the movement is rarely vertical, the antenna usually is curled along a more horizontal plane from an initial position lateral of the head, and is usually drawn rapidly through the open mouthparts; less frequently it is chewed by the maxillae. In the much rarer *assisted* mode, the ipsilateral foreleg pulls the antenna into the mouth and in both families is either returned to the substrate or held in mid-air; in addition, the japygids were occasionally observed using the ipsilateral foreleg to help hold the antenna in the mouth by placing the leg crosswise in front of the mouthparts. Pagés (1967) points out that in *Dipljapyx* the foreleg holds the antenna during chewing by the maxillae, but is not used when the antenna is drawn through the maxillae without chewing movements.

Palp Clean. A maxillary palp is passed unassisted through the mouthparts in the *anterior* mode in which the palp tip projects posteriad and is drawn anteriad out of the mouth. This was observed clearly in *Metajapyx.* (In *Campodea,* maxillary palpi are one segmented and the labial palpi are vestigial.)

Foreleg Clean. A foreleg is raised and extended forward while the head turns to the side to reach it; the leg is essentially in a ventrolateral position during cleaning, and is drawn posteriorly through the mouth, tarsal claws last. This occurs in both families and all three genera.

Midleg Clean. A midleg is brought forward alongside the body and the head turns and dips to reach it, the limb moving posteriorly through the mouth, tarsal claws last. There are three modes: *under* L_1, in which the foreleg is raised out of the way, in both families; L_1 *pull,* in which the raised foreleg is used to pull the midleg into the mouth, seen rarely in *Campodea* and reported in *Dipljapyx* by Pagés (1967); and *over* L_1, where the foreleg remains on the substrate and the midleg crosses above is, seen in *Metajapyx.*

Hindleg Clean. A hindleg is brought forward alongside the laterally arched body and the head turns and dips to reach it, the limb moving posteriorly through the mouth, tarsal claws last. There are three modes in Diplura: *under* L_{1+2}, where fore and mid legs are raised out of the way, in both families; *under* L_1, *over* L_2, which is self-explanatory and occurs in both families (in this mode both families usually raise and partly extend L_1, and japygids sometimes flex L_1 and position it under the body); and L_1 *pull,* in which the foreleg helps pull the hindleg to the mouth, in *Campodea* and *Dipljapyx.*

Fore-Midleg Clean. Ipsilateral fore and midlegs are passed simultaneously through the mouth in anterior-posterior sequence. This infrequent action occurs in both *Campodea* and *Metajapyx.* Sometimes both tarsi are involved, but usually the fore tarsus and mid tibia are the parts cleaned.

Fore-Hindleg Clean. As above, the ipsilateral limbs moving posteriorly through the mouthparts, observed rarely in *Campodea.*

Mid-Hindleg Clean. As above, except that the movement seems to be a rare continuation of *Hindleg Clean, under* L_{1+2}, where the midleg becomes involved; in no case was the movement initiated independently of *Hindleg Clean.* This movement was observed rarely in *Metajapyx.*

Body Clean. Both families can bend double and use their mouthparts to groom body surfaces from the thorax to the cerci. These movements are less frequent than other grooming, so it is not known if the differences between the two families are real or sampling error. Watching these animals, the observer rapidly gets the impression that they can probably reach any body part they wish except the pronotum. At present, the campodeids have been seen cleaning all three coxae with the head directed ventro-posteriad;

they also clean the lateral edge of the body, the styli, and the cerci with the body curled laterally. Cercal grooming techniques appear to be very diverse and are more controlled by position and substrate irregularities than by a stereotyped program. For example, the cerci can be held by L_1, or by L_{1+1}, or by L_{1+2}, in each case the remaining ipsilateral legs are under the cercus; other variants involve L_3 raised out of the way, L_2 raised out of the way, and the cercus positioned over all three ipsilateral legs. Body cleaning in japygids extends at least from the mesonotum or mesosternum to the cerci, including dorsal, lateral, and ventral surfaces; during cercal grooming, the mouth can work the outer margin of a forceps from base to apex, around the tip, then the inner margin to and across the anal area, and out the inner margin of the contralateral forceps to its tip; the far outer margin is not groomed until the insect straightens and bends to the opposite side. In *Dipljapyx* Pagés (1967) reports that the thoracic legs hold the abdomen when the body is tightly curved to clean from the mesothorax to the fifth abdominal segment.

RUBBING. Involves progressive contact of body parts with each other or with the substrate. In Diplura, all rubbing is of low frequency.

Antenna-Foreleg Rub. The fore tarsus or tibia is used to rub the dorsal surface of the ipsilateral antenna. This occurs in *Campodea* where the movement is confined to the basal antennal segments, and is sometimes combined with and precedes *Antenna Clean, assisted.*

Head-Foreleg Rub. In *Campodea,* the fore tarsus is used to rub the venter of the head and the mouthparts; in *Dipljapyx,* Pagés describes head capsule rubs but does not indicate the areas involved.

Head-Midleg Rub. Also in *Campodea,* a midleg is used to rub the venter of the head.

Head-Substrate Rub. *Dipljapyx* was observed rubbing the labial region of the head on the substrate with a sideways motion.

Body-Midleg Rub. In *Metajapyx,* the midleg is used to rub the dorsal and lateral surfaces of the thorax.

Body-Midleg-Midleg Rub. Also in *Metajapyx,* this is the bilateral version of the previous movement, both midlegs rubbing different thoracic regions simultaneously.

Body-Hindleg Rub. In *Metajapyx,* the hindleg is occasionally used to rub the dorsal or lateral surfaces of the thorax. *Body Rubs* can be combined, for on one occasion the thorax was rubbed simultaneously by a mid and hind leg from opposite sides.

Body-Substrate Rub. Pagés (1967) reports that *Dipljapyx* rubs the thoracic sternum and abdominal base energetically on the substrate. He recognizes that this may be territorial marking, but believes that grooming is more probable.

DISCUSSION

The grooming patterns of Campodeidae and Japygidae are basically similar with one major exception. In *Antenna Clean,* campodeids chew the antenna with the maxillae during passage through the mouth, while japygids usually open the mandibles and then scrape the antenna rapidly through the open maxillae without chewing motions. Japygids can also chew the antenna but do so less frequently. The differences in grooming suggest different maxillary structures. Dissection of *Metajapyx* reveals an extraordinarily complex lacinia with five pectinate lamellae along the mesal face. Since we believe that these lamellae are the structures with which the antennae are cleaned; their distribution and function should be considered in future dipluran studies. Illustrations of these structures can be seen in the following works.

Japygidae: (note that the last genus is sometimes listed in a separate family).
  Indjapyx crivellari (Silvestri) as *Parindjapyx* (Silvestri, 1932, fig. XXXI, 4).
  Burmjapyx major (Grassi) as *Japyx* (Silvestri, 1922, fig. IV).
  Metajapyx confectus Silvestri (Silvestri, 1947, fig. 2).
  Monojapyx simplex profusa Silvestri as *Japyx* (Silvestri, 1932, fig. XXI, 2).
  Catajapyx confusus (Silvestri) as *Japyx* (Silvestri, 1929, fig. 2–5).
  Heterojapyx gallardi Tillyard (Snodgrass, 1935, fig. 79).
  Evalljapyx hubbardi (Cook) as *E. sonoranus* (Silvestri, 1947, fig. 3).
  Parajapyx isabellae (Grassi) (Paclt, 1957, fig. 37).
Anajapygidae:
  Anajapyx vesciculosus Silvestri (Silvestri, 1905, fig. 4).
  Anajapyx hermosus Smith (Smith, 1960, fig. 9).
Projapygidae:
  Symphylurinus stangei Smith (Smith, 1960, fig. 7).

The general localities of these twelve species are, in sequence: Is. Rhodes; Mediterranean; Washington, D.C.; Greece; Greece; Australia; se. Arizona; semi-cosmopolitan; Italy; California; Mexico; Mexico.

The remaining two families of Diplura: Procampodeidae and Campodeidae are described by Paclt (1957, p. 5) as having tongue-like processes ("languettes") on the lacinia, but lacking pectinate lamellae, while Smith (1960) simply states that the two campodeiform families are without "pectens". In *Procampodea* the lacinial apex has a mesal row of 4 projections, one of which is bifid; these structures are illustrated by Silvestri (1905b: pl. XII, fig. 21). The functional morphology of dipluran mouthparts is further complicated by another feature: the presence of an antebasal serrate prostheca (sometimes called a "lacinia mobilis") on the mandibles of campodeids (see Paclt, 1957, fig. 7), anajapygids and projapygids (see Smith, 1960, figs. 10, 13 respectively), and anteapically on procampodeids (see Silvestri, 1905b, pl. XII, fig. 19, 20). The functions of these maxillary and mandibular structures have not been demonstrated, but based on our observations, grooming is one of the most probable uses of the pectinate lamellae.

Jander (1966–842) states that grooming ". . . the antennae and all of the legs with the mouthparts . . . is . . . to be regarded as the primordial mode of grooming . . ." in tracheate arthropods. It is true that oral cleaning movements predominate in diversity and frequency in primitive taxa, but it is also true that virtually all primitive arthropods have rubbing movements too. In most cases it is impossible to decide objectively which came first.

Many factors affect grooming, and all act on both primitive and derivative taxa. For example, grooming movements have constraints imposed by body flexibility and degree of leg movement. The configuration of a coxa and its cavity can be primitive or derivative, but superimposed on this basic structure are the results of selection for plane of leg movement, rotation, strength, speed, body height, and grooming requirements. The resolution of these diverse pressures must result in a morphological compromise which affects grooming capability, but has little to do with primitiveness. Additional examples are numerous. An elongate, flexible, soft-bodied organism has different grooming patterns from a fatter, more rigid, sclerotized organism; one with easily abraded scales will be different from one with firm setae; and an interstitial inhabitant will be different from a subcortical or leaf-litter inhabitant. The point is that all of these kinds of organisms occur in Apterygota and all are among the most primitive known hexapods.

In Diplura, grooming of the antennae, mid- and hindlegs involves at least fourteen cleaning positions, all of which appear to be satisfactory. This diversity is quite remarkable and is unequaled in other insects (Valentine, unpubl.). The grooming of dipluran forelegs involves only one mode. The stereotypy of foreleg grooming contrasts sharply with the diversity of antennal, mid- and hindleg grooming. The logical explanation is that the single foreleg technique works in most or all situations, while no one technique works for the other appendages. Environmental constraints appear to require that the insect reach and groom its antennae, mid- and hindlegs in several alternate ways. Diplura are basically interstitial organisms. Almost all specimens were found in the soil under undisturbed stones or boards, or in soil clods in gardens. A standard technique for finding campodeids was to break up the damp clods in a freshly plowed field or while digging potatoes. The very fine tunnels and cracks in this unyielding substrate are inhabited principally by small myriapods, Collembola, and Diplura. Since campodeids do not burrow and japygids do so very weakly (Pagés, 1967), they primarily use the interstices already present. In such a habitat body configurations are subject to an infinite diversity of living spaces. A grooming behavior possible in one crack may be impossible in another; however, a modification may work. We believe that the unequal grooming diversity in Diplura is a response to the problems of an interstitial life style. Foreleg grooming, where the leg is simply raised to the mouth, does not require any special bending or movement, so one technique does the job. Antennal, mid- and hindleg grooming require unusual movements of the appendage or of the body. Such movements may be limited by the varied configurations of the crawl space, and must accommodate to those configurations; thus, a variety of alternate positions appears to be a necessity.

It is important to contrast the remarkable freedom of grooming positions of Diplura, with the very high degree of stereotypy in such orders as Diptera and Hymenoptera. The point is that a discussion of insect grooming based on Diptera or Hymenoptera is as biased towards stereotypy as a discussion of Diplura is biased towards lack of stereotypy. Present literature emphasizes the stereotyped aspects of grooming, but it should be obvious that generalizations based on highly derivative or primitive orders are not valid for the entire class and may be skewed in opposite directions. The order Thysanura would be a heuristic study because of the diversity of surface textures. There are scaly lepismatids, campodeid-like nicoletiids, and sclerotized, non-scaly lepidotrichids. Grooming in these three families may further clarify why the degree of stereotypy varies from taxon to taxon.

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THE DACETINE ANT GENUS *PENTASTRUMA* (HYMENOPTERA: FORMICIDAE)[1]

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The genus *Pentastruma* was established by Forel (*loc. cit. infra*) on the basis of a single Taiwanese worker specimen that he described (*P. sauteri*) as having 5 antennal segments, a very unusual number even for a member of the Dacetini, to which tribe he indicated that it belonged. In several ways, the description read as though based on a depilated species of *Smithistruma,* and when, several years ago, Dr. Masao Kubota sent specimens of a nearly hairless short-mandibulate dacetine from Japan, WLB suspected that it might be close to *Pentastruma sauteri,* despite the fact that its antennae displayed the 6-merous condition usual in strumigenite dacetines.

Now we have finally discovered the location of the Hans Sauter Collection of Taiwanese ants, in the Institüt für Pflanzenschutzforschung (BZA) der Akademie der Landwirtschaftswissenschaften der Deutsche Demokratik Republic in Eberswalde. Through the kind offices of Dr. G. Morge we have been able to borrow some critical formicid types from the Sauter material, among them the unique specimen of *Pentastruma sauteri.* This worker proves to be close to the Japanese species received from Dr. Kubota, but it is specifically distinct. It does also have 6 antennomeres, with the normal strumigenite proportions, and not 5 as stated by Forel. In its general form, *P. sauteri* is a rather typical *Smithistruma,* except for its complete lack of standing or other conspicuous hairs on head, trunk and petiole, and the new Japanese species matches it in these respects.

It seems logical that *Pentastruma* should eventually be merged with *Smithistruma,* but the latter genus is itself not stable at this

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time, because new species have been discovered (mostly unpublished) that seem likely to link it with such senior genera as *Trichoscapa* and *Codiomyrmex.*

Until more of these new species have been formally described and properly analyzed, no firm classification of the short-mandibulate strumigenites is practicable. It seems best to retain some of the available generic names for now, if only to avoid excessive combinatorial changes as the classification develops.

Accordingly, we retain the name *Pentastruma* for the time being. We figure for the first time the type species, *P. sauteri,* and supplement its original description, and we describe a second species, *P. canina,* from Japan, based on all 3 castes.

Measurements and proportions, and their abbreviations, are those standard in papers on Dacetini, e.g., Brown, 1953, Amer. Midl. Nat. **50:** 7 ff., and 1973, Pacific Insects **15:** 259.

Pentastruma

>*Pentastruma* Forel, 1912, Ent. Mitt. **1:** 50. Type species: *Pentastruma sauteri* Forel, monobasic.

Worker: Like *Smithistruma* in size, and form of head, mandibles and remainder of body, including the 6-merous antennae; small funicular segments II and II separate and distinct. Clypeus with median tumulus and broadly extended anterolateral apron; anterior margin concave in outline. Mandibles depressed, porrect, with rounded basal lamella and no diastema, up to 15 acute teeth and denticles of varying length, including small apical tooth. Labrum with 2 long, tapered lobes, as in *Smithistruma.*

Body densely reticulate-punctulate and opaque (feebly shining in some views), but postpetiolar disc and gaster smooth and shining, except for basigastric costulae. Head, trunk, petiole and appendages without erect hairs, and even the pubescence reduced to a virtually invisible (at 50×) dilute vestiture of minute, appressed to decumbent hairs. The under-mouthparts have some small standing hairs. Postpetiole and gaster with a few short, blunt-tipped or remiform, standing hairs, mostly arranged symmetrically. Color testaceous to light ferruginous.

Queen: Like the *Smithistruma* queen, but with differences corresponding to those of the worker. Thoracic dorsum with a few short, slender but stiff, erect hairs. Pronotum with a flat, C-shaped, marginate dorsal platform; scutum rising abruptly above this.

Male: As in *Smithistruma.*

Distribution as known: Japan (Honshu and southward); Taiwan. Almost certainly occurs on the Asian mainland, but not yet collected there.

Pentastruma sauteri

Fig. 1

Pentastruma sauteri Forel, 1912:51, worker. Type loc.: Pilam, Taiwan. Holotype worker: TL 2.2, HL 0.62, HW 0.43, ML 0.06, WL 0.55 mm; CI 69, MI 10.

The figure shows well the full-face outline view of head and mandibles. The head is shorter, with vertex more convex, than in *P. canina,* and the mandibles are shorter and more "set into" the anterior clypeal concavity. Although we have been unable to view the mandibular dentition directly and in detail in the lone holotype specimen, it seems that a rounded basal lamella is present, and that a series of sharp teeth follows without a diastema. The number of teeth (12?) may be slightly smaller than in *P. canina,* and the sizes of the teeth seem to be more evenly graded.

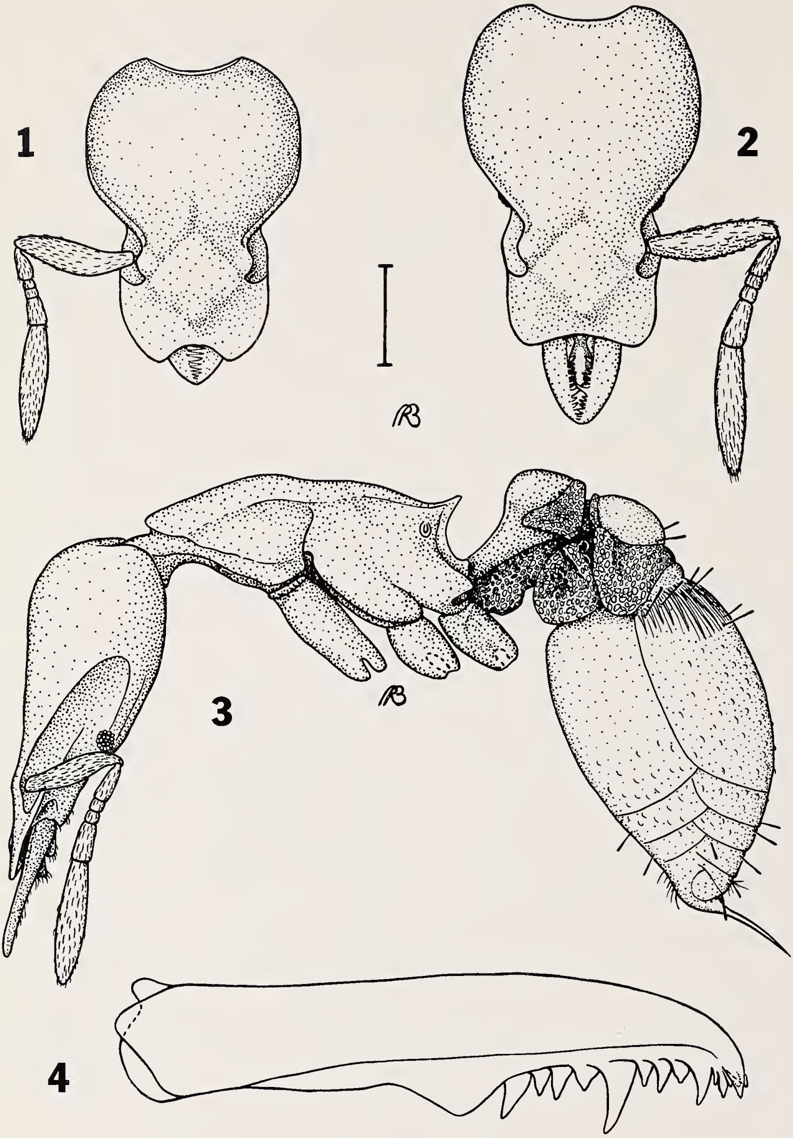
Viewed from the side, *P. sauteri* is much as shown in the side view of *P. canina* (Fig. 4), except that in *sauteri,* the upper vertex is more prominent, so that the head is thicker at this point dorsoventrally, and the transition from frontal to occipital faces of vertex more abrupt. The truncal dorsum is more strongly sinuate in side view; the propodeal teeth are also shorter and less acute than in *canina,* and the propodeal lamella wider. The erect pilosity of the gastric dorsum and apex is even more reduced, in hair number and size, than in *canina.* In the *sauteri* type, the middle of the mesopleura is weakly shining, though still sculptured, and the dorsolateral margins of the trunk are completely lacking.

P. sauteri still remains known only from this single specimen from Taiwan.

Pentastruma canina new species

Figs. 2, 3, 4

Holotype worker: TL 2.9, HL 0.77, HW 0.55, ML 0.16, WL 0.72, petiole L 0.30, eye L 0.05, scape L 0.32, hind femur L 0.46, hind tibia L 0.35 mm; CI 71, MI 21.



Figures 1–4. *Pentastruma* spp., workers. Fig. 1, *P. sauteri* holotype, head in full-face dorsal view. Fig. 2, *P. canina* new species, paratype from type nest series, head in full-face dorsal view. Fig. 3, same, side view. Fig. 4, same, another paranidotype, mandible greatly enlarged. Figs. 1–3 to same scale; scale line = 0.2 mm. Drawings by Ronald G. Boisvert.

Habitus as shown for the paratype in Figs. 2 and 4. Note the depressed, flat mandibles and the 6-merous antennae, with segments proportioned as in *Smithistruma,* and also the broadly extended, sharp-edged, lamelliform, free lateral margins of the clypeus, translucent in bright light. Mandibular armament shown in detail in Fig. 3. After the broadly rounded basal lamella there follow without a diastema 15 teeth, of which the first, fifth, and ninth are the longest. Between these, 2 groups of 3 smaller teeth each, in each such triplet, the middle tooth a little longer than the 2 flanking it. A similar triplet follows the ninth tooth, and after this 2 small subapical teeth and a robust apical tooth. Labral lobes at rest extending beyond the midlength of the mandibles. Mandibular surface very finely sculptured, weakly sericeous-shining.

Pronotum with rounded, strongly marginate anterior margin (excluding cervix), faintly indicated but rounded humeri, feebly marginate or submarginate dorsolateral margins, widest (W about 0.31 mm) behind midlength, tapering caudad into subparallel-sided posterior half of trunk (W about 0.16 mm across propodeal dorsum), which even widens again very slightly caudad. Metanotal groove obsolete or nearly so as viewed from above; propodeal teeth approximately parallel. Faint margins extend the length of the dorsolateral borders of the trunk, but these are visible only in certain views and lights.

Petiolar node subquadrate (rounded in front), slightly wider (W about 0.15 mm) than long, its dorsal surface with sculpture partly effaced, weakly shining. Postpetiolar disc transversely elliptical, nearly twice as wide as long (L 0.15, W 0.27 mm), smooth and shining, with a widely spaced pair of inclined hairs near posterior border. Gaster with weak basidorsal costulae, effaced mesad, the longest extending about a quarter of the length of the first tergum. Erect, feebly enlarged hairs: 4 near base of first gastric tergite, a pair near midlength, and a pair near posterior border of first tergite; remaining segments with 2 or 4 hairs each on tergites, and a few fine ventral, erect hairs also on apical half of gaster. The fine, short, extremely dilute, appressed and decumbent pubescence is invisible except at high magnifications (over 50×) and in special, strong lights, and is best developed on mandibles, antennae, vertex, legs, and gaster, though nowhere evident without a special effort to find it.

Color medium testaceous; spongiform apendages sordid whitish-testaceous.

Type deposited in the Museum of Comparative Zoology, Harvard University.

Queen (Based on 7 specimens from 4 localities, including type nest series): TL 3.0–3.3, HL 0.77–0.80, HW 0.57–0.59, ML 0.17–0.18, WL 0.80–0.84, forewing L (3 specimens) 2.4–2.6 mm; CI 73–75, MI 22–23. Largest specimen (from Kiyosumiyama, HL 0.80 mm) with scape L 0.33, eye L 0.13 mm.

With the usual differences from the worker. Pronotum with flat dorsal pronotal platform, as seen from above, markedly constricted before it joins the mesothorax. Scutellum rounded and bulging caudad. Petiolar node broader than in worker, and tending to be medially sulcate in front. Scutum irregularly reticulate-punctate, its surface weakly shining in some lights, opaque in others. Color testaceous to medium ferruginous, usually slightly darker than worker.

Male (3 specimens from Manazuru and Shirahama): TL 2.7–2.8, HL 0.56–0.60, HW including eyes 0.45–0.47, eye L 0.20–0.22, WL 0.82–0.83, forewing L 2.3–2.4 mm.

Color blackish-brown, gaster dark reddish-brown, legs and antennae sordid, pale, dull brown; wings hyaline. Mandibles slender, each with a weak tooth-like angle apicad of midlength, only slightly curved, probably not opposable, tapered to a very acute apex. Labrum broad, the 2 lobes short and separately rounded.

Antennal scape broader and longer than pedicel, and about as broad as the apical antennal segment; segments III through XII slender and cylindrical, all longer than scape or pedicel. Pronotum forming a flattened, C-shaped platform, something like that of female. Mesonotum large and bulging; notauli present but short, and not meeting behind to form a V or Y; parapsidal lines present. Scutellum bulging, rounded caudad. Propodeal teeth low, subacute, with narrow, concave infradental lamellae. Mesokatepisternum and a patch on the side of the propodeum with sculpture effaced, nearly or quite smooth and shining.

Petiole claviform, with low, rounded, scarcely differentiated node that is mainly smooth and shining above; spongiform appendages reduced to a narrow mid-ventral strip and a fine, cariniform posterodorsal collar. Postpetiole broader than long, rounded, smooth and shining, with a narrow, posterior collar of transparent lamella and an anteroventral spur trimmed narrowly with transparent lamella. Gaster unadorned at base, smooth and shining, with an extremely sparse, inconspicuous sprinkling of tiny, appressed pubescence hairs, and a very few obliquely erect, short, fine hairs on tergum of basal segment, plus some more of these nearer the gastric apex. Legs with dilute, fine, inconspicuous, decumbent and appressed pubescence. Head, trunk, antennae, legs and sides of petiole predominantly finely reticulate-punctulate, opaque, with the exceptions noted above.

Paratypes: 38 workers, 8 queens (alate and dealate) and 2 males, all from JAPAN. HONSHU: Manazuru, Kanagawa Pref. (type locality), 3 nest series; 4 April 1968 (with males), 20 Oct. 1968, 5 Jan. 1973 (with winged queens), all leg. M. Kubota. Hamaoka, Shizuoka Pref., 15 Nov. 1976, leg. R. Egawa. Kiyosumiyama, Chiba Pref., 17 Aug. 1976, leg. T. Kannari. Shirahama, Wakayama Pref., 6 Jan. 1971 (with males), leg. M. Kubota. KYUSHU: Miyazaki-jingu, Miyazaki Pref., 18 July 1971, leg. M. Shindo. Deposited in the collection of Dr. Masao Kubota, at Odawara, Kanagawa Pref., Japan; in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; and in the Department of Entomology, British Museum (Natural History), London.

The variation of worker paratypes is most marked in body size, relative head width, acuteness and width of propodeal teeth and trailing lamellae, and in depth of ferruginous coloration, often varying to faded straw color (in callows?). TL 2.5–2.9, HL 0.68–0.78, HW 0.48–0.56, ML 0.14–0.16, Eye L 0.04–0.06, WL 0.62–0.72 mm; CI 66–74 (mean 71 for n = 16), MI 19–22.

P. canina, widespread in central and southern Japan, is readily distinguishable from *P. sauteri* by the form of the head and mandibles (Figs. 1 and 2). From the known *Smithistruma* and *Trichoscapa* species of eastern Asia, the *canina* worker may be separated by its head shape and by the total lack of standing pilosity on head, scapes and trunk.

Dr. Masao Kubota, of Odawara, Kanagawa Prefecture, Japan, deserves thanks, not only for the opportunity to study the many excellently prepared specimens of *P. canina,* but also for notes on the biology of the species summarized below.

P. canina is an uncommon species, found in the Kantō District and southward. It inhabits the floor of coastal evergreen broadleafed forest, which is generally subtropical. Nests are found in small pieces of rotten wood, rotten fallen branches, under moist leaf litter, or at a slight depth in the humus. The largest colony censused contained one queen and 57 workers.

OBSERVATIONS ON A POPULATION OF *SIALIS ITASCA* ROSS IN WEST VIRGINIA (MEGALOPTERA: SIALIDAE)

By C. K. Lilly[1], D. L. Ashley[2], and D. C. Tarter[2]

Observations on the ecology of each species in an aquatic community are necessary for the total understanding of community dynamics. Several authors, including Davis (1903), Ross (1937), Townsend (1939), Flint (1964), Azam and Anderson (1967), Woodrum and Tarter (1973), Pritchard and Leischner (1973), Tarter and Woodrum (1973), Tarter (1973), Tarter et al. (1976), and Tarter et al. (1978) have reported on the taxonomy, distribution, life history, and ecology of several *Sialis* spp. Other authors, including Roback and Richardson (1969), Warner (1971), Nichols and Bulow (1973), Tarter and Woodrum (1972) and Woodrum and Tarter (1973), have noted the extreme tolerance of *Sialis* to acid mine drainage.

The primary objectives of this investigation were: (1) to make observations on the life history and ecology of the alderfly *S. itasca* in a small farm pond and (2) to determine the pH tolerance of this population under laboratory conditions.

Materials and Methods

The population of *S. itasca* inhabits a small farm pond, 0.1 hectare, near Shoals, West Virginia which is 8 km south of Huntington, West Virginia. This pond is located in the north-central region of Wayne County. It is located at 82° 29′40″W longitude and 38° 21′50″N latitude.

This investigation was initiated in May 1975 and continued until April 1976. Monthly samples were taken by a small seine (0.25 inch mesh). The seine was placed in the water vertically and the mud and debris on the bottom of the pond between the seine and the bank were disturbed. The seine was then moved toward the bank while dragging the bottom of the net on the bottom of the pond collecting

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mud and debris in the net. The larval alderflies were collected and preserved in 70 percent ethanol.

Temperatures were taken with a Taylor maximum-minimum thermometer placed on the pond bottom 0.5 meter below the water surface. They were recorded in degrees Celsius once per month at the time benthic samples were taken. Water chemistry tests were performed in the field with a Hach chemical kit, Model AL-36-WR. All tests were completed within one hour. Hydrogen-ion concentration (pH) was measured colorimetrically. Dissolved oxygen, carbon dioxide, hardness (magnesium and calcium), phenolphthalein and methyl orange alkalinity, free acidity, and total acidity were measured and recorded in mg/1.

Size classes were determined by length frequency distributions arranged in 1 mm length groups. Total length (exclusive of the caudal filament) was measured under 7× magnification with calipers and a plastic ruler (nearest 0.5 mm). Head width was measured with an ocular micrometer between the inner edges of the eyes (nearest 0.01 mm). Differences in head width of 124 larvae were determined to show the mean, range and standard deviation.

A total of 84 foreguts were examined to determine food habits. The head was removed and the abdomen was split open to remove the intestine. The contents of the intestine were removed and examined under a dissecting microscope and a compound microscope to identify their contents. The percent frequency of occurrence of each item was determined, and the monthly and seasonal averages and various sizes were compared.

For the pH tolerance test, forty mature larvae collected from the pond in April were taken to the laboratory for acclimatization over a 24 hr period. The larvae were placed in groups of 10 in 4 finger bowls. One bowl was filled one-third of the way with pond water. A one molar solution of potassium dihydrogen phosphate (KH_2PO_4) was diluted approximately into the other three bowls, to set pH values at 5.5, 4.0, and 2.5. The pH value of the control was 7.0. A Model 5 Corning Scientific pH meter was used to determine pH values. Oxygen was constantly supplied with air stones. The temperature did not change significantly during the experiment and averaged 12 C. The 96 hour TL_m (median tolerance limit) test (APHA, 1965) was used to measure the effect of low pH. The pH value at which 50 percent of the alderfly larvae died after 96 hours was determined by straight-line graphical interpolation.

Fifteen larvae were collected in April and returned to the laboratory for rearing in vials containing pond water. These vials were connected to vials containing sand by a short section of rubber tubing (Pritchard and Leischner, 1973). Wire mesh and strips of foam rubber were placed in the vials and rubber tubing to enable the larvae (one per vial) to move freely between the vials. The vials were kept at room temperature which was approximately 70 F.

Fecundity was determined by a direct count of ovarian eggs under a compound microscope. The ovaries of 3 adults were removed and a total of 1616 eggs were counted. The diameters of 90 eggs were measured to the nearest 0.01 mm with an ocular micrometer using a Bausch and Lomb compound microscope.

RESULTS AND DISCUSSION

Pond Environment

Temperature. — The average annual temperature for the pond was 18.1 C. The extreme monthly temperatures were 0.5 C in February and 35.0 C in August and September.

Water Chemistry. — The average annual pH was 8.4 (7.5 to 9.0). The average annual dissolved oxygen was 8.5 mg/l (6.5 to 10.0). The average annual total hardness was 139.6 mg/l (102.6 to 153.9). The average annual carbon dioxide concentration was 9.6 mg/l (5.0 to 25.0). The average annual alkalinity was 110.5 mg/l (68.4 to 145.4). The average annual total acidity was 12.4 mg/l (5.7 to 28.5).

Larval Stage

Development. — Length-frequency histograms indicated that the population of *S. itasca* contained one size class (Fig. 1). Hatching occurred at the end of May. There were 18 egg masses located in the field at the end of May. The egg masses were found on the leaves of hornbeam and buckeye trees. Three egg masses which were returned to the laboratory hatched within 2 days. In July all the egg masses were empty but no larvae were located. The earliest and smallest larvae were collected on August 2, 1975. Their average length was 6.45 mm, and their average head width was 1.02 mm. The last and largest larvae were collected on April 6, 1976. Their average length was 13.67 mm, and average head width was 1.59 mm.

Head width was used to show the monthly variation in growth rate and the percent increase in growth rate (Fig. 2). Due to the

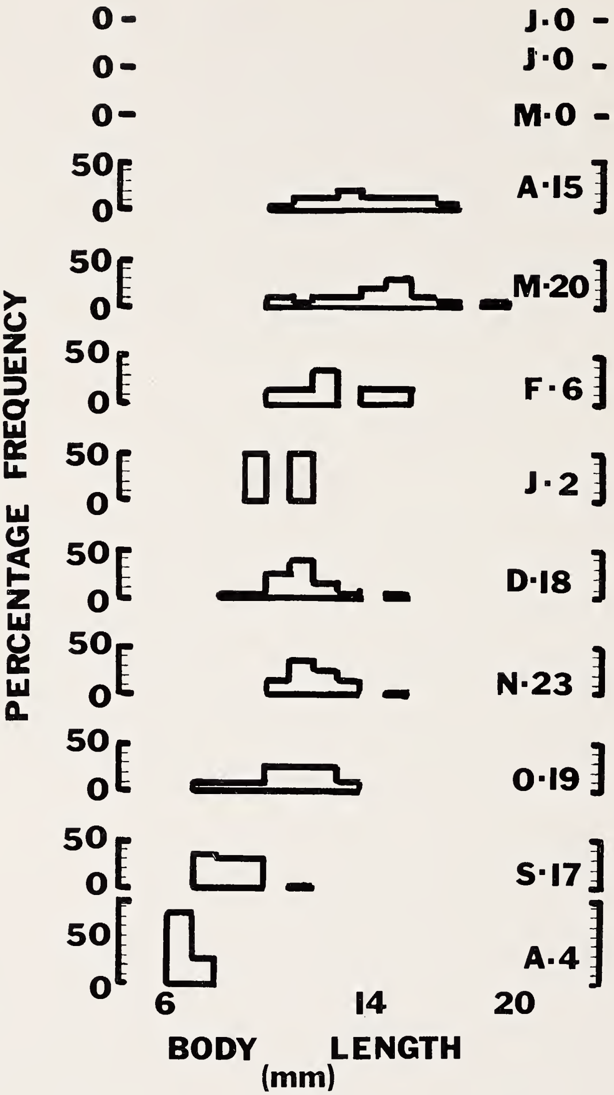

Figure 1. Length-frequencies at monthly intervals of *S. itasca* larvae from a farm pond near Shoals, W. Va. The number of larvae is given for each month.

small sample size (4) in August, no statement can be made concerning the growth rate from August to September. An eighteen percent increase in growth rate was recorded from October to November. There was a decrease in growth rate in December. Small sample sizes in January (2) and February (6) prevented any growth rate information. There was a six percent growth rate from March to April. The largest mean head width was measured in April at 1.59 mm and ranged between 0.95 and 1.86 mm September and November, respectively. No larvae were located in May, June and July.

Woodrum and Tarter (1973) also found a decrease in growth during the winter months in *S. aequalis.* Azam and Anderson (1969) found a decrease in the growth rate for *S. rotunda* and *S. californica* during the winter months.

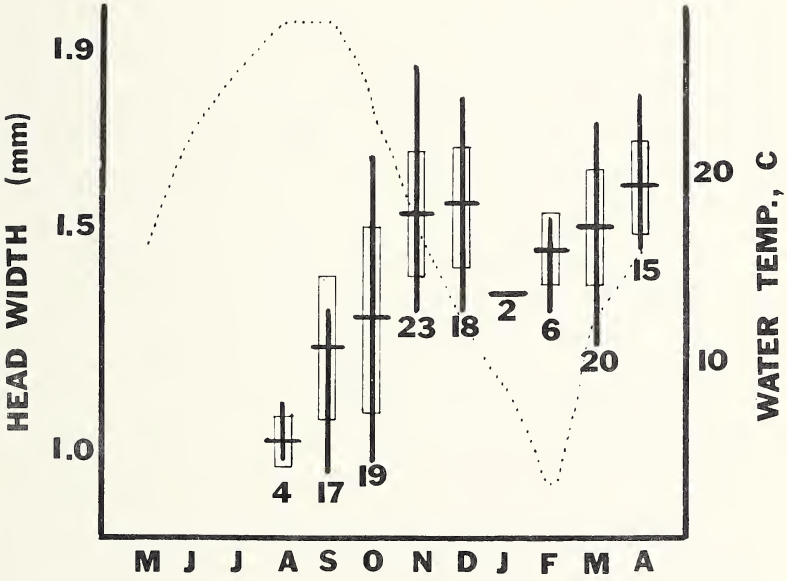

Figure 2. Monthly variation of the head width in *S. itasca* larvae. Vertical lines = ranges, horizontal lines = means, open rectangle = one standard deviation, numbers = sample sizes, and dotted lines = temperature (C).

Food Habits. — This population of *S. itasca* was found to feed almost exclusively on the ostracod, *Cyclocypris* sp. The only other food items were 3 midges, *Chironomus* sp., which were found on 3 different occasions. Of the 84 foreguts analyzed, 21 percent were empty and 79 percent contained food. Ostrocods were found in 71 percent of the foreguts, and midges were found in 4 percent of the foreguts.

Excluding the month of August when a very small sample size (4) was used, the largest number of empty foreguts occurred in January (50%). The percent of empty foreguts increased again in April supporting the findings of Woodrum and Tarter (1973) in *S. aequalis* that the larvae probably do not feed just before pupation.

Azam and Anderson (1969) reported *S. rotunda* and *S. californica* to be indiscriminate feeders and reported cannibalism to be frequent. Woodrum and Tarter (1973) found *S. aequalis* to be more restricted in its feeding due to the limited choices of organisms found in the acid mine stream in which they were located. They also reported cannibalism to occur to a lesser extent. The *S. itasca* in this investigation were found to be more restrictive feeders preying almost exclusively on ostracods while having an abundant supply of other organisms upon which they could feed. Cannibalism was observed in the laboratory when larvae were confined for three days without food.

Predation. — The stomachs of 18 odonates and 10 sunfish were examined. No alderfly remains were found in the sunfish and only one alderfly head was found in the odonates. Schwiebert (1973) noted that the hellgrammite and trout are predators of the alderfly.

pH Tolerance. — The 96 hour TL_m value for *S. itasca* was found to be 3.1. All ten larvae survived the 96-hour period at pH values of 7.0 and 5.5, 70 percent survived in a pH of 4.0, and 30 percent survived at a pH of 2.5. Tarter and Woodrum (1972) found *S. aequalis* from an acid mine stream to have a TL_m value of 2.1. These values would indicate that *S. itasca* and *S. aequalis* are quite tolerant of low pH. *Sialis* spp. have been noted to be tolerant to low pH conditions in western Pennsylvania streams (Roback and Richardson, 1969), Roaring Creek in eastern West Virginia (Warner, 1971), and in the East Fork of the Obey River in Tennessee (Nichols and Bulow, 1973).

Pupal Stage

Larvae placed in the laboratory rearing chambers moved to the sand for pupation within 2 to 4 days. The pupal stage lasted for approximately 2 weeks. The adults emerged during the night. No pupae could be located in the bank of the pond.

Azam and Anderson (1969) reported *S. rotunda* and *S. californica* to pupate during April, May and June. Pritchard and Leischner (1973) reported that *S. cornuta* pupated from May to mid-June. Woodrum and Tarter (1973) found *S. aequalis* to crawl 1.5 to 5 m out of the water onto a moist sandbank when the water temperature reached 11 to 13 C and pupated in an earthen cell 1 to 7 cm below the surface. They found the pupae to respond to a disturbance but otherwise remained rather dormant.

Adult Stage

Number and Size of Eggs. — Fecundity of 3 adult alderflies showed a range of 454 to 587 eggs per female; the average was 539 eggs. The eggs were cylindrical, rounded on the ends, had a curved micropylar tubercle on one end, and averaged 0.31 mm in length by 0.14 mm in width. The number of eggs found in *S. itasca* was similar to those of *S. aequalis* (657) (Woodrum and Tarter, 1973), *S. rotunda* (300–500) and *S. californica* (400–700) (Azam and Anderson, 1969), and *S. cornuta* (615) (Pritchard and Leischner, 1973). Egg masses of *S. itasca* were found on the underside of hornbeam and buckeye leaves 0.5 to 3 m above the water surface. The eggs are laid in rows in a nearly vertical position much like those of *S. rotunda* (Azam and Anderson, 1969).

Mating. — Although copulation was not observed, a courtship behavior was observed in the laboratory much like that described by Azam and Anderson (1969) for *S. rotunda* and by Woodrum and Tarter (1973) for *S. aequalis.*

Longevity. — Adults in the laboratory lived for 4 to 6 days. Only one adult was captured in the field on 3 May 1975. *Sialis rotunda* was first seen in mid-April and reached their peak in May (Azam and Anderson, 1969) while *S. californica* was seen in May but did not peak until mid-June (Azam and Anderson, 1969). *Sialis aequalis* was observed in the field between April 21 and May 4 (Woodrum and Tarter, 1973). Since the adults serve only to reproduce the species, it is apparent that they have a brief life span to perform this function. Azam and Anderson (1969) observed the female of *S. rotunda* laying eggs within a day after emerging.

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STRUCTURE AND RELATIONSHIPS OF THE UPPER CARBONIFEROUS INSECT, *PROCHOROPTERA CALOPTERYX* (DIAPHANOPTERODEA, PROCHOROPTERIDAE)

By Frank M. Carpenter[1] and Eugene S. Richardson, Jr.[2]

Prochoroptera calopteryx was described by Handlirsch (1911) from a single specimen in a concretion from the Francis Creek Shale (Pennsylvanian) in northeastern Illinois. Although poorly preserved, the fossil showed several unusual features. Because of these and its very incomplete preservation, the insect's relationships have been decidedly controversial. Fortunately, after a lapse of nearly seventy years following the publication of Handlirsch's account, three more specimens have recently been found in concretions from the same deposit. These additional fossils, which have been turned over to us for study, provide considerably more information about the insect than the type and enable more reliable conclusions about its relations with other Paleozoic insects, even though much of its body structure still remains unknown. It clearly belongs to the extinct order Diaphanopterodea and is only the second species of that order known from Pennsylvanian strata in North America. Descriptive accounts of all four specimens of *calopteryx* are included below, with a discussion of the relationships of the family Prochoropteridae.

For the opportunity of studying these new specimens we are indebted to Helen and Ted Piecko of Chicago, and Mr. J. J. Fagan of Burbank, Illinois. Handlirsch's type of *calopteryx* has been placed at our disposal by Jean S. Lawless, Division of Invertebrate Paleontology, Peabody Museum, Yale University. Partial support of this research is gratefully acknowledged to the National Science Foundation, Grant No. DEB 78-09947, F. M. Carpenter, Principal Investigator.

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ORDER DIAPHANOPTERODEA

Diaphanopteroidea Handlirsch, 1919, p. 575.
Diaphanopterodea Rohdendorf, 1962, p. 69; Carpenter, 1963, p. 253.
[= Palaeohymenoptera Haupt, 1941, p. 99.]

Family Prochoropteridae

Prochoropteridae Handlirsch, 1911, p. 375.

Fore wing: similar to that of the Elmoidae but with SC extending much farther beyond the origin of RS than in *Elmoa;* stem of R without a prominent bend at the point of divergence of CUA; cross veins weakly developed, without branching. Hind wing: similar to the fore, so far as known, but relatively broader and with its hind margin more curved; coalescence of RS with MS apparently less than in the fore wing. Thorax large, but prothorax small and conical; head small (from above).

Type-genus: *Prochoroptera* Handlirsch. A second genus, *Euchoroptera* Carpenter (1940), from the Pennsylvanian of Kansas (Stanton Formation), also appears to belong to this family; little is known of its wing venation, but the body structures are like those of other Diaphanopterodea.

Genus *Prochoroptera* Handlirsch

Prochoroptera Handlirsch, 1911, p. 376.

Since this genus is monospecific, its characteristics can only be suggested. In all probability the coalescence of MA with RS and the distal forking of MP are in this category. *Prochoroptera* differs from *Euchoroptera* in having the branching of RS pectinate, instead of dichotomous.

Type-Species: *Prochoroptera calopteryx* Handlirsch.

Prochoroptera calopteryx Handlirsch
Figures 1–3

Prochoroptera calopteryx Handlirsch, 1911, p. 376; 1919, p. 586; 1920, p. 172. Haupt, 1941, p. 99. Laurentiaux, 1953, p. 444. Carpenter, 1940, p. 638; 1947, p. 45; 1963, p. 248.

The fore wing is known to a length of 20 mm; estimate of complete length (based on *Euchoroptera*), 36 mm; maximum width, 6 mm. Hind wing: known to a length of 20 mm; maximum width, 6

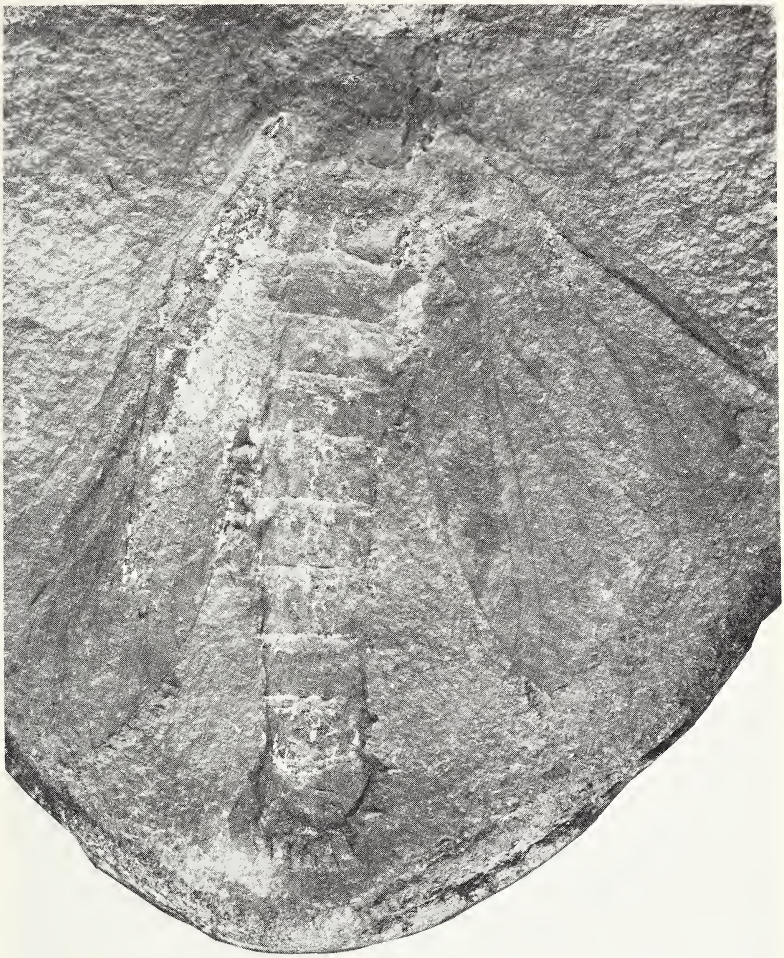

Figure 1. *Prochoroptera calopteryx.* Photograph of reverse of specimen HTP 12523 (× 3.8).

mm. The details of venation are shown in figure 2. Body length, from front of mesothorax to end of abdomen, 25 mm; length of abdomen, 18–19 mm; width, 4–5 mm.

Holotype: no. YPM67, Peabody Museum, Yale University (obverse and reverse).

As shown in Handlirsch's figure, this fossil includes the thorax, abdomen, and parts of both pairs of wings, which rest obliquely backward. His figure of the wings is essentially accurate, although his attempted restoration of the complete wing turns out to be incorrect, at least to the extent that we now know it. The body is also satisfactorily represented in his figure, although the prothorax is too large. The abdominal segments of this specimen possess paired lateral expansions, apparently strongly sclerotized and similar to those present in at least some Palaeodictyoptera. Handlirsch's figure depicts these as membranous areas bordering the terga, but there is nothing in the fossil to support that interpretation. The 9th abdominal segment bears a pair of longitudinal ridges, converging distally, as shown in Handlirsch's figure. These are almost certainly the basal portions of the valves forming the ovipositor. Cerci are not preserved.[3] The dimensions of this specimen are as follows: fore wing, length (as preserved), 20 mm; width uncertain; hind wing, length (as preserved), 20 mm. Body length (from front of mesothorax to end of abdomen), 25 mm; pterothorax, length, 6.3 mm; width, maximum, 6 mm; abdomen, length, 18 mm; width, maximum (3rd segment), 4.5 mm; prothorax, length, 3.5 mm; head absent.

The three recently discovered specimens of *calopteryx* are as follows:

1. No. JJF-IL11–007, collected by J. J. Fagan in Pit 11 (strip mine in Will and Kankakee Counties, 3 to 5 miles south of Braidwood, Illinois).[4] This specimen is preserved in almost the same position as the type. The prothorax and the wing veins are clearer than in the type. Its dimensions are as follows: fore wing, length (as

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[3] Most of the "whole" specimens of insects preserved in these concretions lack the distal parts of the wings and the distal anterior and posterior appendages, such as antennae and cerci. The insect's body is ordinarily in the center of the concretion, which is usually too small to include the distal portions of these appendages.

[4] Mr. Fagan has now deposited this specimen in the Field Museum of Natural History, where it bears the number PE 25667.

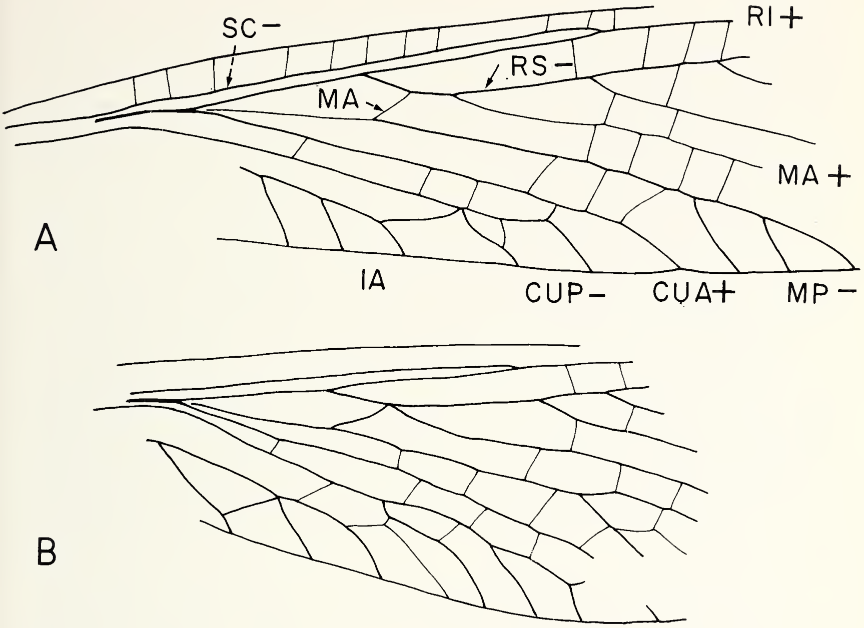

Figure 2. *Prochoroptera calopteryx.* Drawing of fore and hind wings, as known; based mainly on specimen HTP 12523, with some details added from the holotype and specimen JJF 1L11-007. SC, subcosta; R1, radius; RS, radial sector; MA, anterior media; MP, posterior media; CUA, anterior cubitus; CUP, posterior cubitus; 1A, first anal vein; +, convex vein; −, concave vein.

preserved), 18 mm; width, 6 mm; hind wing, length (as preserved), 18 mm; width, 6 mm. Body length (from front of mesothorax to end of abdomen), 25 mm; pterothorax, length, 6.3 mm; width, 4.8 mm; abdomen, length 19 mm; width, 4.8 mm; prothorax, length, 2.5 mm; width at posterior edge, 3 mm; head absent.

2. No. HTP 12523, Helen and Ted Piecko collection. This is the best specimen known. The obverse half represents a ventral view of the insect and the reverse (figure 1), a dorsal view.[5] The wings,

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[5] In our terminology, the *obverse* is the counterpart that shows the topography of the veins as seen on the dorsal surface of the living insect (i.e., SC, concave; R1, convex, etc.); the *reverse* shows the veins in the opposite topography. Generally speaking, the reverse shows the dorsal surface of the insect, and the obverse shows the ventral surface.

pterothorax, and abdomen are especially clear, but the prothorax and head are not preserved. The wings on one side, although lacking the apical portions, are very clearly preserved; those on the other side are twisted and folded together. Widely spaced pits in the impressions of the veins and cross veins indicate the original presence of trichia or small setae. The segmentation of the abdomen is especially clear and the lateral extensions of the segments, mentioned above in the type, are faintly preserved in the obverse half of the fossil. Also, in that counterpart, which shows the ventral view of the abdomen, the bases of the ovipositor valves can be seen in the 8th and 9th segments. The ovipositor appears to be about 5 mm long before disappearing at the edge of the concretion. The cerci are not preserved. The following are the dimensions of this fossil: fore wing (as preserved), 15 mm; width, uncertain; hind wing, length (as preserved), 15 mm; width, 6 mm. Body, length (from front of mesothorax to end of abdomen), 25 mm; pterothorax, length, 5 mm; width, 4.8 mm; abdomen, length, 18.5 mm; width, maximum, 4.6 mm.

3. No. HTP 415, Helen and Ted Piecko collection. This is a poorly preserved specimen, resting in the same position as the previous one. The venation is clear enough for identification of the species, and the prothorax and even the head, which is not shown in other specimens, are discernible. Neither the ovipositor nor the cerci are visible. The dimensions of this specimen are as follows: fore wing (as preserved), 20 mm; width, uncertain; dimensions of hind wing uncertain. Body length (from front of mesothorax to end of abdomen), 25 mm; pterothorax, length, 6 mm; width, maximum, 4 mm; abdomen, length, 20 mm; maximum width, 4.5 mm; prothorax, length, 3.3 mm; posterior width, 2.5 mm; anterior width, 1.5 mm; head, length, 3 mm; width 3 mm. The head as preserved shows somewhat protuberant eyes; the head is obviously seen in dorsal view, with no indication of the beak.

Discussion of Structure

The wings of *calopteryx,* as far as they are known at present, are shown in figure 2, which is based mainly on specimen HTP 12523, with some details added from the other specimens. The figure shows more of the basal parts of both wings than was known to Handlirsch. The homologies of the veins are obvious, the convexities and concavities being clearly preserved. Handlirsch (1911) confused MA with a branch of the media, but his interpretations were the conventional ones at the time. In all four specimens the amount of coalescence between MA and RS is distinctly less in the hind wing than in the fore wing, but in other respects the venational patterns are nearly identical, so far as they are known. The shape of the hind wing, as preserved, suggests that it may have been slightly shorter than the fore wing, the hind margin having a greater curvature. The fore wing was apparently somewhat more elongate than indicated in Handlirsch's figure.

Figure 3, showing all of the known parts of the insect, is based mainly on HTP 12523, with the prothorax and head as preserved in HTP 415. The wings have been added to the figure to show their size relative to the body, which appears to be surprisingly robust compared to the wings (See figure 1). The prothorax, which is preserved in HTP 415 and the holotype, is clearly conical in shape and unusually small with respect to the rest of the thorax. The

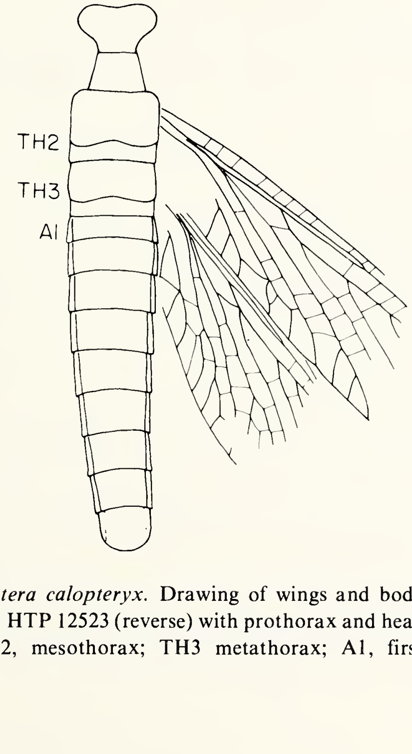

Figure 3. *Prochoroptera calopteryx.* Drawing of wings and body, as known; based mainly on specimen HTP 12523 (reverse) with prothorax and head added from specimen HTP 415. TH2, mesothorax; TH3 metathorax; A1, first abdominal segment.

outline of the head is faintly indicated in specimen HTP 415. Handlirsch's drawing (1911) of the type includes a suggestion of the head or part of it, but we have been unable to discern the structure that he has drawn. However, the head as shown in specimen HTP 415 is very small with respect to the rest of the insect, although of course the head as preserved in the fossil is seen from above and does not show its full length. The meso- and metathorax, on the other hand, appear large relative to the rest of the insect. The abdominal segments are virtually homonomous, with only a slight reduction in the width posteriorly.

Affinities of the Prochoropteridae

Opinions of the affinities of *calopteryx,* based on the type, have been diverse. Handlirsch (1911, 1919, 1920) considered it to belong to the Megasecoptera. Carpenter (1940), following the discovery of another and apparently related Pennsylvanian insect (*Euchoroptera longipennis*), concluded that the family Prochoropteridae had close affinities with the Permian family Asthenohymenidae, then considered to be the most highly specialized of the Megasecoptera. However, Haupt (1941), basing his conclusions on Handlirsch's brief account of *Prochoroptera,* designated a new order, Palaeohymenoptera, for the family Prochoropteridae, assigning it to his "Legion Hymenopteroidea", which also included the Hymenoptera. Unaware of that publication[6] Carpenter (1947, 1954) proposed that the families Prochoropteridae and Diaphanopteridae (Commentry, France), along with two other Permian families, be placed in a separate suborder of the Megasecoptera. However, Rohdendorf in 1962 adopted the ordinal name Diaphanopterodea for that series of families, since the taxon had been named by Handlirsch (1919) for the Diaphanopteridae. That term has subsequently been generally accepted.

The order Diaphanopterodea is now recognized as belonging to the Palaeoptera and as allied to the Palaeodictyoptera and Megasecoptera, all of their members possessing haustellate mouthparts and long cerci. Alone in this series, however, the Diaphanopterodea had the ability to "fold" their wings at rest along the abdomen. The

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[6] The journal containing Haupt's 1941 paper (Zeitschrift für Naturwissenschaften, Halle) was not received by the library at Harvard University until January, 1958.

most distinctive feature of their venation is the coalescence of CUA and M basally, and, except in the Diaphanopteridae, the coalescence of CUA and M further basally with R. In all the families of the order, M appears to arise at the point of divergence of R and CUA.

Although the body structure of *Prochoroptera* is very incompletely known, the wing venation clearly shows the diagnostic features of the order Diaphanopterodea, and of course, as noted above, in all known specimens the wings are folded along the abdomen. However, the position of the Prochoropteridae within the order is still uncertain. As far as known, the most obvious evolutionary changes within the Diaphanopterodea are the narrowing of the wing base and the consequent increased coalescence of MA with RS and ultimately with R itself (See Carpenter, 1963, plate 10, figs. 1–6). However, it now seems probable that these changes occurred independently within several lines of the order (Kukalova-Peck, 1974). As a result, diagnoses of some families are very difficult to make, especially of those in which the wings are not completely known, such as the Prochoropteridae. However, it seems advisable to retain the family Prochoropteridae as valid and as distinct from such Permian families as Elmoidae and Martynoviidae on the basis of its venational features as presently known.

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DIVISION OF LABOR WITHIN THE WORKER CASTE OF *FORMICA PERPILOSA* WHEELER (HYMENOPTERA: FORMICIDAE)*

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Introduction

Polymorphism, in the study of social insects, is defined as the existence within an individual colony of two or more phases or castes belonging to the same sex, without particular regard to their genetic or environmental origin (Wilson, 1953). The adaptive result of the development of female polymorphism is the division of labor within the colony. In most ants this division is clearly seen between reproductive and non-reproductive caste, but less evident within the worker caste (Oster & Wilson, 1978). The present article utilizes the Fagen & Goldman (1977) method for estimating the total repertory size of behavioral categories of each worker subcaste listed on an ethogram or behavioral catalog.

Ethograms are the essential first step of the comparative study of behavior (Wilson, 1974). A behavioral catalog of *Formica perpilosa* Wheeler, a weakly polymorphic species of the *neogagates* group (Buren, 1968), was constructed in order to investigate behavioral differences between the major size groups, defined here arbitrarily as three worker subcastes. *Formica perpilosa* is a common ant in the southern United States and northern Mexico (Gregg, 1963). It feeds mainly on plant exudates and tends membracids of the genus *Pubilia* (LaBerge, 1952). Its physiology has been relatively well studied by Schumacher & Whitford (1974), Kay & Whitford (1975), Whitford, Kay & Schumacher (1975) and Schumacher & Whitford (1976). The genus *Formica* is of unusual interest because its species are either monomorphic or weakly polymorphic and thus span the early stage of caste evolution. Yet close studies of the polymorphic species have not been undertaken.

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MATERIAL AND METHODS

Founding queens were collected near Portal, Arizona, in May, 1975, by B. Hölldobler and individually placed in test tubes, 14.8 cm long by 23 mm inner diameter, kept moist by compact cotton plugs that trap water at the bottom of the tubes. As the selected colony grew the tube was moved to a plexiglass box 28 cm × 45 cm and 15 cm deep, the sides of which were coated with Fluon GP-1 (Northeast Chemicals Co., Woonsockett, R.I.) to prevent escape, and four similar tubes added. The colony has since been maintained on an artificial diet for ants (Bhatkar & Whitcomb, 1970) and honey water three times a week and fed freshly killed cockroaches (*Nauphoeta cinerea*) once a week.

Before the first set of observations the colony was moved to a glass nest made of two square plates 12.5 cm on a side, held apart by small pieces of non-toxic plasticin and taped on three sides. This simple nest permits close observation of the behavior of the entire colony. The assemblage was put on the floor of the original container next to the water tubes. The remainder of the floor served as foraging space and was kept clear for observation.

The container was small enough to be placed under a swinging arm dissecting microscope. During a period of 4 weeks, a total of 18 hours were dedicated to cataloging behavior; 2809 separate behavioral acts were recorded. The observation hours ranged randomly from 9:00 A.M. to 11:00 P.M.; no differences in level or pattern of activity were noted, related to time of day.

This species is polymorphic in the sense of Wilson (1935); for the purpose of this investigation the workers were classified in 3 groups, minors, medias and majors. Samples of 15 specimens of each group were selected later for head width measurements in order to check the adequacy of the classification. Specimens that could not be readily placed in one of the size classes were not included in the ethogram.

RESULTS

The behavioral catalog of *Formica perpilosa* is presented on Table 1. Twenty-eight behavioral categories were observed in the minor category, 34 in the media, and 11 in the major. By fitting the frequency data to a lognormal Poisson distribution (Fagen & Goldman, 1977), the total numbers of categories, including those

Table 1. Relative frequencies of behavioral acts by the three worker categories of a single colony of *Formica perpilosa.* (N, total number of behavioral acts recorded for each caste). Approximate population of the nest: one nest queen, 150 minor workers, 270 media workers, 30 major workers, 50 eggs, 7 larvae and 5 pupae.

Behavioral Acts	minor workers N = 996	media workers N = 1679	major workers N = 134
A—*Grooming*			
1—Autogrooming head, 1st pair of legs	.167	.131	.224
2—Autogrooming 2nd pair of legs	.060	.062	.052
3—Autogrooming abdomen, 3rd pair of legs	.023	.022	0
4—Allogrooming minor workers	.054	.019	0
5—Allogrooming media workers	.043	.095	.052
6—Allogrooming major workers	.007	.012	.030
7—Allogrooming nest queen	.011	.049	.022
B—*Brood Care*			
8—Standing at the brood pile	.066	.077	.134
9—Carry egg (or eggs in succession)	.033	.055	0
10—Lick egg (or eggs in succession)	.016	.053	0
11—Carry larva (or larvae in succession)	.009	.024	0
12—Feed larva	0	.004	0
13—Lick larva (or larva in succession)	.011	.031	0
14—Carry pupa	0	0	0
15—Lick pupa	0	0	0
16—Assist eclosion to adult	.002	.024	0
C—*Regurgitation Behavior*			
17—Regurgitation with minors	.070	.024	.052
18—Regurgitation with medias	.040	.165	.291
19—Regurgitation with majors	.007	.021	.045
20—Donating to the Queen	0	.009	.008
21—Lay trophic egg	0	0	0
22—Feed queen trophic egg	0	.001	0
23—Feed larva trophic egg	0	.001	0
24—Carry infrabucal pellet	.003	.009	.090
25—Feed on infrabucal pellet	.007	.011	0
D—*Working*			
26—Foraging outside the nest	.082	.021	0
27—Feed on diet	.022	.004	0
28—Feed on honey	.029	.025	0
29—Feed on cockroaches	.020	.007	0
30—Carry live nestmate	0	.001	0
31—Carry dead nestmate	0	.003	0
32—Drag the nest Queen	0	.001	0
33—Handle nest material	.018	.005	0
34—Carry debris	.033	.003	0
35—Lick nest wall	.059	.034	0
36—Excavating	.092	.012	0
E—*Other Behaviors*			
37—Antennal tipping	.001	.002	0
38—Jittering	.016	0	0
Total	1.0	1.0	1.0
no. behavioral categories observed per caste	28	34	11

not seen, were estimated to be respectively 29, 36 and 11, with 95 per cent confidence intervals of (25, 33) (25, 47) and (5, 19).

COMMENTS ON TABLE 1:

Some behavioral categories deserve special mention:

1. *Carry pupa or lick pupa:* Care of pupae consisted exclusively of assisting eclosion to adult. The pupae remained in the brood chamber and only when the colony was disturbed (which did not happen during the drawing of the catalog) media workers carried them to the new nest.

2. *Lay trophic egg:* The actual laying of trophic eggs was not seen, but 3 times media workers were seen offering the larvae and the queen small, round, shiny objects, looking like eggs, but different from the normal ones laid by the nest queen. It is not impossible that the laying of trophic eggs is a real but rare event.

3. *Recruitment behavior:* In order to determine whether the workers utilize any kind of food recruitment, the colony was deprived of food for one week and the nest connected to an arena by a bridge of round sticks. Honey water was presented on the arena floor. Two periods of one hour observation were recorded. Initially all ants that reached the food source were collected and not allowed to return by the bridge. Between the two experiments the honey source, the bridge and the arena floor were changed to avoid recognition by the ants. In the first period 35 ants reached the food source, in the second 262. This experiment clearly shows that this species uses food recruitment. Returning ants were observed to rub the tips of the abdomen on the bridge sticks (probably laying a scent trail) and to display no nestmates. During the construction of the catalog, however, no recruitment behavior was noted, probably because the colony was kept fed to saturation.

4. *Jittering and antennal tipping:* These behavioral categories were described by Wilson (1976), but nothing is known about their meaning.

5. *Defensive behavior:* Our *perpilosa* colony was not stressed to ellicit defensive behavior. However, a stray individual of the ant *Novomessor cockerelli* was found on the nest floor being attacked by media and minor workers of *Formica perpilosa;* not even in this situation the majors were observed outside the nest. This of course does not mean that majors cannot play a role in defending the nest against predators or raids by other ants, but it is apparent defense is not their characteristic behavior. A more detailed account of the defensive behavior of this species should be useful.

After the behavioral catalog was drawn, 50 specimens had their head widths and lengths measured and plotted. The linear anamorphosis afforded a linear regression of head length on head width, where the coefficient of determination is $r^2 = .964$. When logarithmically plotted, in order to compare with Wilson's model

(1953), the log-log anamorphosis afforded a linear regression of head length on head width. The equation is

$$\log L = .2795 - .8602 \log W$$

or, alternatively,

$$L = 1.9033\ W^{.8602}$$

The coefficient of determination, r^2 is also .964, showing of course an excellent fit.

I have chosen the following criteria for the definition of the categories of workers: minors, head width 1 mm or less; medias, 1 to 1.4 mm; majors, larger than 1.4 mm.

The majors represent only 6.6% of the nest population and their behavioral catalog comprises merely 11 behavioral categories. Their behavior, as seen in Table 2, is mostly directed toward grooming and regurgitation with nestmates.

DISCUSSION AND CONCLUSION

The behavioral catalog and the head shape curve of our *Formica perpilosa* colony show that the worker caste is strongly polyethic, in spite of being only slightly polymorphic. The media category is responsible for most of the behavioral categories. The majors are specialized in regurgitation with nestmates and may act as a trophic subcaste as in *Camponotus* (*Colobopsis*) *fraxinicola* (Wilson, 1974). *F. perpilosa* majors also possess a relatively large abdomen and

Table 2. Relative frequencies of groups of behavioral acts listed on Table 1 by the three worker subcastes in a single colony of *Formica perpilosa*. (N. total number of behavioral acts recorded for each subcaste.)

Groups of behavioral acts (from Table 1)	minor workers N = 996	media workers N = 1679	major workers N = 134
A—Grooming	.365	.390	.380
B—Brood Care	.137	.248	.134
C—Regurgitation	.127	.241	.486
D—"Working"	.355	.116	0
E—Jittering & Antennal tipping	.017	.002	0
	1.0	1.0	1.0

were never observed performing any defensive or "working" behavior. They were recorded as using almost half of their time doing trophallaxis or offering infrabucal pellets to minors and medias.

King and Walters (1950) have found a very similar situation in "*Formica rufa melanotica*" (=*F. obscuripes*) in natural nests. They were able to prove a correlation between polymorphism and polyethism, showing that minor workers were specialized in attending aphids. The major workers again remained inside the nest most of the time.

On Table 2 one can notice that all the categories of *F. perpilosa* spend the same amount of time performing grooming behavior. The minors are almost exclusively responsible for several tasks grouped as "working" and the medias spend a more uniform amount of time performing each group of behavioral acts.

Wilson (1953) proposed a model for the origin and evolution of polymorphism in ants. In 1971 he reviewed the ant caste system and said that five steps can be recognized in the evolution within the worker caste: monomorphism, monophasic allometry, diphasic allometry, triphasic allometry and complete dimorphism.

Age polyethism is the responsible phenomenon for caste structure in monomorphic species, and the polyethic classes are sometimes referred to as physiological classes. Traniello (1978) reported an apparent lack of temporal division of labor in the primitive ponerine ant *Amblyopone pallipes,* which appears to have the most primitive caste system yet documented in ants.

Monophasic allometry is the commonest manifestation of nonisometric growth. Studies on the division of labor in weakly polymorphic species showed a "by preponderance" division of labor, i.e., any given worker should be capable of performing any given normal task.

In *Formica polyctena* size variation is weakly correlated with division of labor. The behavioral variation observed by Otto (1958) consisted mainly of age polyethism and individual peculiarities. Although the *F. perpilosa* subcastes were not divided using age parameters, I believe that age does not account for a large fraction of the total behavioral variation.

Majors of advanced polymorphic ant species, especially completely dimorphic species, where intermediates no longer exist and the two remaining classes are remarkably different in morphology, usually act as soldiers. This is not true in the present case, where another kind of specialization was revealed.

In the complete dimorphic species there is no behavioral overlap between the castes. Each category can be easily distinguished from the others morphologically and behaviorally.

Majors of *Zacryptocerus varians* (members of one of the nine genera in which complete dimorphism is easily recognized) function primarily in defense (Wilson, 1976) and deserve the title of soldiers. Yet they sometimes wash and manipulate larvae and pupae. But during a high intensity attack, majors block the nest entrance with their saucer-shaped heads and are more persistent and effective than minors in forcing the enemy back to the entrance and finally out of the nest.

Dr. Edward O. Wilson, reviewing the manuscript, was kind enough to suggest that *F. perpilosa* majors represent an early stage in the evolution toward repletes, as seen in *Proformica* and *Myrmecocystus* (Wilson, 1971). The specialization shown by *perpilosa* majors (see Table 2) agrees with this view.

F. perpilosa seems to occupy, from the viewpoint of evolution of division of labor, an intermediary position between monomorphic and completely dimorphic species.

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CULTURE TECHNIQUES FOR *ACANTHOPS FALCATA,* A NEOTROPICAL MANTID SUITABLE FOR BIOLOGICAL STUDIES (WITH NOTES ON RAISING WEB BUILDING SPIDERS)*

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Introduction

"It is both expensive and difficult to maintain a year-round colony of mantids and a continuous supply of living insects upon which to feed them. Because of their cannibalism, mantids must be raised in individual containers, and the smaller males are invariably in short supply." Roeder, 1963, p. 141.

We think that we have found the solutions to these problems. We have devised a simple and inexpensive culture regime and found a species that is easy to manage in captivity. This species, *Acanthops falcata* Stol, is small enough to raise in large numbers in a modest amount of space and large enough to be convenient for a wide number of biological investigations. Females that are sexually receptive can be triggered to mate by a dark/light transition and males also become sexually active following such a transition. Matings are thus readily manipulable by the experimenter. In addition, the species is fecund and hardy.

Our interest in solving the problems of raising predatory arthropods began in 1971, when we needed naive predators in order to investigate instinctive behavior. We used two species of araneid spiders, *Argiope argentata* and *A. aemula,* feeding them on dead drosophiloid flies (Robinson & Robinson, 1976a). Since then we have raised several generations of *A. argentata* and successfully hand reared two other species of web building spiders from egg cocoons, without the restriction of using dead prey, which makes the problem simpler.

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Later we became interested in the developmental biology of sexual size dimorphism and intrasexual size poymorphism (Robinson & Robinson, 1976b, Robinson, B. & M. H. Robinson, 1978). However, orb-weaving spiders are not easy subjects for this type of study, and we turned our attention to mantids, in particular to the dead leaf mantid, *Acanthops falcata. A. falcata* proved to be an ideal subject and could become a most useful laboratory`animal. It is an extremely efficient predator, attacking, at all instars, any live prey from drosophiloid flies up to insects of almost its own size. In captivity it becomes very 'tame' and will wait for food to drop when the cage lid is raised, and will often take food directly from the forceps. Although the species has to be raised in separate cages, the containers we used were small, inexpensive, readily available and easily manageable.

We think that *A. falcata* has great potentialities as an experimental animal. It has an extensive behavioral repertory, with an efficient predatory strike and a complex startle display (first described by Crane, 1952). We have demonstrated (Robinson & Robinson, in prep.) that receptive females secrete an attractant to which males fly. The pheromone remains to be isolated. The female has a relatively large head capsule and brain and the large eyes have excellent movement detection and depth perception. It should be an excellent subject for neurophysiological studies. Our success rate of rearing nearly 1,000 individuals over several generations has been about 95%, and out methods should prove of interest to ethologists, neurophysiologists, biochemists and developmental biologists wishing to work with this mantid.

CULTURE METHODS

THE INSECT.

Acanthops falcata is a small neotropical mantid of the family Hymenopodidae. For a mantid it has an unusual degree of sexual dimorphism. The flightless female (Figure 1) resembles a curled dead leaf and weighs 400–500mg. The male, which flies well, resembles a flat dead leaf, and weighs under 200mg.

A brief summary of the life history is given here. Details of instar duration, sizes and weights at each instar, variability of number of instars and mating behavior are to be published separately (Robinson & Robinson, in prep.).

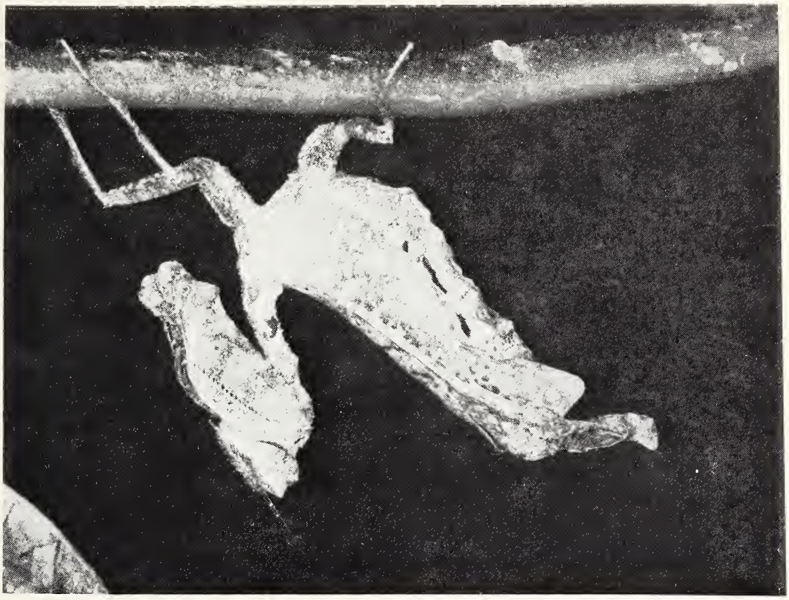

Figure 1. A female *Acanthops falcata* hanging from a twig in its cryptic posture. Body length *ca* 45mm.

In captivity the females have a life expectancy of about 6 months. They lay long slender oothecae which may contain as many as 60 eggs, but more usually, 25–35. Eggs can be produced every 8 days and hatch in 16–19 days. We have records of females, that after one mating, laid 16 fertile oothecae. In Panama, at ambient temperature (about 25° C-30° C), development from egg to adult is usually accomplished in 7 molts, including the molt from pronymph to first instar, that takes place at eclosion. Postembrionic development takes about 2 months, depending on food supply. We have kept males alive for over a month and for most of this time they remain sexually active. Even old males can be effectively mated. Unmated females secrete a pheromone for a limited period each day until they are mated. The period of secretion coincides with the brief daily period when males fly. In the wild, this period is immediately after dawn, but in the laboratory will occur after a dark/light transition (Robinson & Robinson, in prep.).

Cannibalism does not appear to be part of the mating behavior, as it is in many other species of mantids (Roeder 1935, 1963). Although males fall within the prey range of females, they seem to escape readily unless conditions are overcrowded. Copulations last from 20 minutes to 1 hour. After mating, the male drops from the female and usually survives to inseminate several females.

THE CAGES.

To raise large numbers of mantids in individual cages we made use of materials that are readily available and inexpensive. Transparent plastic party "glasses" need only a loose fitting cover to make a single plastic container into a cage. We found that the covers of plastic (disposable) petri dishes would fit one brand of 6oz shot "glasses" while the bottoms would fit another. These lids can be drilled to take a cotton ball insert that can be wetted to provide a high humidity within the cages. (In Panama's 80–100% relative humidity, this is not necessary.) The plastic cages can be stored on wooden trays, and stacked so that several hundred mantids occupy relatively little space. Fiber-tipped pens, sold as freezer markers, are excellent for marking index numbers and other data on the plastic cages. In natural conditions, *A. falcata* rests hanging from a thin twig. To provide a perch, we placed a piece of bamboo in each cage, resting diagonally from the top at one side to the bottom of the opposite side (Figure 2).

6oz shot "glasses" are large enough for an adult female, but occasionally prove too small for an adult female to emerge successfully from the final molt. Ecdysis is diurnal, quick and usually without complications, taking about 30 minutes for all but the final molt, which takes about twice as long. As the majority of the insects ecdyse between 10am and 3pm, we solved the cage size problem by watching individuals that were due to molt and removing them from the cage. Once molting had started, the stick with the molting mantid on it was placed in a piece of florists' clay or Play-Doh. Here the mantid ecdysed, turned and extended its wings. After a successful molt we returned the mantid, on its stick, to the cage.

We used several different cages in which to introduce males and females for mating. Out of doors we used a 2m × 1m × 1m screened cage which was placed over several shrubs. Pheromone secretion by females, male flights and mating occurred only in the first 15 minutes after dawn. We also used a twelve gallon glass aquarium as

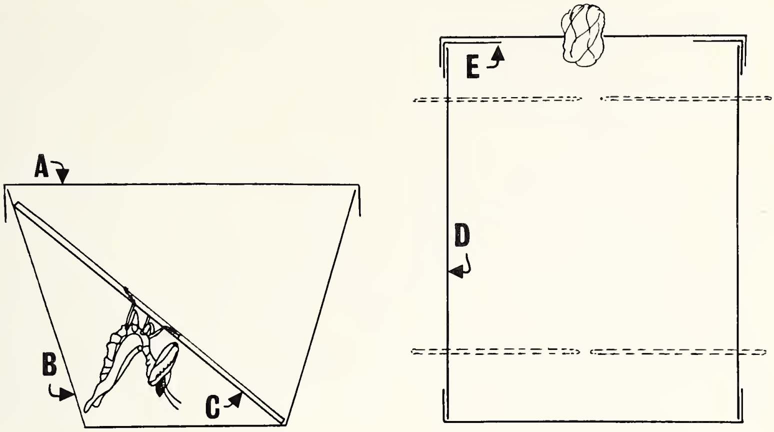

Figure 2. Left. Rearing cage for *Acanthops falcata.* (See text) A is a plastic petri dish and B a 6oz shot "glass". The female is shown in her resting posture on a piece of bamboo (C).
Right. A larger cage, suitable for spiders and large mantids. (See text) D is a cylinder of transparent acetate sheeting, 10cm high, joined with cellulose tape. E shows the double lid made from a plastic petri dish and cover. The inner section has a hole of 5 cm diameter cut from it. The outer section, which is plugged with a moist cotton ball, can be raised to introduce food, without disturbing the animal. The positions of the cylindrical toothpicks which provide web attachment points and footholds are indicated.

a mating arena. This was fitted with a screen top and held two or three potted plants. In the enclosed space males seemed to have difficulty locating a secreting female and if males and females were left together in such a container outside the mating period, males were eaten. Several males can be left together, however, and females can be introduced when they are secreting. The aquarium had the advantage that the mantids could be kept in it in the dark, and we could initiate mating behavior without disturbing them, by bringing them into a lighted area. Later we developed a 1m × 1m × .5m screened cage as a mating arena. Mantids from the dark phase of a controlled light regime can be brought into the light and released into such a cage, where they immediately become sexually active. Results are better if the light intensity is low. Since secreting females maintain a specialized posture (Robinson & Robinson, in prep.) it is easy to determine when they are receptive.

Females produce perfectly normal oothecae in the rearing cages. These are long and they hang down from the substrate to which they are attached by a long stalk. We removed oothecae from rearing cages, dated them and put them in 8oz clear plastic tunblers to hatch. To allow the pronymphs to emerge normally and complete their first molt on the outside, the ootheca must be attached to the lid of the hatching cage so that it can hang downwards, surrounded by free space. We tried various methods of attaching the ootheca stalk to the lid. This can be done with adhesive tape, but the small, fragile nymphs may stick to the exposed edges of the tape. It is more satisfactory to pass the stalk through a small hole and tape it to the outside of the lid. No additional moisture was necessary for most of the year in Panama, but during the dry season eggs were sprayed towards the end of the developmental period.

The pronymphs develop within the ootheca and at eclosion ecdyse to the first instar. They stand on the ootheca for several hours before dispersal and are easier to transfer to individual rearing cages at this stage. During the first instar they are not cannibalistic and can be kept communally but should be separated soon after the next molt.

CULTURE TECHNIQUES.

Normally mantids will not strike at motionless prey. The first three instars were fed exclusively on live drosophiloid flies. Sometime during the 4th instar the diet was changed to include live domestic crickets, *Acheta domestica,* supplied by Fluckers Cricket Farm, and by the 5th instar, only live crickets were fed. The *Drosophila sp.* were caught over a massive outdoor fruit culture in a fine meshed net, which was then placed in a freezer. By trial and error we determined the length of time necessary to immobilize the flies without killing them, and how long it took for them to become active again. The fastest way of introducing the flies into the cages was also the simplest. We transferred a quantity of immobile flies from the net onto a sheet of paper, and lifting each lid in turn, we shook the required number of prey into each cage. At the first instar this number was only two or three; towards the end of the fourth instar it was about ten. We quickly learned by experience how many mantids we could feed before the flies recovered on the paper, and, by looking at the cage debris, could tell if the mantids were under or overfed. The stage at which we changed the diet to crickets depended on the size of the crickets which were available. *A. falcata* will reach maturity entirely on a diet of *Drosophila,* but the developmental period is longer, and the adults that we raised on this diet were abnormally small (Robinson, B. & M. H. Robinson, in prep.). To make the crickets easier to handle, they too were placed in a freezer for a short time, or stored in a refrigerator before being dropped into the cages from forceps. Uneaten crickets left in cages will eat ecdysing mantids or oothecae. The former is not a serious problem with *A. falcata* which molts during the day, as it is with species which molt at night, or whose molting time is longer. We have raised two other species of mantid, *Phyllovates chlorophaea* (see below) and *Chaerododis rhombicollis* (see Robinson 1969). Both these species were vulnerable to cricket attack for about two hours during each molt, which takes place at night. We had to remove live crickets from their cages at the end of each day.

In the humid tropics drinking water does not seem to be necessary for mantids that are fed daily. However, when they were transferred to the mating cages containing wet plants, they were observed to drink, males more than females. In air-conditioned or heated laboratories, it may prove necessary to supply moisture. As described above, cotton balls can be inserted into holes in the lids of the cages. These can be sprayed to keep them moist. Care should be taken that water does not form in droplets in the cages of first instar nymphs, as they will not be able to escape from the surface tension. We always use rainwater rather than tap water for spraying insects or providing moisture in cages.

CAGES AND CULTURE TECHNIQUES SUITABLE FOR OTHER ARTHROPODS.

We have also raised several other species of mantids successfully, using the above methods for small species. For larger species we used these techniques for early instars adapting them as necessary as the mantids grew too large for the cages. *Phyllovates chlorophaea* is a large, long-legged mantid, which we have raised successfully. For this large insect 6oz shot glasses were suitable until the 4th-5th instar. This species hangs below a leaf rather than from a twig. In order to give it a foothold on the lid of the cage, we attached a piece of masking tape, approx. 3cm - 5cm to the undersurface. The cages that we used for later instars and adults are adaptations of lepidoptera rearing cages, designed by R. Silberglied and A. Aiello.

These consisted of a cylinder of metallic hardware cloth, 10cm high and with a diameter very slightly larger than that of a plastic petri dish. The petri dish fitted snugly inside the cylinder as a base, and a cover was placed over this, enclosing the bottom of the cylinder between the two. The top was bound with masking tape, and a second petri dish cover was used as a lid. Screened cages cannot, of course, be used until the mantid has transferred to a diet of crickets. For the final molt, when the mantid hangs from its exoskeleton until the legs harden, a 20cm high cage was needed. Rather than build new cages for this very short period, two cages were joined together, by removing the base of the upper one and attaching it to the top of the lower one with masking tape. After ecdysis, the double cage was disassembled and the adult mantid was returned to its original cage.

Feeding procedures were exactly the same for *P. chlorophaea* as those described for *A. falcata* (above). However, either *P. chlorophaea* attacks smaller prey, or domestic crickets are not preferred prey. It was necessary to feed several small crickets daily, and to remove any uneaten prey at the end of each day. We raised *P. chlorophaea* to study its life history. It needs more care, more space and more complex cages than *A. falcata.* In addition, its mating behavior is similar to that of *Mantis religiosa* (Roeder, 1935), where males frequently do not survive to inseminate more than one female.

The lepidoptera rearing cage (above) can be modified so that live *Drosophila* can be fed, if the cylinder is made of transparent acetate sheeting. With the following modifications we found that they made excellent cages for raising web-building spiders, particularly those with horizontal webs. (See Figure 2.) The acetate cylinder was made to fit tightly into a plastic petri dish base. An inner lid was made by cutting a circle of 5cm diameter out of a second petri dish, using an electric soldering iron. A petri dish cover was used as an outer lid. The outer lid, which was plugged with a cotton ball to keep the cage humid, could be raised for feeding the spiders, without disturbing web foundation lines. To give the spiders web attachment points, four cylindrical toothpicks were pushed through the acetate until they almost met in a cross, 2cm from the top and 2cm from the bottom of the cage.

We initially kept web building spiders in glass vials with snap caps (Robinson & Robinson, 1976a). These are not ideal, as the web is often attached to the cap, and the spider cannot be fed without the web being damaged. Later we discovered the 1 inch diameter transparent plastic storage tubes, supplied by Forestry Supplies Inc.

These come in 18 inch lengths, with separate plugs. They can be cut to the required size and fitted with a removable plug at each end. One cap was fitted with a moist cotton ball and either cap could be used to introduce food. Webs were rarely attached to both caps.

FEEDING SPIDERS.

Drosophila, the most readily available food, are probably larger than the natural prey of 2nd instar spiderlings of most species and when used live usually break the fragile web and escape. Dead *Drosophila* placed in a spiderling's web are usually found and eaten soon after being introduced. If they are ignored at this stage, the spider feeds on them when the web is taken down. For later instars, prey of an appropriate size, immobilized in the freezer, can be placed or dropped in the webs. Spiders drink water from their webs, and even in the humid tropics, once the spider has been transferred from a vial to a cage we spray the webs with rain water daily.

We are (September 1978) presently undertaking a long research trip to Papua New Guinea and have given our culture of *Acanthops falcata* to the Insect Zoo, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, who hope to maintain it.

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SEARCHING BEHAVIOR OF *HIPPODAMIA CONVERGENS* LARVAE (COCCINELLIDAE: COLEOPTERA)*

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Introduction

Survival and development of predaceous Coccinellidae depend in large part on their ability to find food (Hodek, 1973). Coccinellid larvae exhibit different searching patterns before and after finding prey; the path of a larva just after consuming a prey item is generally more tortuous than before the encounter (Banks, 1954; Banks, 1957; Kaddow 1959). When the prey are gregarious, this type of altered searching behavior is thought to increase the chance of finding additional prey (Banks, 1957). In the present study I describe the searching behavior of larvae of the convergent lady beetle, *Hippodamia convergens* (Guerin), before and after feeding on the spotted alfalfa aphid, *Therioaphis maculata* (Buckton).

Materials and Methods

Adult *H. convergens* were collected from a field of alfalfa located at the Arizona State University Experimental Farm, Tempe, AZ. Copulating pairs were isolated for 48 hrs, then the females were removed and placed in six-dram plastic vials lined with paper toweling. The toweling was moistened periodically. Isolated females were supplied daily with thirty fourth-instar or adult *T. maculata* (Nielson and Currie, 1960) collected from the alfalfa field by sweep netting. The vials were incubated at 32° C for 4 or 5 days during which time the fertilized females deposited clusters of eggs on the toweling; then the female beetles were removed and the brood chambers incubated for another two days. After hatching, the first instar larvae remain clustered around the egg shell, but because of cannibalism it was necessary to immediately separate the newly hatched larvae. Individual larvae were transferred to new vials, by

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the use of a fine camel-hair brush, together with five immature aphids. After moulting to the second instar and thereafter the larvae were provided thirty aphids per day. Following the third molt the new fourth instar larvae were used for experimentation.

To study searching behavior before and after feeding, an artificial searching arena was constructed similar in design to the arenas of Fleschner (1950) and Banks (1957). A twelve inch square plywood board was covered with buff-colored art paper and surrounded by an electrically heated wire. The arena was uniformly illuminated by a fluorescent light suspended two feet above the center, and all tests were performed at room temperature. Tracks of the larvae were recorded by tracing lightly with a pencil, and 30 sec intervals were noted on the tracks. Track diagrams were enlarged with an overhead projector. The number of degrees of each turn, whether to the right or left, was measured with a protractor. The data were expressed as the total number of degrees turned, which was a function of the number and type of turns the larvae made. Statistical analysis was done with Student's t-test.

RESULTS

Sixteen fourth instar *H. convergens* larvae were starved for 4 hrs prior to testing. Each larva was placed in the center of the arena under a vial, and timing commenced when the vial was removed. The larva was followed by a pencil tracing and 30 sec intervals were recorded on the track for a total test period of 5 min. At this time an adult *T. maculata* was placed directly in front of the larva; the aphid was seized and rapidly consumed. The track was again traced when the larva began to move after feeding, and 30 sec intervals were recorded for 5 min. This test procedure was repeated for each of sixteen larvae.

The movements of larvae before feeding were less tortuous and a much larger portion of the arena was searched; after feeding the larvae concentrated their search in the vicinity where the aphid was discovered. The track consisted of numerous turns and frequently areas previously searched were revisited several times. Analysis of the tracks confirmed these observations (Fig. 1). For three minutes following the consumption of an aphid the larvae made more turns than they did prior to feeding, but in the final two minutes of observation the fed larvae appeared to revert to their pre-fed

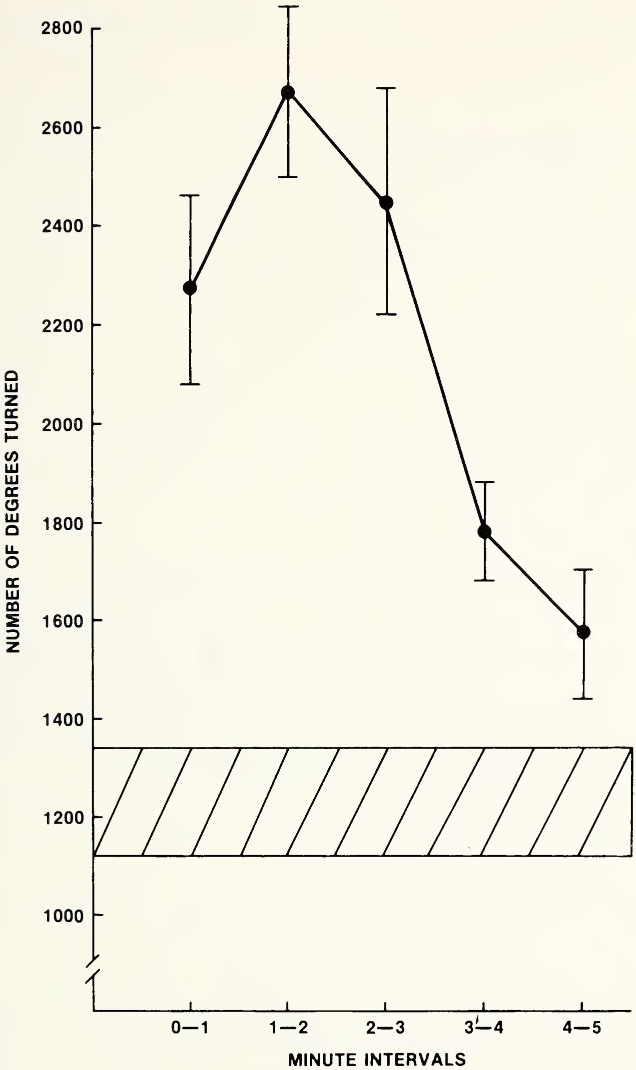

Figure 1. Searching movements of fourth instar *H. convergens* larvae during a five minute interval before and after consuming one adult *T. maculata.* The bar represents the cumulative mean ± one standard deviation of the numbers of degrees turned by larvae for five 1-minute-intervals prior to feeding.

searching pattern. The total number of degrees turned was 6200.3 ± 992.0 before feeding and 12058.8 ± 1798.8 after feeding ($p < 0.001$).

DISCUSSION

The searching movements of fourth instar *H. convergens* larvae before finding prey generally consist of wide sweeping turns. After consuming one adult *T. maculata* the searching movements are modified; initially movements consist of many small turns in the immediate vicinity of the previously consumed prey. With time the movements become more characteristic of the pre-fed state. Banks (1957) noted a similar searching behavior in a study of *Adalia bipunctata* (L.) and the aphid *Myzus persicae* (Sulz.), and Kaddow (1959) found the same searching movements in larvae of *Hippodamia quinquesignata* (Kirby) fed pea aphids, *Macrosiphum pisi* (Kaltenbach). Modification of turning movements after finding the first host is common to other entomophagous and parasitic insects (Fleschner, 1950; Laing, 1937).

It appears that coccinellid larvae lack sophisticated sensory apparatus and do not discover their prey until actual contact occurs (Hodek, 1973). Furthermore, this undirected searching is very inefficient in that much time and energy are wasted revisiting areas previously searched (Banks, 1957). If one assumes that the searching behavior of coccinellid larvae is indeed undirected, then the number of encounters between predator and prey would be merely a function of their respective population densities. However, this assumes that the chance of finding a second prey is the same as that for the first. On the other hand, if after the first prey encounter the predator alters its pattern of search in such a way as to increase the likelihood of capturing additional prey, then the predator has become more efficient even though its searching is still undirected (in terms of sensory capability). *T. maculata* are colonial and not uniformly dispersed throughout their habitat. With this characteristic in mind it would seem advantageous for *H. convergens* larvae, having encountered a single *T. maculata,* to modify their searching behavior in order to exploit the gregarious nature of their prey. Since survival and reproduction of predators like *H. convergens* is dependent upon finding adequate food (Hodek, 1973), a strong selection pressure probably exists for behaviors which improve food finding capabilities. Therefore, it is suggested that the change of searching pattern by *H. convergens* larvae after finding one prey item is adaptive.

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FURTHER STUDIES OF THE MYRMICINE STING APPARATUS: *EUTETRAMORIUM, OXYOPOMYRMEX,* AND *TERATANER* (HYMENOPTERA, FORMICIDAE)*

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INTRODUCTION

In an earlier investigation (Kugler, 1978, 1979) I described the sting apparatus of representatives of 63 genera of myrmicine ants. In so doing, it was shown that this complex structure has clear potential for defining myrmicine genera and perhaps generic groupings. Furthermore, its morphology may have played an important role in the evolution of some genera.

Here I present descriptions of members of 3 genera that could not be included in that work. Structural affinities with the sting apparatus of other genera are discussed in order to assist those reclassifying this taxonomically problematical subfamily.

METHODS

The materials and methods used are described in detail in Kugler (1978). For the sake of brevity, figures from that earlier study are cited here in italics; new figures of this paper are cited in Roman type. Voucher specimens are deposited in the Harvard Museum of Comparative Zoology, labeled "Kugler study 1978." Scale lines in the figures are in millimeters.

EUTETRAMORIUM

Species examined: *E. mocquerysi,* 2 workers.

Spiracular plate: (Fig. 1) Body subtriangular, only slightly longer than wide. Anterior apodeme wide along nearly whole length, ending abruptly near dorsal margin of plate. Ventral and posterior

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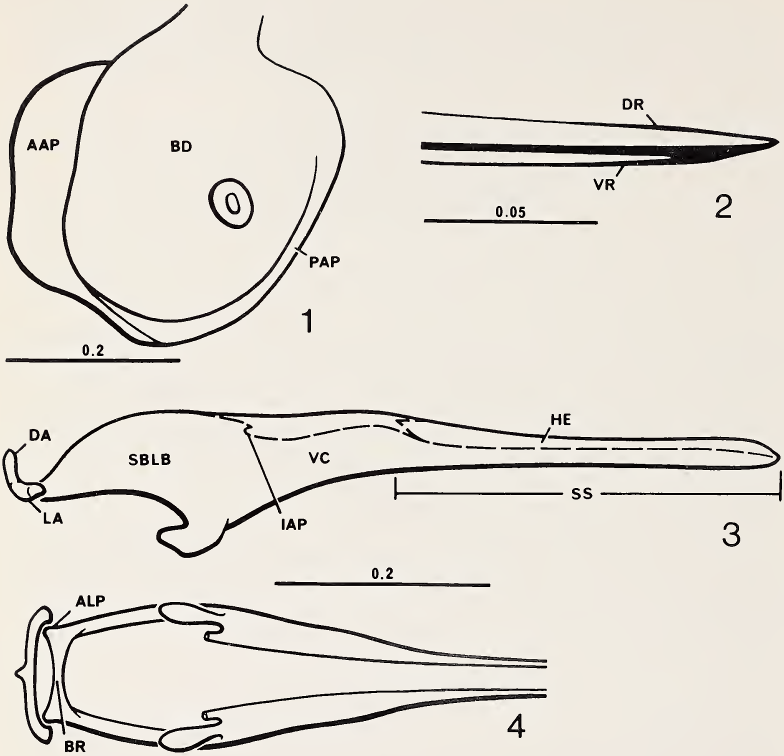


Figures 1–4. Sclerites of the sting apparatus of *Eutetramorium mocquerysi*. Fig. 1, spiracular plate, side view. Fig. 2, apical ¼ of lancet, side view. Fig. 3, sting and furcula, side view. Fig. 4, sting and furcula, ventral view. Abbreviations: AAP, anterior apodeme; ALP, anterolateral process of sting base; BD, body; BR, basal ridge; DA, dorsal arm of furcula; DR, dorsal ridge; HE, hemocoel; IAP, internal apodeme; LA, lateral arm of furcula; PAP, posterior apodeme; SBLB, sting bulb; SS, sting shaft; VC, valve chamber; VR, ventral ridge.

apodemes present, well sclerotized. No dorsal notch or posterodorsal lobe. Spiracle relatively small, located caudad of center.

Quadrate plate: Body and apodeme both subrectangular, equal in width; body extends well ventrad of apodeme. Dorsal edge of plate convex, with moderately wide medial and lateral lobes terminating in an acute anterodorsal corner.

Anal plate: Very poorly sclerotized, ill-defined; no sensilla.

Oblong plate: Posterior arm with narrow, well sclerotized apodeme, body widens abruptly just caudad of articulation with fulcral arm, a lightly sclerotized ventral ridge arcs from intervalvifer articulation to opposite fulcral arm. Anterior apodeme wide, prominent, bluntly rounded. Ventral arm wide, broadly spindle-shaped fulcral arm meets posterior arm perpendicularly, postincision deep.

Gonostylus: Two-segmented as indicated by bimodal sensilla pattern and ill-defined membranous region; evenly tapered to end, neither long and slender nor short and wide, not strongly dorsoventrally compressed. Distal segment with 7 long setae and isolated dorsoterminal chaeta; proximal segment with 10 setae of varied lengths. Distal segment grades evenly into terminal membrane. No distal notch or basiconic sensilla.

Triangular plate: Body wide, basal portion abruptly tapered; ventroapical process a distinct extension from body, narrowly rounded apically. Dorsal and medial tubercles present.

Lancet: (Fig. 2) Straight, acute, well sclerotized, with distinct ventral ridge and, distally, a dorsal ridge. Each lancet with 2 valves of moderate size; the caudal one smaller, less sclerotized. No barbs present.

Sting: (Figs. 3, 4) Long, slender, well sclerotized; sting bulb, valve chamber and sting shaft regions distinguishable in profile. Sting base not arched, anterolateral processes present. Valve chamber internally much lower than sting bulb. Sting shaft with distinct hemocoel throughout length, height of hemocoel greater apically than subapically. No terminal flange. Campaniform sensilla present on sting shaft and distal 2/3 of valve chamber. Index of reduction 26.8.

Furcula: (Figs. 3, 4) T-shaped in anterior view, lateral arms wrap around sting base, dorsal arm well developed.

Discussion

The sting apparatus of *Eutetramorium mocquerysi* seems most closely related to those of the Tetramoriini and the *Leptothorax* genus group (see Kugler, 1978). Some common characters are: the wide anterior apodeme and overall shape of the spiracular plate (*Fig. 57*); the medial and lateral lobes, and shape of the anterodorsal corner of the quadrate plate (*Fig. 58*); the shape of the anterior apodeme, ventral ridge and body of the posterior arm of the oblong plate (*Figs. 52, 59*); much of the shape of the sting (*Figs. 55, 56*). The gonostyli are much like those of *Leptothorax* (*Fig. 53*), but not as long and narrow, and they lack the companion seta. The sting base and furcula have characteristics of those of *Liomyrmex* cf. *aurianus* (*Figs. 69, 70*).

In spite of its similarities with the Tetramoriini, *E. mocquerysi* lacks the dorsal flange on the end of the sting and the characteristically stubby gonostyli of that tribe. On the basis of the flange character and other external characters Bolton (1976) removed *Eutetramorium* from its traditional association with the Tetramoriini. He prefers to place it in the Myrmicini, but as an alternative hypothesis, based admittedly on one character system, I would suggest a position nearer *Leptothorax* and related genera.

OXYOPOMYRMEX

Species examined: *O. tuneticus,* 1 worker; *O. tuneticus* var. *thoracicus,* 1 worker.

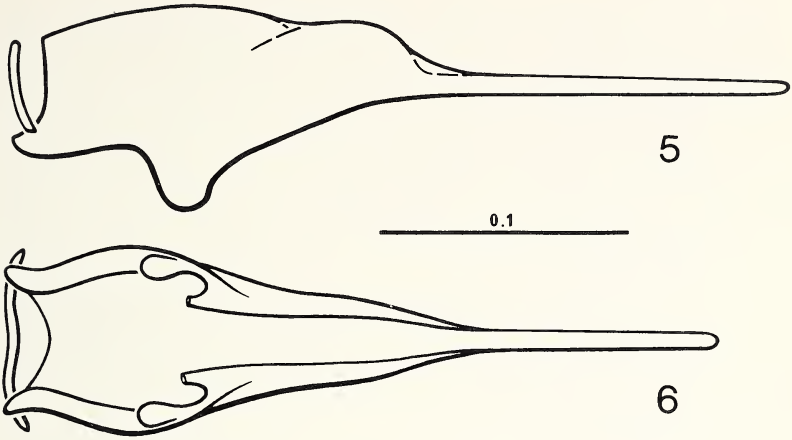
Spiracular plate: Body subrectangular, with straight anterior edge, slightly concave posterior edge and convex dorsal and ventral edges. Anterior apodeme forms a square anteroventral corner, then a thin margin along anterior edge to dorsad of body of plate; medial connection membranous. Large V-shaped dorsal notch present; no distinct posteroventral tubercle or posterodorsal lobe.

Quadrate plate: Subtriangular, both body and apodeme much narrowed at base. Dorsal edge straight, anterodorsal corner broadly rounded. Anterior edge poorly sclerotized, expecially dorsad.

Anal plate: Weakly sclerotized, longer than wide, with 4 long setae on terminal edge in *O. tuneticus,* 2 setae in *O. t.* var. *thoracicus.*

Oblong plate: Dorsal ridge and body of posterior arm long and narrow, uniform in width, without ventral ridge. Anterior apodeme very long and slender. Ventral arm tapered and subtruncate distally; fulcral arm slender, weak, diffuse dorsad, forming acute angle with posterior arm.

Gonostylus: In *O. t. thoracicus,* narrow from side view, with no indication of segmentation; 17–20 setae scattered more or less evenly along distal 2/3 of ventrolateral surface. Dorsoterminal chaeta, companion seta and terminal membrane present. No basiconic sensilla. Gonostyli of *O. tuneticus* lost in preparation.



Figures 5–6. Sting and furcula of *Oxyopomyrmex tuneticus*. Fig. 5, *O. tuneticus*, side view. Fig. 6, *O. tuneticus* var. *thoracicus*, ventral view.

Triangular plate: In *O. tuneticus* body and ventroapical process very slender and distinct; in *O. t.* var. *thoracicus* body wider dorsad and merging more with ventroapical process. In both specimens, body evenly tapered to ramus; neither dorsal nor medial tubercle present.

Lancet: Long, weak, and spatulate distally, with broadly rounded apex; about twice as deep as end of sting shaft. One large lancet valve per lancet.

Sting: (Figs. 5, 6) Sting bulb large with weak basal ridge and distinct anterolateral processes. Valve chamber well developed, clearly distinguishable from sting bulb and sting shaft in profile and in ventral view; internal apophysis long. Sting shaft short, very slender and weak; no dorsal flange. Index of reduction 21.9 for *O. tuneticus,* 20.4 for *O. t.* var. *thoracicus.*

Furcula: (Figs. 5, 6) Slender arch, uniform in diameter; no dorsal arm.

Discussion

The sting apparatus of *Oxyopomyrmex tuneticus* and *O. t.* var. *thoracicus* are very similar to those of *Messor* and *Aphaenogaster.* The large dorsal notch and thin anterior apodeme of the spiracular plate (*Fig. 130*); the subtriangular quadrate plate (*Fig. 131*); the long slender posterior arm and anterior apodeme and the inclined fulcral arm of the oblong plate (*Figs. 132, 133*); and the shape of the sting bulb, valve chamber and furcula (*Figs. 138, 139*) are common characteristics of the species so far examined in these 3 genera. The *Oxyopomyrmex* species, however, are distinct in two important respects: the sting shaft has no dorsal flange (*Fig. 138*), and the lancets are spatulate and broadly rounded apically, rather than acute (*Fig. 137*).

The close affinities of *Oxyopomyrmex, Messor* and *Aphaenogaster* as suggested by the sting apparatus are consistent with the views advanced by Emery (1922) and Wheeler (1910: 139–140, 268; 1922).

TERATANER

Species examined: *T. alluaudi,* 2 workers.

Spiracular plate: (Fig. 7) Body subrectangular. Anterior apodeme narrow, well sclerotized, continues dorsad to make completely sclerotized connection with opposite side. Dorsal notch and ventral and posterior apodemes present.

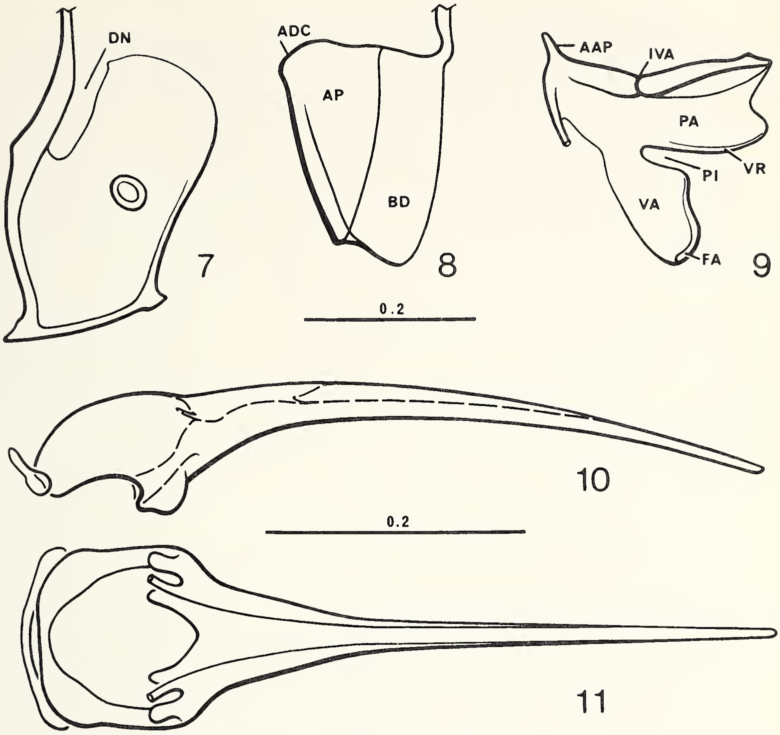
Quadrate plate: (Fig. 8) Apodeme subtriangular, no medial or lateral lobes, anterodorsal corner rounded. Body subrectangular, extending below apodeme.

Anal plate: Wider than long, clear suture between plate and anal arc; moderately well sclerotized proximally, posterior and lateral borders unsclerotized, undefined. Thirty-one long setae cover plate; no sensilla basiconica.

Oblong plate: (Fig. 9) Posterior arm short and straight, dorsal ridge strong, ventral ridge weak, ill-defined. Ventral arm wide apically with narrow fulcral arm perpendicular to posterior arm; postincision deep. Anterior apodeme rather short, acute.

Gonostylus: One-segmented. Dorsal surface free of sensilla, broadly triangular. Lateral surface narrower, uniformly and densely covered with long thin setae along distal ½ of length, longest setae proximad; small dorsoterminal chaeta embedded among setae; no obvious companion seta; no basiconic sensilla. Short terminal membrane present.

Lancet: Long, slender, weak and flagelliform. Two intermediate-sized valves per lancet, caudal valve smaller.



Figures 7–11. Sclerites of the sting apparatus of *Erataner alluaudi.* Fig. 7, spiracular plate, side view. Fig. 8, quadrate plate, side view. Fig. 9, oblong plate, side view. Fig. 10, sting and furcula, side view. Fig. 11, sting and furcula, ventral view. Abbreviations: AAP, anterior apodeme; ADC, anterodorsal corner; AP, apodeme; BD, body; DN, dorsal notch; FA, fulcral arm; IVA, intervalvifer articulation; PA, posterior arm; PI, postincision; VA, ventral arm; VR, ventral ridge.

Sting: (Figs. 10, 11) Sting bulb wide, with heavy basal ridge. Valve chamber small, indistinguishable from sting shaft in profile; topped by heavy internal ridge; 2 large ventrolaterally projecting prongs seem to originate on the internal apophysis. Sting shaft long, slender, tapering to weak apex; hemocoel clearly visible in basal 2/3. Index of reduction 20.1.

Furcula: (Figs. 10, 11) A simple low arch, no dorsal arm; extremities dilated at articulation with base of sting.

Discussion

The sting apparatus of *Terataner alluaudi* bears most resemblance to several genera normally considered unrelated by most modern myrmecologists. It has a variety of derived characters in common with *Atopomyrmex mocquerysi,* such as: shape of the anal plate; form of the gonostyli; long, flagelliform lancets (*Fig. 215*); form of the bulb, valve chamber and shaft of the sting, including 2 prongs extending into the sting bulb from the internal apophysis (*Figs. 216, 217*). These species, however, differ markedly in the shapes of the spiracular and oblong plates, and in the lack of a furcula and anal setae in *A. mocquerysi.* With the Cephalotini, *T. alluaudi* shares the following characters: complete medial connection of the anterior apodeme of the spiracular plate (may not be derived); anal plate wider than long and with numerous dorsal sensilla; long, well-defined fulcral arm of the oblong plate; gonostylus shape and setation (*Fig. 192*); shape of the lancets (*Fig. 194*); sting bulb shape, low valve chamber and flagellate sting shaft as in *Procryptocerus scabriusculus* (*Figs. 196, 197*). The main differences are the shape of the spiracular plate (*Fig. 198*); and in *T. alluaudi* the lack of the long pollicate anterodorsal process of the quadrate plate (*Figs. 189, 198*), the furcula not appressed to the sting base, the more elongate sting shaft containing a hemocoel, and the prongs in the sting bulb (cf. *Figs. 190, 191, 196, 197*). With *Cataulacus tardus, T. alluaudi* shares the medial connection of the spiracular plate anterior apodemes; the shape and setation of the gonostyli; flagelliform lancets (though much shorter in *C. tardus*); and prongs in the sting bulb (the number of which is different, *Figs. 203, 204*). Such prongs are known only from *Terataner, Atopomyrmex* and *Cataulacus.*

Both Emery (1922) and Wheeler (1922) placed *Terataner* in the tribe Myrmecinini with *Podomyrma, Lordomyrma, Atopomyrmex, Myrmecina, Pristomyrmex* and *Acanthomyrmex,* along with other genera, the stings of which have not yet been examined. Emery more specifically placed it with the first 3 genera in the subtribe Podomyrmiti after earlier creating the genus *Terataner* from some of the species then in *Atopomyrmex* (Emery, 1912). The sting apparatus does not support the groupings of the above genera into tribe Myrmecinini (see also discussions in Kugler, 1978), but the view of *Terataner* and *Atopomyrmex* as distinct, related genera is seen here as likely. Sting apparatus morphology also suggests a relationship between *Terataner,* the Cephalotini and possibly *Cataulacus* that should be considered in future classifications of the Myrmicinae.

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AN UNUSUAL ASCALAPHID LARVA (NEUROPTERA: ASCALAPHIDAE) FROM SOUTHERN AFRICA, WITH COMMENTS ON LARVAL EVOLUTION WITHIN THE MYRMELEONTOIDEA*

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Ascalaphidae is a fairly large family of planipennian Neuroptera that has received little attention from taxonomists since Weele's 1908 monograph. Life history and behavioral studies of the group have suffered even greater neglect; what is known has been summarized in a previous work (Henry, 1977). As an order, Neuroptera is taxonomically intractable, largely due to difficulty in interpreting wing venation: extreme convergence is common in distantly related families, yet divergence often occurs within a single subfamily or genus. For this reason, the immature stages have proven to be more reliable indicators of relationship than the adults, and our present understanding of evolution within the order is based more on larval than adult features (Withycombe, 1925; MacLeod, 1970). Since such considerations apply as strongly to Ascalaphidae as they do to other Neuroptera, all larval or life-history data are of paramount importance to phylogenetic studies of the family.

Described here is a peculiar ascalaphid larva from Mkuze Game Park, Natal, collected in November of 1967 by J. A. Slater and T. Schuh. Although it shows all the diagnostic features of the family, certain details of its setal morphology and of the form and distribution of its thoracic and abdominal extensions (scoli) are unique and of great phylogenetic importance. As the larva is (necessarily) unassociated with an adult, I will describe its major features informally and compare them critically with those of larvae of known taxa in an attempt to deduce the general systematic position of the insect. In addition, I will summarize what is known of larval morphology in the superfamily Myrmeleontoidea, so that conclusions concerning the Mkuse specimen can be placed in perspective.

**Manuscript received by the editor December 12, 1978.*

METHODS AND MATERIALS

The larva was preserved in 70 percent ethanol. Wild™ M5 and M5A stereoscopic dissecting microscopes were used to observe the specimen, while drawings were made by means of integral camera lucida attachments for these instruments.

DESCRIPTION OF LARVA

The African specimen is a typical ascalaphid immature in most respects (Fig. 1), displaying robust jaws with three mandibular teeth, large squarish head with pronounced occipital angles, prominent ocular tubercles each bearing six dorsal and one ventral stemmata, and compact, lightly sclerotized body fringed by numerous finger-like, setigerous extensions. It measures about 7 mm from labral margin to anal spinneret and is probably a partially grown second instar. Previous studies of ascalaphid immatures (Henry, 1976) indicate that important features of the mature larva that may be absent or distorted in the first instar are expressed quite clearly by the second stadium; for this reason, the following description can be compared with existing descriptions of third instar larvae.

The head capsule is of the generalized ascalaphid type in shape, more square than cordate, without extreme dorso-ventral flattening. Ocular tubercles (Fig. 2-A) are cylindroid, and the ventral stemma on each is but slightly reduced compared with the dorsal ones. The antennal tubercles are poorly developed. Jaws are straight-shanked, each tapering smoothly from proximal tooth to tip; the distal tooth is markedly smaller than the others. Ventrally, sclerites of the mouthpart bases and the pieces of the labium (Fig. 2-B) have a generalized form and relationship to one another (Henry, 1976). The manner of ventral articulation of the mandibles to the head capsule is also relatively unspecialized: each condyle bears against a median lobe at the end of the subgenal ridge rather than being retained more positively by a U-shaped socket.

The body of the specimen also exhibits several apparently primitive traits. Twelve pairs of long primary scoli fringe the body from mesothorax to eighth abdominal segment (Fig. 1); in addition, a pair of equally prominent ventro-lateral secondary scoli occurs on abdominal segments I-VII (Fig. 3). All scoli are slightly flattened dorso-ventrally and possess a border of specialized setae (see below). The eight pairs of abdominal spiracles are situated laterally

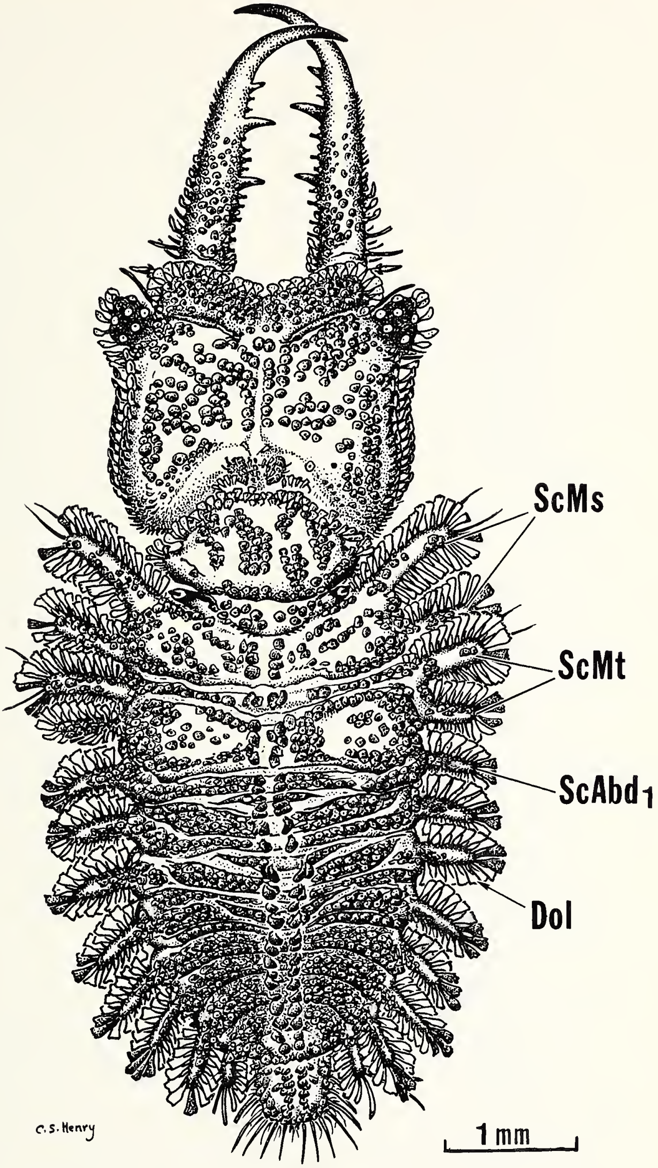

Figure 1. Mkuze ascalaphid larva, probably second instar. ScMs = mesothoracic scoli, ScMt = metathoracic scoli, ScAbd$_1$ = scoli of first abdominal segment, Dol = dolichasterine seta.

in a linear arrangement between the primary and secondary series of scoli; the eighth abdominal segment, lacking ventral scoli, bears its spiracles beneath the primary scoli.

Nearly all setae are highly modified (Figs. 1–3). Those clothing most of the dorsal and ventral surfaces of the head, body, and scoli are very short and flattened into round discs or scales. Large, dorsoventrally flattened dolichasters project from the labral margin and fringe the ocular tubercle and each primary and secondary scolus. Spoon-shaped dolichasters occur dorsally in a double row down the mid-line of the body and in a triple series on each side of the head capsule. Long setae of conventional shape are present in small numbers on the tips of the first and third scoli of the thorax and singly on the tip of each scolus of the ventral abdominal series; the last primary scolus also bears a few terminal setae of this type.

The pigmentation pattern of the specimen is due primarily to the scale-like setae that cover nearly all parts of the body. In general the insect has a mottled appearance, as though adapted for crypsis in a relatively exposed or open microhabitat; however, its true colors are of course unknown. The ocular tubercles are conspicuously darker and the tips of the scoli lighter than other parts of the larva; otherwise, mottling is quite uniform.

DISCUSSION

The Ascalaphidae is one of six families in the superfamily Myrmeleontoidea, a complex defined by a common larval type exhibiting an array of cephalic traits that apparently evolved together to provide structural support for the large muscles and condyles of the jaw "trap" mechanism (MacLeod, 1964, 1970). In contrast to the hemerobiiform larva of other Planipennia, that of Myrmeleontoidea (=Infraorder Myrmeleontiformia) displays 1) maxillary blade lance-like, never as broad as mandible; 2) robust, sickle-shaped mandibles; 3) ventral surface of large quadrate head convex and heavily sclerotized, with sclerites of maxillae and labium confined to medial anterior region; 4) pronounced anteriad migration and torsion of the tentorium so that it assumes a dorso-ventral orientation connecting the anterior tentorial pits above to the posterior ones directly below; 5) relatively short antenna with thick scape but filiform distal portion; and 6) two- to four-segmented labial palps each arising from the tip of a large, palpimere-like structure that actually represents half of the divided prelabium.

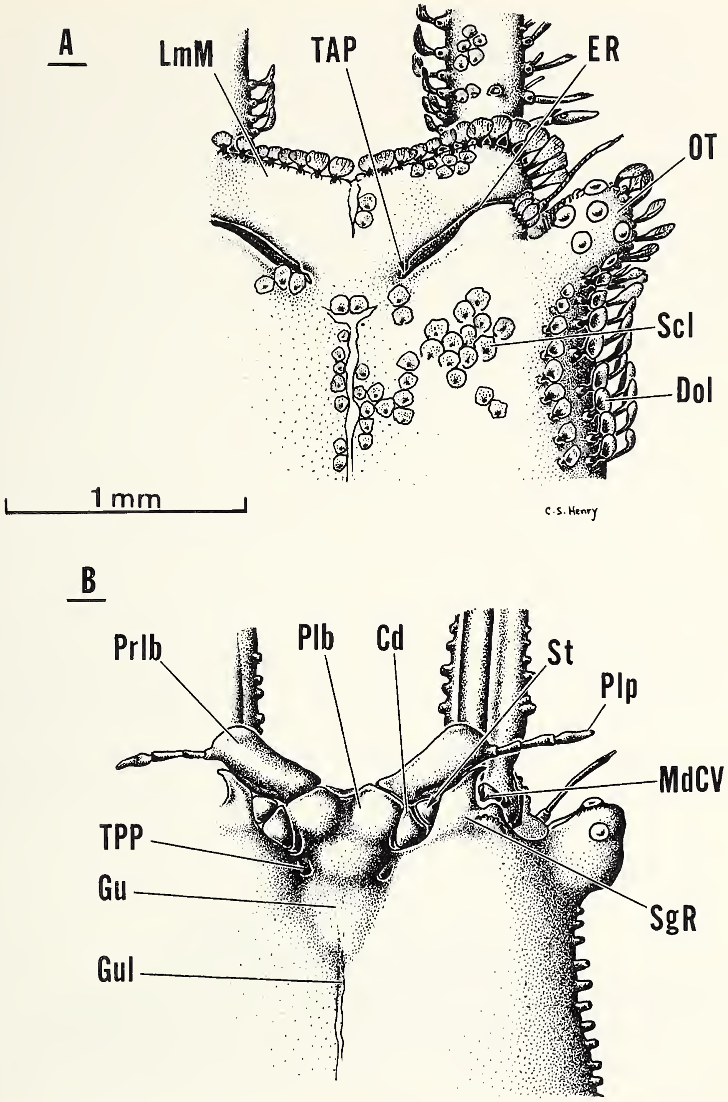

Figure 2. Mkuze larva, details of head capsule. A = anterior dorsal aspect, B = anterior ventral aspect. Cd = maxillary cardo, Dol = dolichaster, ER = epistomal ridge, Gu = gular area, Gul = gular line, LmM = labral margin, MdCV = ventral mandibular condyle, OT = ocular tubercle, Plb = postlabium, Prlb = prelabial lobe, Plp = labial palp, Scl = scale-like seta, SgR = subgenal ridge, St = maxillary stipes, TAP = anterior tentorial pit, TPP = posterior tentorial pit.

Psychopsidae appears to be the most generalized of myrmeleontoid families with respect to these larval features (Fig. 4). Basic specializations that have originated within the assemblage include the development of mandibular teeth (all families except Psychopsidae), elaboration of setigerous tubercles or scoli on the sides of the body (all except Psychopsidae and Nemopteridae), increase in the number of pairs of stemmata to seven (all except Psychopsidae and most Nymphidae), appearance of distinct ocular tubercles (Ascalaphidae, Stilbopterygidae, and Myrmeleontidae), fusion of tarsus with tibia in the metathoracic leg (same three families), and great enlargement of hind tarsal claws (Stilbopterygidae and Myrmeleontidae). Available evidence suggests a sister-group relationship between Nymphidae and all other families except Psychopsidae (MacLeod, 1970); Ascalaphidae in turn is probably the sister-group to Myrmeleontidae (Riek, 1976), while the stilbopterygids—at least, those from Australia—may prove to be nothing more than specialized ant-lions (manuscript in preparation).

As discussed in an earlier paper (Henry, 1976), several larval specializations appear within the Ascalaphidae (Fig. 4). For example, New World ascalaphine (split-eyed) forms of the genus *Ululodes* Currie and *Colobopterus* Rambur manifest extensively modified cordate heads and a complex of mouthpart specializations, all relating to an extreme 270° "trap" position of the jaws; these larvae also possess fewer and longer body scoli (ten pairs) than other taxa, show no trace of a ventral scolus series, and bear al

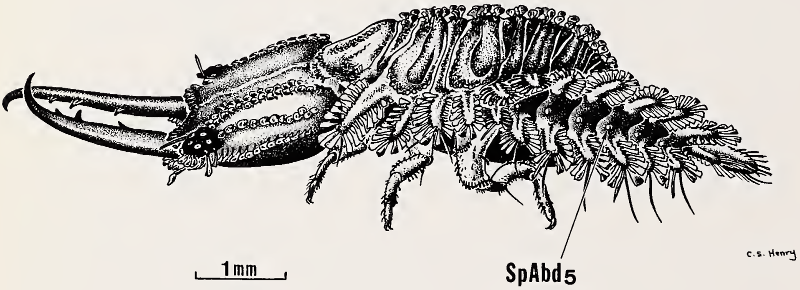

Figure 3. Mkuze larva, lateral view. $SpAbd_5$ = spiracle of fifth abdominal segment.

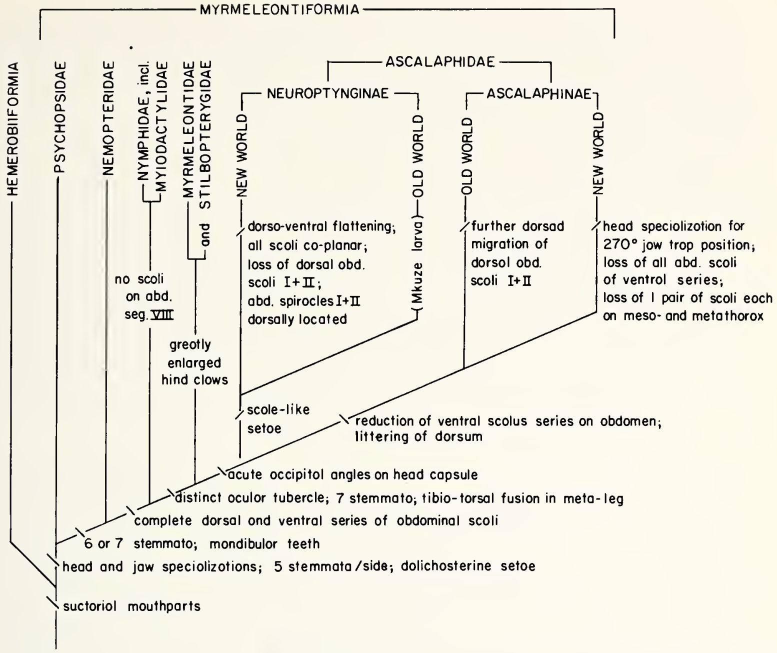

Figure 4. Cladogram of myrmeleontoid families of planipennian Neuroptera, based upon larval features.

abdominal spiracles ventrally. In contrast, New World neuroptyngine (entire-eyed) forms like *Ascaloptnyx* Banks and *Byas* Rambur (Henry, 1978) show extreme dorso-ventral flattening and a much larger number of scoli—twelve primary and six secondary (smaller) pairs, the latter placed just anteriad of the former on abdominal segments III-VIII. In addition, abdominal spiracles I and II are dorsally located in these neuroptyngines, and specialized scale-like dolichasters predominate on their body surfaces. Known Old World ascalaphines, on the other hand, resemble Nymphidae in possessing both a dorsal and ventral series of scoli on the abdomen and laterally located abdominal spiracles; however, at least in *Ascalaphus* Fabricius,[1] the ventral series is largely vestigial and the first

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[1] Tjeder (1972) points out that *Ascalaphus* as used here and as previously understood should be replaced for nomenclatural reasons by *Libelloides* Schäffer; *Ascalaphus* Fabricius then replaces *Helicomitus* McLachlan.

two pairs of abdominal spiracles show signs of dorsal migration (Henry, 1976, Fig. 10). Finally, the Oligocene *Neadelphus protae* MacLeod displays ventral spiracle location and is devoid of ventral scoli, vestigial or otherwise, but those it possesses number twelve rather than the ten of *Ululodes* and its relatives; it also shows no setal modification (MacLeod, 1970; Henry, 1976, Fig. 9).

MacLeod (1970) interprets the secondary abdominal scoli of New World neuroptyngines as having migrated from the ventral series of a non-flattened nymphid-like ascalaphid ancestor. My own view, based on analysis of changes in spiracle location and comparison of scolus shapes, is that the primary rather than secondary scoli of these neuroptyngines have been derived from the ventral series, and that the primary abdominal scoli of Neuroptynginae and Ascalaphinae are therefore not homologous (Henry, 1976).

The Mkuze specimen described here shares its general head capsule morphology and its twelve pairs of primary body scoli with *Neadelphus* and known extant Neuroptynginae and Old World Ascalaphinae; in both respects, it is a primitive or generalized ascalaphid. Its most remarkable feature, however, is the double row of scoli on each side of its abdomen with spiracles placed laterally between the rows: although *Ascalaphus* shows traces of the ventral series and New World neuroptyngines bear the latter in the same plane as the dorsal series, no larva possesses such a fully developed double series nor so closely approaches MacLeod's hypothetical nymphid-like ancestor as this specimen.

The setal patterns on the scoli of the specimen may help to homologize these protuberances in this and other ascalaphid larvae. For example, it is not known which (if either) of the two pairs of scoli on the mesothorax or on the metathorax represent the dorsal series, since spiracles are not present on either segment and all known taxa showing the condition bear both pairs in the same plane. The Mkuze larva possesses sharp-tipped setae on the tips of the first and third pairs of thoracic scoli and on all ventral scoli, suggesting a ventral origin for the more anteriorly placed pair of scoli on each thoracic segment. Actually, the same relationship is also present in *Ascaloptynx:* the first and third thoracic scoli resemble in shape those deduced to belong to the ventral abdominal series (Henry, 1976, Fig. 5). It then follows that, in neuroptyngine larvae bearing all acoli in a common plane, the anterior scoli on each thoracic segment did not originate from the same series as did the anterior ones on each abdominal segment. This conclusion should be tested further.

Although the African specimen is primitive or generalized in most respects, its scale-like setae and flattened dolichasters are a significant specialization shared only with New World Neuroptynginae. Based upon this single apomorphy, the larva could be classified with the Neuroptynginae, for which no larvae are known from the Old World; the dorsal location of abdominal spiracles I and II of New World forms could then be interpreted as an additional specialization within a subgroup of the subfamily, associated with scolus migration in response to dorso-ventral flattening and exposed living habits.

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THE EVOLUTIONARY SIGNIFICANCE OF REDUNDANCY AND VARIABILITY IN PHENOTYPIC-INDUCTION MECHANISMS OF PIERID BUTTERFLIES (LEPIDOPTERA)*

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One of the major discoveries in the study of seasonal polyphenism in butterflies was the role of larval photoperiodic exposure (Danilevskii, 1948). Following this discovery, experiments on two Pierid species — *Colias eurytheme* Bdv. (Watt, 1969; Hoffman, 1974) and *Pieris protodice* Bdv. & LeC. (Shapiro, 1968) — appeared to establish that temperature played no role in the seasonal polyphenisms of that family. This was clearly not the case in at least one Nymphalid, *Araschnia levana* (L.): Süffert (1924) had shown a temperature effect, and later work by Danilevskii (1948), Müller (1955, 1956, 1960), Reinhardt (1969, 1971), and Müller and Reinhardt (1969) showed that photoperiod and temperature interact in a characteristic way. Long-day larvae or young pupae, normally destined to produce the summer form *prorsa,* if experimentally cooled will produce either the winter form *levana* or an intermediate form (*porima*). Short-day larvae give rise to diapause pupae which always give *levana,* regardless of temperature. Thus photoperiod, acting on 4th- and 5th-instar larvae, can irreversibly determine the vernal phenotype, but not the estival one, which can be overridden by temperature acting on the young pupa.

Shapiro (1977) established that pupal diapause and adult phenotype, normally tightly coupled in the *Pieris napi* (L.) group of Pieridae, could be decoupled in *P. n. venosa* Scudder. In *napi* generally, diapausing pupae give rise to vernal phenotypes and nondiapausing ones to estival phenotypes. Populations consist of a mixture of obligate diapausers, apparently determined genetically, and facultative ones responsive to daylength. In some but not all populations, inducing photoperiods can be overridden by high

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developmental temperatures, but low temperatures cannot induce diapause in long-day animals. (This system was first demonstrated for *P. rapae* (L.) by Barker, Mayer, & Cohen (1963).) When non-diapause, long-day pupae of *P. n. venosa* are chilled, they produce vernal phenotypes; thus diapause is not necessary to produce them. However, it is not known whether all diapause individuals are irreversibly determined phenotypically, because they have a mandatory chilling requirement and break diapause in mid-winter, thus assuring that every individual will receive some post-diapause chilling. The entire system is summarized in Fig. 1.

Although the necessary experiments to clarify this point have not been completed with *P. n. venosa,* they have been in the literature for 50 years in a very important paper which has been universally overlooked by English-speaking workers (Lorković, 1929). Lorković worked with *P. rapae* and, to a lesser extent, *Pontia daplidice* (L.). It is worth quoting at some length from a translation of the summary ("homodynamic" pupae are non-diapausers; "heterodynamic" are diapausers):

> "Not only the homodynamic but also the heterodynamic pupae of *P. rapae* are strongly influenceable in respect to the butterfly's markings. If the homodynamic pupae are put in heat (25–30° C) during the sensitive period (which at 25° sets in about 12 hours after pupation), they produce strongly black-spotted butterflies, while cold (5° C) brings about a disappearance of these spots as well as a densely dark powdering of the hindwing underside. Naturally there are formed at corresponding temperatures also all intermediates between the two extremes. The heterodynamic pupae produce as a whole intermediate forms . . . but, contrary to the results of Süffert (on *A. levana* — A.M.S.), the heat form can also be produced by a high temperature of 32° C; but the black marking of the forewing always approaches the heat form more than the hindwing underside, which can never attain the extreme grade of the heat form. At lower temperatures the spotless form is occasioned. The influencing of the heterodynamic pupae by temperature is successful only during the last section of development; pupae which for 3 months were kept at lower temperatures (−5° to +10°) produced heat forms after 6–8 days of exposure to higher temperature (32°).

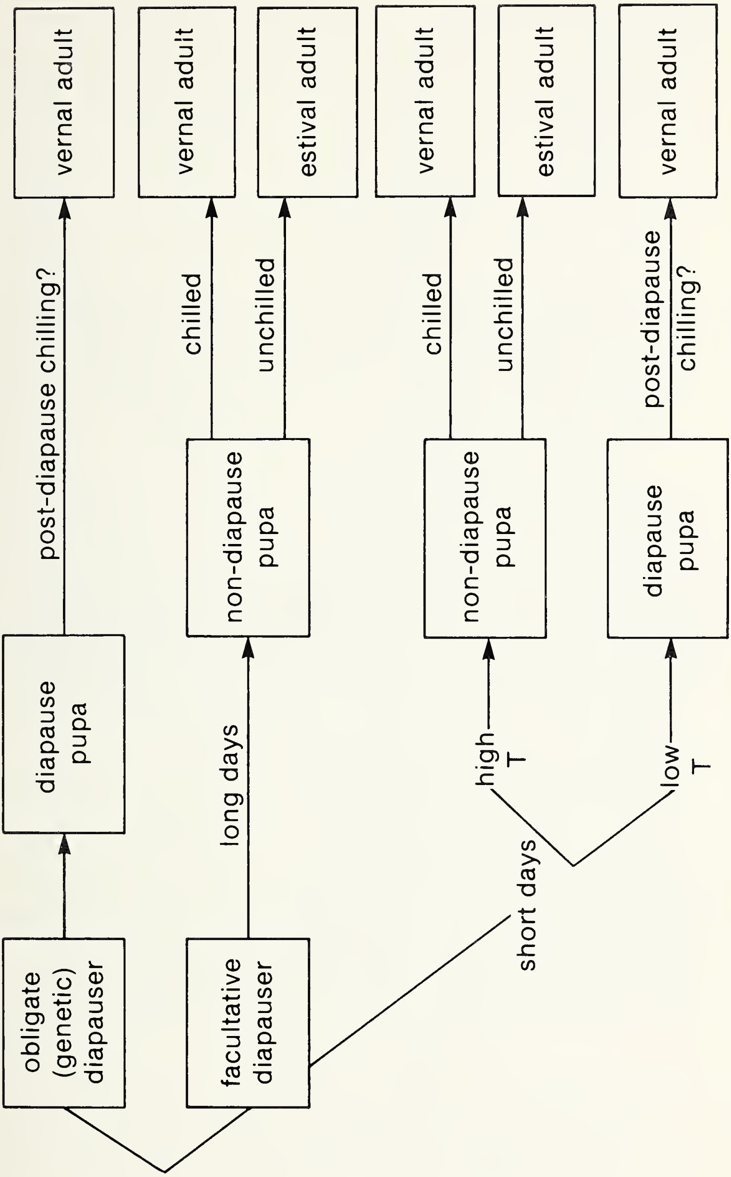

Fig. 1. Schematic representation of developmental and phenotypic options available to *Pieris napi*. Not all options found in all populations, but all except those queried have been demonstrated in the laboratory.

> (Lorković used pupal weight to estimate time of breaking of diapause. — A.M.S.) It must therefore be taken that the "heterodynamic sensitive period" sets in only after the completed latency. (Compare *Papilio zelicaon* Lucas, Shapiro, 1976. — A.M.S.) There are species in which the duration of the pupal dormancy shows great lack of uniformity, varying from 1–8 years, without the difference being reflected at all in the markings of the butterflies . . ."

Indications of the same phenomena are apparent in temperature-manipulation experiments with the aforementioned *P. protodice* and *C. eurytheme,* which had been thought to employ photoperiodic cues alone. In both species vernal phenotype *is* irreversibly determined by short days (actually long nights), regardless of temperature and with no linkage to diapause (there are no obligate diapausers in *P. protodice,* and *C. eurytheme* has no diapause at all). However, as in both *A. levana* and *P. n. venosa,* long-day animals *can* be induced to develop the full vernal phenotype by pupal chilling. Examples are shown in Fig. 2. That these responses have been missed in the past is not surprising; they are difficult to work with. In a given group of sibs a few individuals will respond strongly to a given treatment, while others respond slightly or not at all. It is difficult to keep track of precise pupation times for large numbers of individuals and to obtain statistically meaningful numbers of even-aged pupae for treatment, and the precise characterization of the responses will take several years, just as it did for the Nymphalid *Nymphalis urticae* (L.) (history reviewed in Shapiro, 1976). However, it is already clear that there is considerable intrapopulational variability in the timing of the "sensitive period," that it is quite short (there is no statistical difference in the distribution of phenotypes in batches of *P. protodice* chilled at the same age and held for 1, 2, 3, or 4 weeks), and that the mean responses among geographic conspecific populations differ.

Precisely the same phenomena emerge in previous studies of phenotypic plasticity which is not involved in regular seasonal polyphenism: *Aricia* spp. (Hoegh-Guldberg, 1974a, b; Jarvis, 1974) (Lycaenidae); various moths (Kettlewell, 1963); and especially the *"elymi"* series of aberrations in *Vanessa* spp., and similar aberrations in *Nymphalis* spp. (all Nymphalidae; see Shapiro, 1976). These temperature-induced variations are "morphoses" (Schmalhausen,

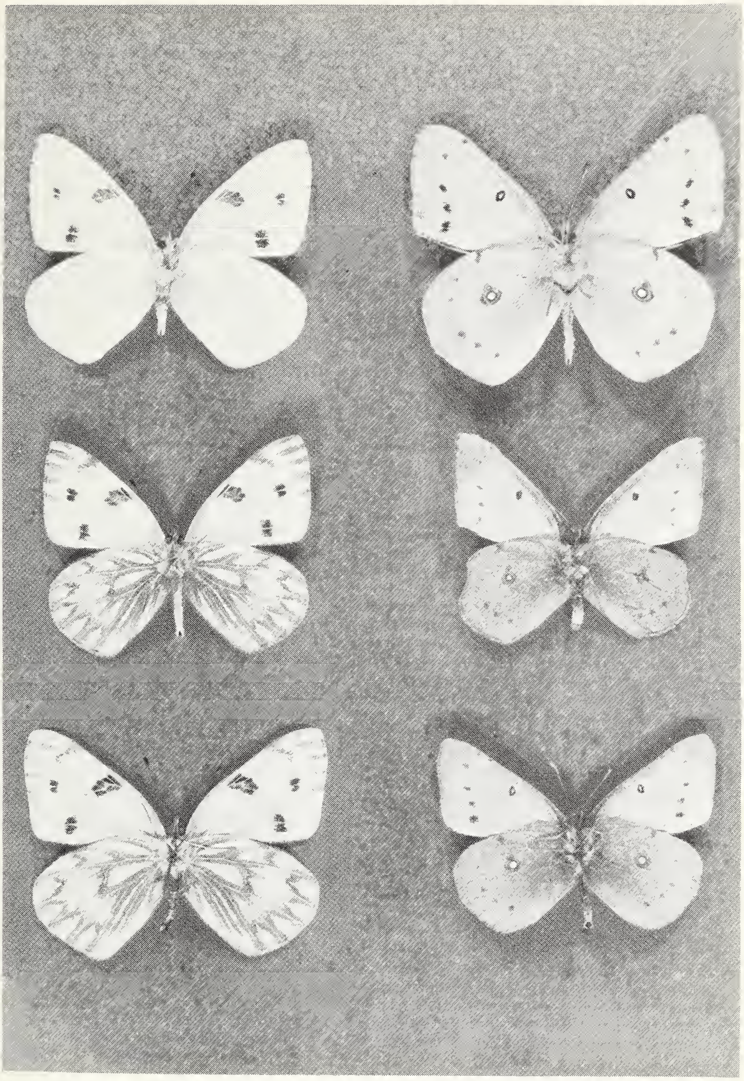

Fig. 2. Examples of redundant mechanisms in phenotypic induction. Ventral surfaces of males of *Pieris protodice* (left) and *Colias eurytheme* (right). Top: estival phenotypes, 24 L:O D, 25° C, pupa unchilled. Center: vernal, same conditions, young pupa chilled. Bottom: vernal, 10L: 14D, 25° C, pupa unchilled.

1949), nonadaptive developmental reactions. But the reactions of Pierids are the same as those regularly produced by photoperiod, and are presumably *adaptive*.

Probably most or all individuals of *P. protodice* and *C. eurytheme* can be switched from an estival to a vernal phenotype by some degree of chilling at some time in the first 24 hours after pupation. If this is true, then temperature can reinforce photoperiod in producing seasonally appropriate adult phenotypes in multivoltine species. For diapaused individuals of *P. protodice* and the closely related *P. occidentalis* Reak., the irreversibly determined vernal phenotype may be reinforced by post-diapause chilling, producing the characteristically greater phenotypic expression than is seen in lab-reared animals. The same is perhaps true for the (non-diapausing) late winter pupae of *C. eurytheme*. The period of post-diapause or late-winter chilling is so prolonged in the wild that virtually all overwintered animals will be affected. This process will tend to smooth over, or conceal, not only the aforementioned genetic variance in "sensitive period" but that which characteristically occurs for chilling requirement (strength of diapause), as well. Yet all of this variance is potentially adaptive in fluctuating environments, particularly when the suitability of spring weather for butterflies is highly uncertain, and we should expect selection to match norms of reaction to environmental uncertainty in populations with sufficient genetic integrity. Does it?

Hoffman (1978) reports that Rocky Mountain *Colias philodice eriphyle* Edw. differs from both *C. eurytheme* and *C. p. philodice* Godart in having adult phenotype decoupled from photoperiodic control (though it may be temperature-sensitive). He attributes this to high environmental uncertainty which renders photoperiod a poor seasonal predictor. Similar predictions about developmental phenology were made by Bradshaw (1973) and Istock (1978). Similarly, Shapiro (1973) found phenotype less reliably cued by photoperiod in the montane *Pieris occidentalis* than in *P. protodice,* a lowland species. Crosses of *C. p. philodice* × *C. p. eriphyle* would be informative as to how simple or complex genetic control of photoperiodic coupling can be. Right now everything which is known points to a definite evolutionary sequence in the history of insect polyphenism: a pre-existing phenotypic response to temperature which happens to be adaptive in some environments but not others is subject to selection for modifiers which affect threshold of expression and ultimately couple it to a reliable seasonal predictor, normally a pre-existing photoperiodic control of diapause.

This postulated evolutionary sequence can be further rationalized by noting that the pattern of interaction among genetics, photoperiod, and temperature is completely in accord with Darwinian predictions. For multivoltine species, which in Pieridae are weedy colonizers, photoperiodic determination of diapause can be overridden by high temperature in some individuals, allowing them to gamble on an extra generation in an unusually warm autumn. But photoperiodic determination of vernal phenotype is absolute; this makes sense insofar as autumn is colder than summer and any direct-developing butterflies will be aided in their feeding and reproductive activities by the thermoregulatory properties of the vernal phenotype. Estival phenotypes are not irreversibly determined by summer photoperiods. Cold can act on the young pupa just a few days before hatch to produce more or less of the vernal phenotype, giving rise to darker animals on short notice in unseasonably cold conditions. Hoffmann's Rocky Mountain *C. p. eriphyle* and Shapiro's coastal *P. n. venosa* are commonly exposed to unseasonable cold and switch readily without regard to photoperiod. But lowland *C. eurytheme* and *P. protodice,* which rarely face such conditions, are arcane enough in their "sensitive period" characteristics that they were missed altogether in laboratory experiments for years.

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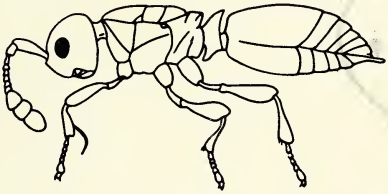

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TERGAL AND STERNAL GLANDS IN ANTS*

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Introduction

Chemical signals, or pheromones as they are generally called, play a central role in the complex communication system of ant societies. During the last 20 years a number of exocrine glands have been identified as the anatomical sources for a diversity of pheromones which mediate sexual and social behavior in ants (for reviews see Wilson 1971, Blum 1977, Hölldobler 1978).

In recent years, however, several hitherto unknown exocrine glandular structures have been discovered in ants and the behavioral functions of some of them have already been determined. In this paper we will review these findings and will report the new results of our comparative morphological study of tergal and sternal glands in ants.

Material and Methods

For histological investigations live specimens were fixed in alcoholic Bouin (Dubosqu Brasil) or Carnoy (Romeis 1948), embedded in methyl methacrylate, and sectioned 8μ thick with a Jung Tetrander I microtome (Rathmayer 1962). The staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A Scanning Electron Microscope. For some of the species which could only be identified to the generic level, the respective number is given of the voucher specimens, which are deposited in the ant collection of the MCZ (Harvard University).

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RESULTS

Tergal glands

a. Pygidial gland

In a detailed anatomical study of *Myrmica rubra* Janet (1898) described a pair of clusters of a few glandular cells, located under the third gastric tergum. Each cell sends a duct through the intersegmental membrane between the third and fourth gastral terga. We discovered a similar, but considerably larger paired glandular complex at the same anatomical position in *Novomessor cockerelli* and *N. albisetosus* (Hölldobler et al 1976). Kugler (1978) recently investigated a number of myrmicine ants and in many of them he found the gland, which had "distinct reservoirs, produced by invagination of the intersegmental membrane between abdominal tergum 6 and tergum 7 (pygidium)". Kugler suggested that these glandular organs be called *pygidial glands.* We accept this terminology, because it describes the anatomical designation of the organ more precisely than the term "dorsal gland" or "tergal gland", originally suggested (Hölldobler et al 1976, Hölldobler and Haskins 1977). However, it has to be pointed out that the pygidium of the ants (the last exposed tergum) is the 7th abdominal tergum and is not homologous to the pygidium of the Coleoptera (8th abdominal tergum). Hence, the pygidial glands of ants are not homologous to the pygidial glands of Coleoptera.

In a previous study (Hölldobler and Haskins 1977) we found pygidial glands with large reservoirs in several ponerine and myrmeciine ants (*Amblyopone, Paraponera, Ectatomma, Odontomachus, Pachycondyla, Platythyrea, Rhytidoponera, Myrmecia*) and we demonstrated that the virgin females of *Rhytidoponera metallica* attract males by the release of a pheromone from these glands. In his anatomical studies of *Rhytidoponera metallica* and *R. convexa,* Whelden (1957, 1960) described a pair of cell clusters each comprising 8–15 glandular cells. Each cell sends a duct through the membrane connecting the 6th and 7th abdominal segments. We are now certain that Whelden already had discovered the pygidial gland in *Rhytidoponera;* his histological methods, however, may not have enabled him to detect the large reservoirs associated with the glandular cell clusters. Similar paired glandular structures were found by Whelden (1957) in the ponerine species *Stigmatomma* (=*Amblyopone*) *pallipes.*

Finally, independently of our investigations, Maschwitz (pers. communication) found a pygidial gland in *Leptogenys chinensis,* which he called the "dorsal gland" (Maschwitz and Schönegge, 1977).

The new anatomical investigations presented in this paper reveal that the pygidial glands are much more common in ants than previously assumed. Usually the organ consists of a pair of lateral clusters of glandular cells, each cell sending a duct through the intersegmental membrane between the 6th and 7th abdominal terga. Depending on the species, the intersegmental membrane can be invaginated to different degrees, so that it can form a more or less voluminous reservoir (Fig. 1, 2, 3, 4). If no reservoir is present, the glandular structures can easily be missed during the dissection and histological sectionings are therefore required to determine whether or not the pygidial gland is present. As we have already indicated for *Novomessor* and as confirmed by Kugler (1978) for several other myrmicine species, the pygidial gland can be associated with a special cuticular structure on the pygidium (7th tergum), (Fig. 5, 6, 7). Our histological studies demonstrated, however, that the absence of such structures does not necessarily indicate the absence of

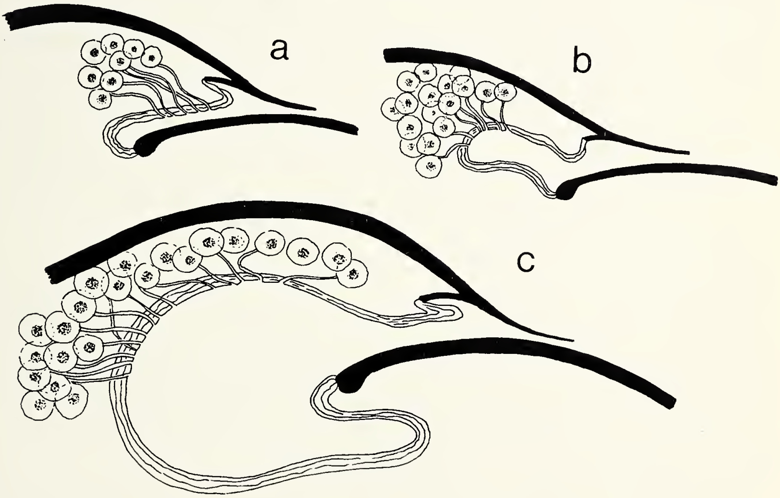

Figure 1. Schematic illustration of glandular cells that send ducts through the intersegmental membrane. When the membrane is increasingly more invaginated, it forms an increasingly larger reservoir (a to c).

pygidial glands. Thus, in several myrmicine species, in which we (Hölldobler et al 1976) and Kugler (1978) previously assumed the pygidial gland to be absent, we find that we now detect this organ by histological methods. Tables 1a and 1b list the species of the major subfamilies that we investigated histologically and indicate the type of tergal glands found.

b. Postpygidial gland

Dorsal glandular structures which open posteriorly to the pygidial gland, between the 7th and 8th abdominal terga (spiracular plate), we call postpygidial glands (Fig. 8). Whelden (1957, 1960) described glands in the 5th gastral segment of *Rhytidoponera convexa* and *R. metallica.* For *R. convexa* he writes: "Even the largest of these is less than half the size of the fourth-segment glands . . . . In the extreme case, there may be but a single gland cell on each side. It is often difficult to distinguish such a unicellular gland from an oenocyte, despite the usually distinct difference in size of the two cell types. Only the identification of a duct certainly distinguishes such a gland from the ductless oenocyte. In many individuals this second pair of glands could not be found". Whelden (1960) makes similar statements for *R. metallica.* Our results are somewhat different. We found well developed postpygidial glands in the 4 species of *Rhytidoponera* investigated (Table 1a). In all specimens we found a pair of clusters of glandular cells. Each cluster contains about 15–20 cells and each cell sends a duct through the intersegmental membrane close to the spiracular plate (Fig. 9, 10). In some ant species the postpygidial gland consists of only a few glandular cells, in others the postpygidial gland is associated with a well developed reservoir (Table 1a, 1b).

Sternal glands

In several species we discovered intersegmental sternal glands (Table 2). They can consist of a few glandular cells that send their channels through the intersegmental membrane, or of large clusters of glandular cells associated with voluminous reservoirs. These reservoirs are formed by invaginations of the intersegmental membranes (Fig. 8).

In several *Leptogenys* species (Fig. 12) we found two large sternal glands with reservoirs between the 7th and 6th, and 6th and 5th sterna. The latter glandular organ is usually associated with a special cuticular structure on the 6th sternum (Fig. 12). In *Paltothyreus* *tarsatus* we found well developed sternal glands between the 7th and 6th, 6th and 5th, and 5th and 4th sterna, but no reservoirs. Instead, the duct openings are associated with filament-like protrusions of the intersegmental membrane (Fig. 13, 14).

Other abdominal glands

The glandular venom apparatus of ants is composed of the Dufour's gland (alkine or accessory gland) and the poison gland. Although the venom apparatus of ants is very well studied (see reviews by Maschwitz and Kloft 1971, Blum and Hermann 1978 a, b), other glands, such as Koschevnikov's gland (sting gland), Bordas's gland and sting sheath glands, known from other Hymenoptera, have not been firmly established in ants.

Koschevnikov (1899) found in honeybees and *Vespa* paired clusters of glandular cells located laterally near the intersegmental membrane between the quadrate plate and the spiracular plate. Each individual cell sends channels into gathering ducts, which connect with the intersegmental membrane. Altenkirch (1962) found similar glands in most Apidae that she had studied.

There are indications that this gland might also be present in some species of the primitive ant subfamilies Myrmeciinae and Ponerinae. Whelden (1957) described a pair of clusters of gland cells, located slightly dorsally on each side of the sting of *Stigmatomma (=Amblyopone) pallipes.* Each cell sends a "rather tortuous duct . . . down and inward, to open through a membrane which is above the sting". Robertson (1968) found "sting glands" in *Rhytidoponera* "toward the region of the triangular plate, where they are attached to the intersegmental membrane". She described similar glands in *Bothroponera* sp. (=*Pachycondyla*), *Leptogenys sjostedji* and *Myrmecia gulosa.* In the latter species the glands are described as "two well formed masses of gland cells, each cell attached to the intersegmental membrane in the region of the triangular plate by a long, simple, cuticular duct".

Table 3 (A) lists the species in which we found paired glandular structures, closely resembling the "sting glands" described by Robertson. In all cases the glandular cells are located near the triangular plate, and from each cell a rather long duct leads downwards and opens through a membrane near the base of the sting (Fig. 15). Although we could not precisely locate the openings of the ducts, we assume they opened in the sting chamber.

Altenkirch (1962) and Maschwitz (1964) discovered a so-called sting sheath gland in several bee species. It consists of a palisade epithelium located in the sheath valves. In some ant species we found a distinct palisade epithelium in the sheath valves and/or single glandular cells with long individual ducts (Table 3 (B), Fig. 16, 17). Janet (1898) describes similar single gland cells, located near the sheath valves, in *Myrmica rubra.*

Bordas's glands, as they were described by Bordas (1895) in Terebrantia and reexamined by Rathmayer (1962) in several sphecid wasps, could not be identified in ants, although some of clusters of the single gland cells which send their ducts through the membrane of the sheath valves could be related to the Bordas's glands. It is obvious to us that the glandular structures, associated with the sting apparatus of ants, need to be investigated in greater detail in future studies.

In several ant species (Table 3 (C)) we found a highly developed palisade epithelium in the 7th sternum (Fig. 8). It is especially conspicuous in several *Leptogenys* species and in the army ants *Eciton* and *Neivamyrmex,* but it is not strongly developed in *Dorylus.* In the dolichoderine species and in *Aneuretus* this epithelium seems to be closely associated with the sternal gland (Pavan's gland).

In the African weaver ant (*Oecophylla longinoda*) we discovered a sternal gland under the 7th sternum, which is quite different from the glandular epithelium described above (Hölldobler and Wilson 1976, 1978). This structure consists of an array of single glandular cells that send short channels into cuticular cups on the outer surface of the sternite. In none of the other formicine species investigated, listed in table 1b, did we find this type of sternal gland. But in *Camponotus sericeus* we detected different clusters of glandular cells in the last sternum. Each cell sends a long channel through the intersegmental membrane near the vagina into the ventral part of the "sting chamber". We discovered similar paired glandular cell clusters in most myrmicine species we investigated. The gland is especially distinct in *Novomessor* and *Veromessor,* where the glandular cell channels penetrate the membrane near the vagina (Fig. 18).

The function of the intersegmental glands:

The functions of most of the glandular structures described in this paper are not yet known, but in a few species the function of the pygidial gland has already been identified. In *Novomessor cockerelli* and *N. albisetosus* the strongly smelling secretion of the pygidial glands releases a "panic alarm" response in workers, apparently specifically designed against army ant predation (Hölldobler in prep.). Kugler (in press) demonstrated that in *Pheidole biconstricta* the pygidial glands produce an alarm-defense secretion. A quite different function has been discovered in *Rhytidoponera metallica.* Here the wingless virgin females attract males by the release of a pheromone from the pygidial gland (Hölldobler and Haskins 1977). Since *Rhytidoponera* workers also have a well-developed pygidial gland and are attracted to its secretions, we believe we have not yet discovered the whole functional spectrum of this organ. In *Leptogenys chinensis,* Maschwitz and Schönegge (1977) demonstrated that the pygidial gland secretions serve together with poison gland substances as a recruitment trail pheromone. We obtained similar results when we recently reexamined the anatomical source of the trail pheromone of *Pachycondyla* (=*Termitopone*) *laevigata.* This ant species conducts well organized predatory raids on termites. During raiding the workers move in a single file, one closely behind another, along a powerful trail pheromone laid down by leading scout ants. Blum (1966) has identified the hindgut as the source of this recruitment trail pheromone. We cannot confirm his findings.

In our experiments with artificial trails laid with extracts from several abdominal glands, only the pygidial gland secretions released massive trail-following behavior in *P. laevigata* (Hölldobler and Traniello in prep.). A careful observational study of the trail-laying behavior of *P. laevigata* workers revealed that not the anus but rather the pygidial gland is dragged over the ground. Although the pygidial gland of *P. laevigata* has no definite reservoir, it is very well developed and is associated with an elaborate cuticular structure on the 7th tergum (Fig. 19, 20). The glandular secretion is apparently stored in the many cavities of this structure. When trailing, the ants rub this structure with its special applicator surface over the ground and deposit thereby the trail pheromone. Traniello (pers. communication) observed species of *Odontomachus* during nest emigrations performing the same trail laying behavior. We suspect that in *Odontomachus* also the pygidial gland secrets a trail pheromone (Fig. 21).

In *Bothroponera* (=*Pachycondyla*) *tesserinoda* we previously analyzed the signals involved in the tandem running recruitment technique (Hölldobler et al 1973, Maschwitz et al 1974). We discovered that the cues responsible for "binding" the follower behind the leader ant include both a surface pheromone and mechanical stimuli. Although we could extract this surface pheromone, we were not able to identify its anatomical source; all experiments with secretions from the known exocrine glands had negative results. After the recent discovery of the pygidial gland in *Pachycondyla* we have begun to conduct tandem running experiments with *Pachycondyla crassa** and *P. harpax**, using dummies contaminated with pygidial gland secretions. Our preliminary results strongly indicate that pygidial gland substance might be the source of the tandem running pheromone in these species.

In the doryline army ants raiding and emigrations are conducted along chemical trails deposited by workers. For *Neivamyrmex,* Watkins (1964) and Watkins et al (1967), and for *Eciton hamatum,* Blum and Portocarrero (1964), identified the hindgut as the source of the trail pheromone. In addition, Chadab and Rettenmeyer (1975) and Topoff and Mirenda (1975) demonstrated that besides the relatively long-lasting hindgut trail-substance, other signals (possibly more volatile secretions) are involved in the organization of "mass recruitment" in *Eciton* and *Neivamyrmex.*

We believe that our morphological investigations provide new possibilities for the analysis of chemical communication in army ants. Both *Neivamyrmex* and *Eciton* have large pygidial glands with distinct reservoirs (Fig. 22, 23). The postpygidial gland is smaller, but still considerably larger than in most of the other investigated species†. In both army ant species the 7th tergum is relatively small. Therefore, the reservoirs of the pygidial gland and postpygidial gland open directly above the anus at the abdominal tip (Fig. 23). In workers (all castes) of *Eciton* the dorsal membrane near the exits of the reservoir of the pygidial glands is conspicuously modified to a brush-like structure (Fig. 24). These morphological features strongly

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* *P. crassa* was observed tandem running by W. L. Brown, Jr. (pers. communication) at the western base of Ubombo Mts., Zululand, and by B. Hölldobler in Shimba Hills Reserve (Kenya). *P. harpax* was observed tandem running by S. Levings (pers. communication) on Barro Colorado Island, Panama.

† Whelden (1963) described two glands at the extreme posterior end of the gaster of *Eciton burchelli* workers. Although the description is not very accurate, from his drawings we can conclude that he found the pygidial gland and postpygidial glands.

suggest that the tergal glands might be involved in the chemical trail communication of army ants. We have begun to test this hypothesis with *Eciton hamatum.* The pygidial gland secretion of *E. hamatum* has a strong, characteristic smell. The secretion is probably skatole (Traniello pers. communication), the substance that gives army ants their typical "fecal odor". Recently Brown et al (1978) demonstrated that skatole is an effective growth inhibitor for bacteria and fungi and repels insectivorous snakes (Watkins et al 1969). Our first, preliminary tests demonstrated that *Eciton* workers follow artificial trails drawn with crushed pygidial glands. When we simultaneously offered trails drawn with hindgut contents and pygidial gland secretions, the latter were significantly preferred during the first minute. When we used trails drawn with secretions of the poison gland or Dufour's gland as controls, the ants always followed the pygidial gland trails. We have to stress, however, that these experiments must be considered pilot tests. The preliminary results, however, are striking enough to warrant a more detailed investigation in the future. It is interesting to note that the anatomy of the pygidial gland in the African army ant, *Dorylus molesta,* is quite different from that of *Eciton* and *Neivamyrmex* (Fig. 25). In this species the 7th tergum is considerably larger than in species of the latter genera, and the reservoirs of the pygidial glands do not open at the abdominal tip. In *Dorylus,* however, we found single glandular cells with channels opening directly at the anus, a feature we have not detected in other ant species (Fig. 25, 26).

Finally, our morphological study of the pygidial gland of *Veromessor pergandei* has led to results that are suggestive of the function of this organ. In this species the 7th tergum is relatively small, and as a result the large reservoirs of the pygidial glands open at the tip of the gaster (Fig. 27). *Veromessor* forages in well-organized columns (Went et al 1972; Wheeler and Rissing 1975; Bernstein 1975). Several observations suggest that these foraging columns are organized by a trail pheromone, though no trail pheromone gland has yet been identified. Clearly, the large pygidial gland has to be considered as a possible source for the trail pheromone.

The function of most of the newly discovered sternal glands is unknown. Only in *Paltothyreus tarsatus* could we demonstrate experimentally that foragers lay a recruitment trail with sternal gland secretions (Hölldobler in prep.).

CONCLUSIONS

Since we first found the pygidial gland widespread in the subfamilies Myrmeciinae and Ponerinae, we speculated that this gland might be a primitive monophylogenetic trait in ants generally (Hölldobler and Haskins 1977). The results reported in the present paper fully confirm this assumption. A well-developed pygidial gland was found in the most primitive ant, *Nothomyrmecia macrops,* and in representatives of all major subfamilies except in the Formicinae (Table 1b). We agree with Kugler (1978) that the "anal glands" of the Dolichoderinae and Aneuretinae are homologous to the pygidial glands of other ant subfamilies. Considering the variation in the morphology of the pygidial glands, even within a single subfamily, we think that the morphological variation of the "anal glands" of dolichoderine and aneuretine species does not warrant a separate terminology. In fact the term "anal gland" is misleading, because the glands do not exit from the anal opening of the gaster, as is sometimes inferred, but between the 6th and 7th abdominal terga (Fig. 28). This was clearly demonstrated by Pavan and Ronchetti (1955). It is our view and also Kugler's (pers. communication) that the "anal glands" should be called pygidial glands.

Kugler (1978) concluded from his comparative studies of myrmicine species that usually those species that have reduced or modified stings also have well-developed pygidial glands. He assumes that the pygidial gland replaces the sting apparatus as a chemical defense device. Our finding that well-developed pygidial glands occur in *Pogonomyrmex,* a genus with a very effective sting apparatus, and in many stinging ponerine species, does not support Kugler's conclusions.

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TABLE 1a

List of species of the poneroid complex (Taylor 1978) that were investigated histologically, and the types of tergal glands found. When the histological series was incomplete and we could not make a definite statement, the column is marked with "?". When the cuticular structure on the pygidium was only slightly sculptured, we marked the column with "–(+)".

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
MYRMECIINAE						
Myrmecia pilosula	R. J. Bartell R. W. Taylor Brindabella Ranges, Australia	+		–	–	+
PONERINAE						
Amblyopone australis	C. P. Haskins Manjimup, W. Australia	+		–	–	–
Amblyopone pallipes	J. Traniello Carlisle, Mass.	+		–	–	–
Platythyrea cribinoda	K. Horton R. Silberglied Shimba Hills, Kenya	+		–		+
Rhytidoponera metallica	C. P. Haskins Blackwell Range, Queensland, Australia	+		–		+
Rhytidoponera perthensis	C. P. Haskins Boddington, W. Australia	+		–		+
Rhytidoponera purpurea	C. P. Haskins Black Mountain, Kuranja, Queensland	+		–		+

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
Rhytidoponera violacea	C. P. Haskins Kings Park, W. Australia	+		−		+
Paltothyreus tarsatus	B. Hölldobler Shimba Hills, Kenya		+	−		+
Pachycondyla crassa	B. Hölldobler Shimba Hills, Kenya	+		−		+
Pachycondyla laevigata (=*Termitopone*)	N. Franks J. Traniello BCI, Panama		+	+	?	?
Plectroctena strigosa	B. Hölldobler Shimba Hills, Kenya	+		+	+	
Leptogenys neutralis	C. P. Haskins Manjimup, W. Australia	+		+		+
Leptogenys pavesii	B. Hölldobler Shimba Hills, Kenya	+		+		+
Leptogenys nitidia	B. Hölldobler Shimba Hills, Kenya	+		+		+
Leptogenys regis	B. Hölldobler Shimba Hills, Kenya	+		+		+
Odontomachus haematoda	C. P. Haskins BCI, Panama	+		+		+

TABLE 1a Continued

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
DORYLINAE						
Neivamyrmex nigrescens	B. Hölldobler Arizona	+		−	+	
Eciton hamatum	A. Aiello R. Silberglied J. Traniello BCI, Panama	+		−	+	
Dorylus molesta	B. Hölldobler Shimba Hills, Kenya		+	+		+
PSEUDOMYRMECINAE						
Pseudomyrmex ferruginea	A. Aiello R. Silberglied Canal Zone, Panama	+		−		+
Pseudomyrmex pallidus	M. Möglich Florida	+		−		?
Tetraponera spec. (78/26)	B. Hölldobler Shimba Hills, Kenya	+				+
MYRMECINAE						
Myrmica americana	J. Traniello Carlisle, Mass.		+	−	−	−
Tetramorium caespitum	J. Traniello Carlisle. Mass.		+	−	−	−
Pogonomyrmex desertorum	B. Hölldobler Arizona		+	−(+)	−	−
Pogonomyrmex californicus	B. Hölldobler Arizona		+	−(+)	−	−

TABLE 1a Continued

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
Pogonomyrmex badius	B. Hölldobler Florida		+	−	−	−
Veromessor pergandei	G. Alpert Mexico	+		−	−	−
Novomessor cockerelli	B. Hölldobler Arizona		+	+	−	−
Novomessor albisetosus	B. Hölldobler Arizona		+	+	−	−
Aphaenogaster rudis	J. Traniello Concord, Mass.		+	−	−	−
Aphaenogaster huachucana	B. Hölldobler Arizona		+	−	−	−
Pheidole militicida (worker & soldier)	B. Hölldobler Arizona		+	−(+)	−	−
Pheidole desertorum	B. Hölldobler Arizona	+		+	−	−
Atta sexdens (several castes)	N. Weber Timehri, Guyana	−	−	−	−	−

TABLE 1a Concluded

TABLE 1b

List of species of the formicoid complex (Taylor 1978) that we investigated histologically, and the types of tergal glands found.

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
NOTHOMYRMECIINAE						
Nothomyrmecia macrops	R. W. Taylor Eyre Peninsula S. Australia	+		−		+
ANEURETINAE						
Aneuretus simoni	E. O. Wilson Ratnapura, Sri Lanka	+		−	−	−
DOLICHODERINAE						
Liometopum apiculatum	B. Hölldobler Arizona	+		−	−	−
Conomyrma bicolor	B. Hölldobler Arizona	+		−	−	−
Iridomyrmex pruinosus	B. Hölldobler Arizona	+		−	−	−
FORMICINAE						
Oecopylla longinoda	B. Hölldobler Shimba Hills, Kenya	−	−	−	−	−
Pachycondyla spec.	R. Silberglied Nairobi Arboretum, Kenya	−	−	−	−	−
Myrmecocystus mexicanus	B. Hölldobler Arizona	−	−	−	−	−
Myrmecocystus mimicus	"	−	−	−	−	−
Myrmecocystus mendax	"	−	−	−	−	−
Formica perpilosa	"	−	−	−	−	−
Camponotus sericeus	M. Möglich Sri Lanka	−	−	−	−	−

TABLE 2

List of species of the poneroid complex in which we found intersegmental sternal glands.

Species	Location of glands between abdominal segments					
	7 and 6		6 and 5		5 and 4	
	reservoir		reservoir		reservoir	
	yes	no	yes	no	yes	no
Myrmecia pilosula		+				
Rhytidoponera purpurea		+				
Paltothyreus tarsatus		+		+		+
Pachycondyla crassa		+		+		?
Leptogenys neutralis	+		+			
Leptogenys pavesii	+		+			
Leptogenys nitida	+		+			
Leptogenys regis	+		+			
Tetraponera sp. (78/26)		+		+		+

TABLE 3

List of species, where sting glands (A), sting sheath glands (B), and a glandular epithelium in the 7th sternum (C) were found. In species marked with "(?)" the histological series was not complete and we could therefore not trace the whole glandular structure. Species which have only a glandular epithelium in the sting sheath are marked with (+); those with glandular epithelium and single gland cells with ducts are marked with (++); in unmarked species only single glandular cells with ducts were found.

A		B		C
Myrmecia pilosula		*Nothomyrmecia macrops*	(++)	*Leptogenys neutralis*
Amblyopone australis	(?)	*Myrmecia pilosula*		*Leptogenys pavesii*
Amblyopone pallipes		*Amblyopone australis*		*Leptogenys nitida*
Rhytidoponera metallica		*Amblyopone pallipes*		*Leptogenys regis*
Rhytidoponera perthensis		*Rhytidoponera purpurea*	(+)	*Eciton hamatum*
Rhytidoponera purpurea		*Platythyrea cribinoda*	(++)	*Neivamyrmex nigrescens*
Rhytidoponera violacea		*Paltothyreus tarsatus*	(++)	*Aneuretus simoni*
Platythyrea cribinoda		*Leptogenys nitida*	(++)	*Iridomyrmex pruinosus*
Paltothyreus tarsatus	(?)	*Leptogenys regis*		*Conomyrma bicolor*
Leptogenys regis	(?)	*Odontomachus haematoda*		*Liometopum apiculatum*
		Myrmica americana	(++)	*Novomessor cockerelli*
				Novomessor albisetosus

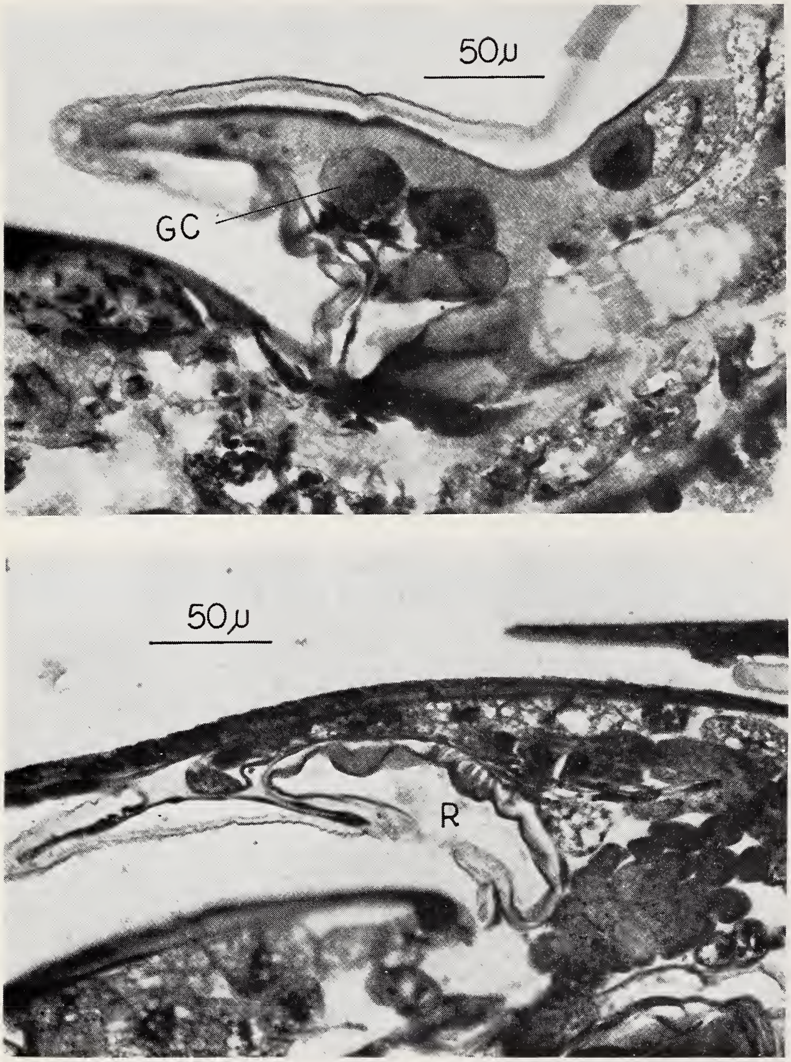

Figure 2. Above: Sagital section through pygidial glands of *Amblyopone australis*. The gland has no distinct reservoir, but 10–15 glandular cells (GC) with channels in each cluster. Below: Pygidial gland of *Amblyopone pallipes* with distinct reservoir (R) and 30–40 glandular cells in each cluster.

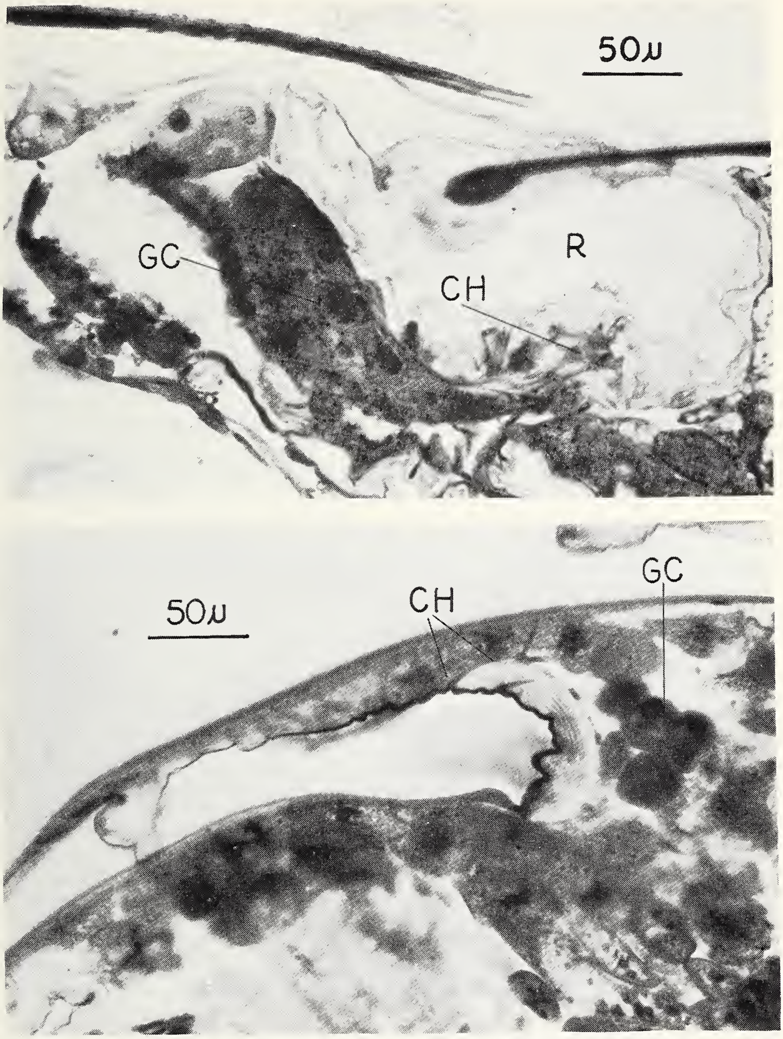

Figure 3. Above: Sagital section through pygidial glands of *Nothomyrmecia macrops:* Very large reservoir (R); each cluster consists of 50–80 cells; GC = glandular cells; CH = channels of glandular cells. Below: Pygidial gland of *Myrmica americana:* No distinct reservoir, 10–15 cells in each cluster.

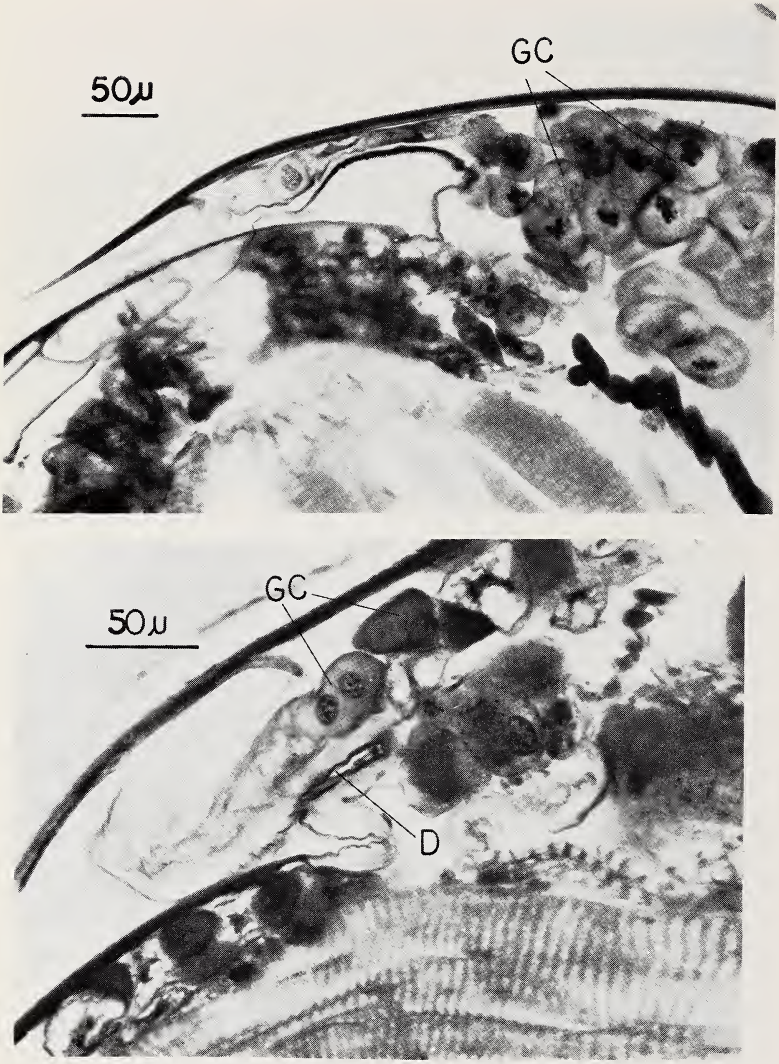

Figure 4. Above: Sagital section through pygidial glands of *Pogonomyrmex californicus:* No definite reservoir, but large cell clusters, each containing 30–35 glandular cells (GC). Below: Pygidial gland of *Pseudomyrmex ferruginea:* No distinct reservoir; intersegmental membrane forms a chitinous duct (D) into which the individual glandular channels open.

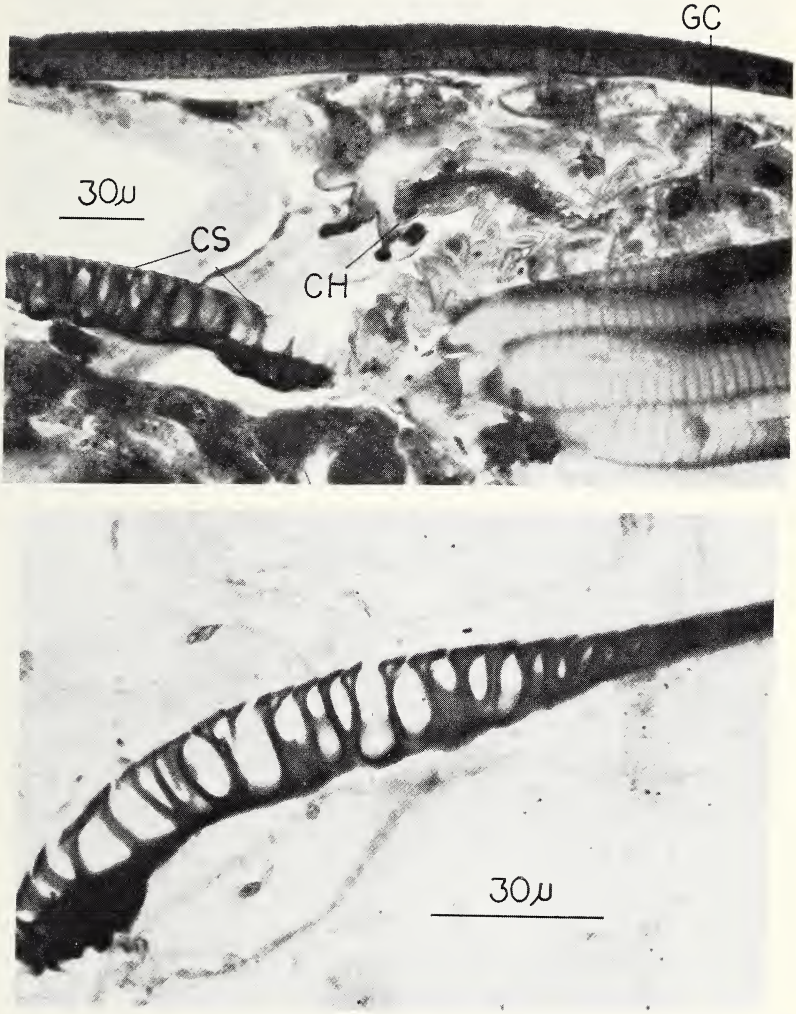

Figure 5. Above: Sagital section through the pygidial gland of *Leptogenys pavesii* (GC = glandular cells; CH = channels of GC; CS = cuticular structure on the 7th tergum). Below: Close-up view of sagital section through cuticular structure of 7th tergum of *Leptogenys neutralis.*

Figure 6. Above: Sagital section through pygidial gland of *Leptogenys regis.* Below: SEM photograph of cuticular structure of 7th tergum of *L. regis.* The tergum is cut so that the well-structured cavities under the surface can be seen. (Lettering as in Fig. 5).

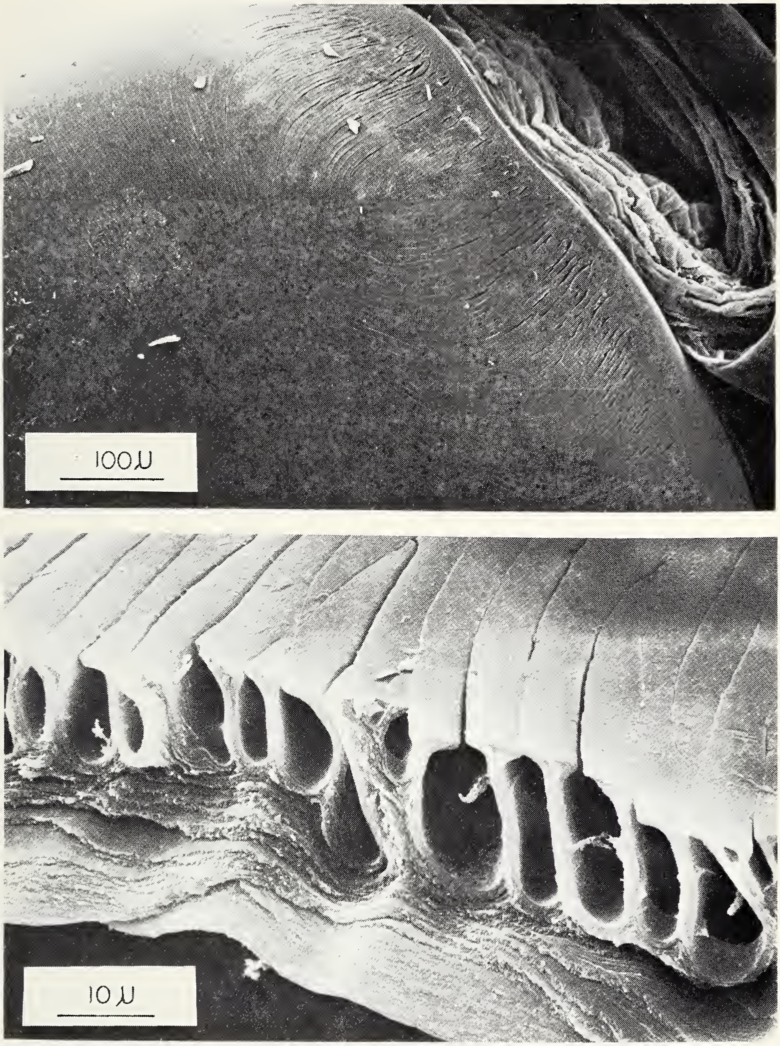

Figure 7. SEM photograph of cuticular structure of 7th tergum of *Plectroctena strigosa.* Above: View of the anterior part of the tergum. The cuticular grooves are clearly visible. Below: Close-up view of cuticular structure; the tergum is cut, so that the cavities beneath the grooves are visible.

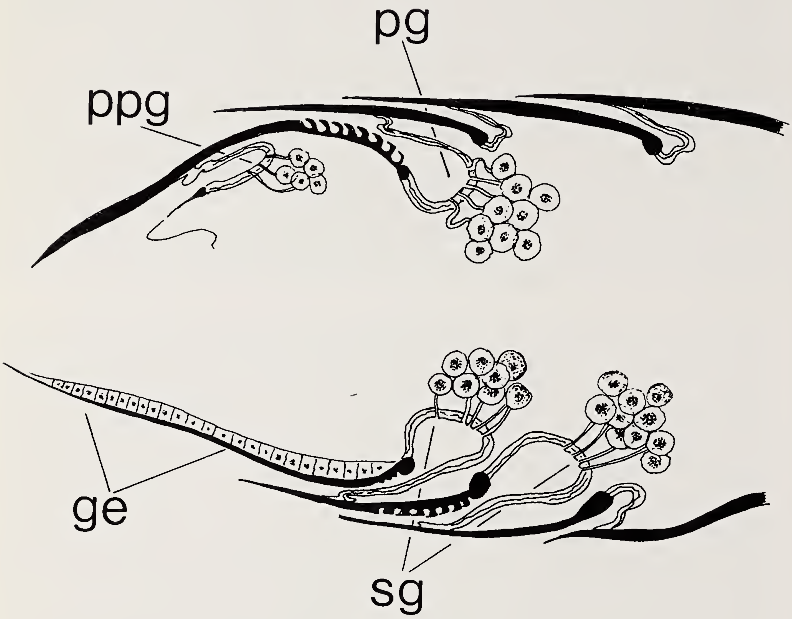

Figure 8. Schematic illustration of tergal and sternal glands in *Leptogenys*. (Lettering as in Fig. 5; sg = sternal gland; ge = glandular epithelium; ppg = postpygidial gland; pg = pygidial gland).

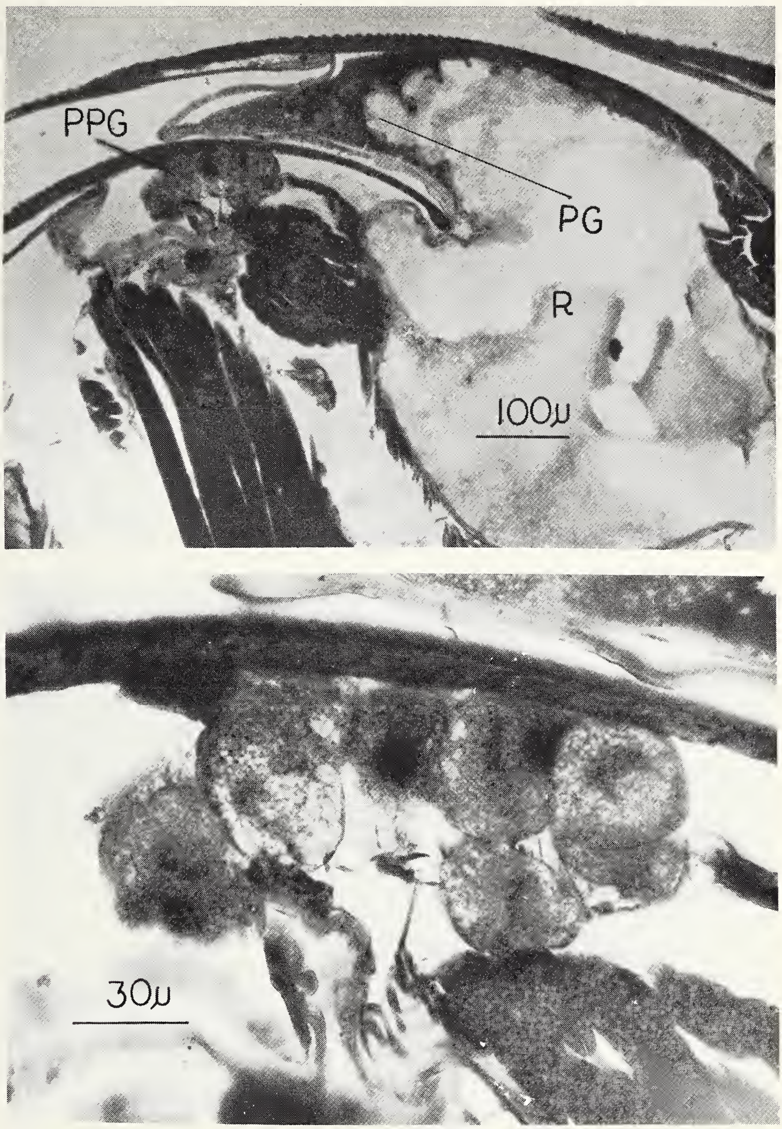

Figure 9. Above: Sagital section through pygidial gland and postpygidial gland, with large reservoirs of *Rhytidoponera perthensis*. Below: Postpygidial gland only; note the glandular cells with channels. (Lettering as in Fig. 8; R = reservoir).

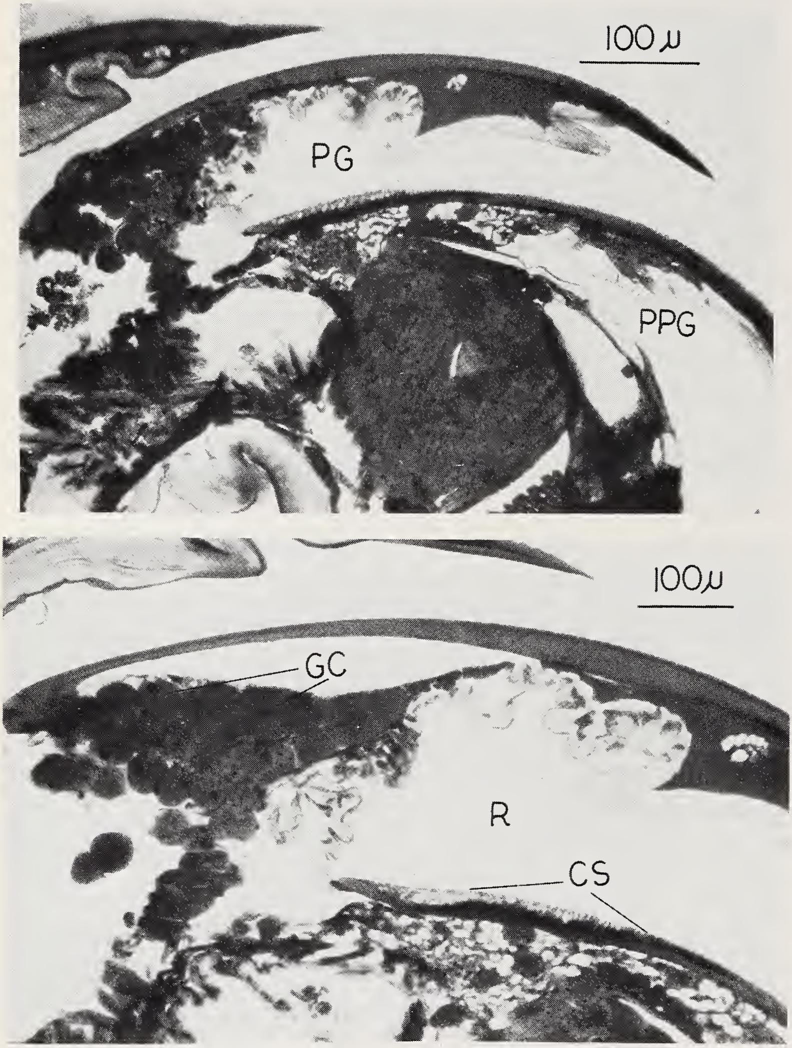

Figure 10. Above: Sagital section through pygidial gland and postpygidial gland of *Plectroctena strigosa.* Below: Pygidial gland. (Lettering as in Fig. 5; PPG = postpygidial gland; PG = pygidial gland; R = reservoir).

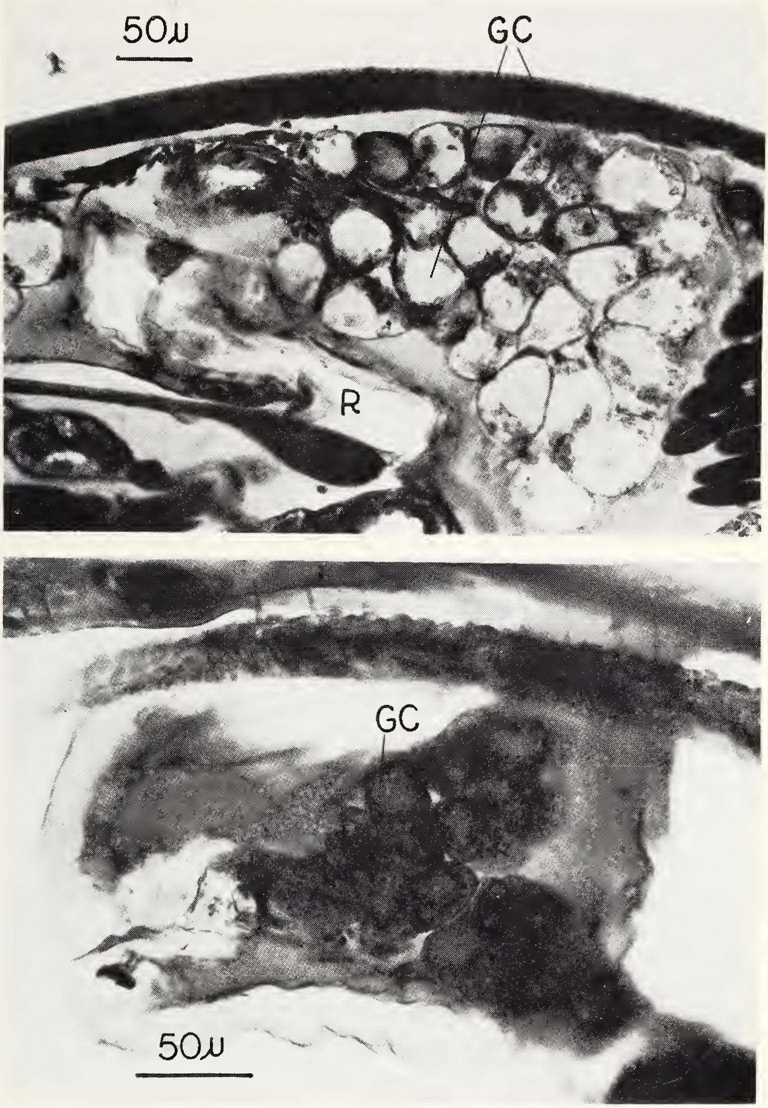

Figure 11. Above: Sagital section through the pygidial gland of *Platythyrea cribinoda*. The large reservoir is folded in this section. Each cell cluster contains 50–70 cells. Below: Section through postpygidial gland of *P. cribinoda;* each cluster contains 15–20 cells. (Lettering as in Fig. 3).

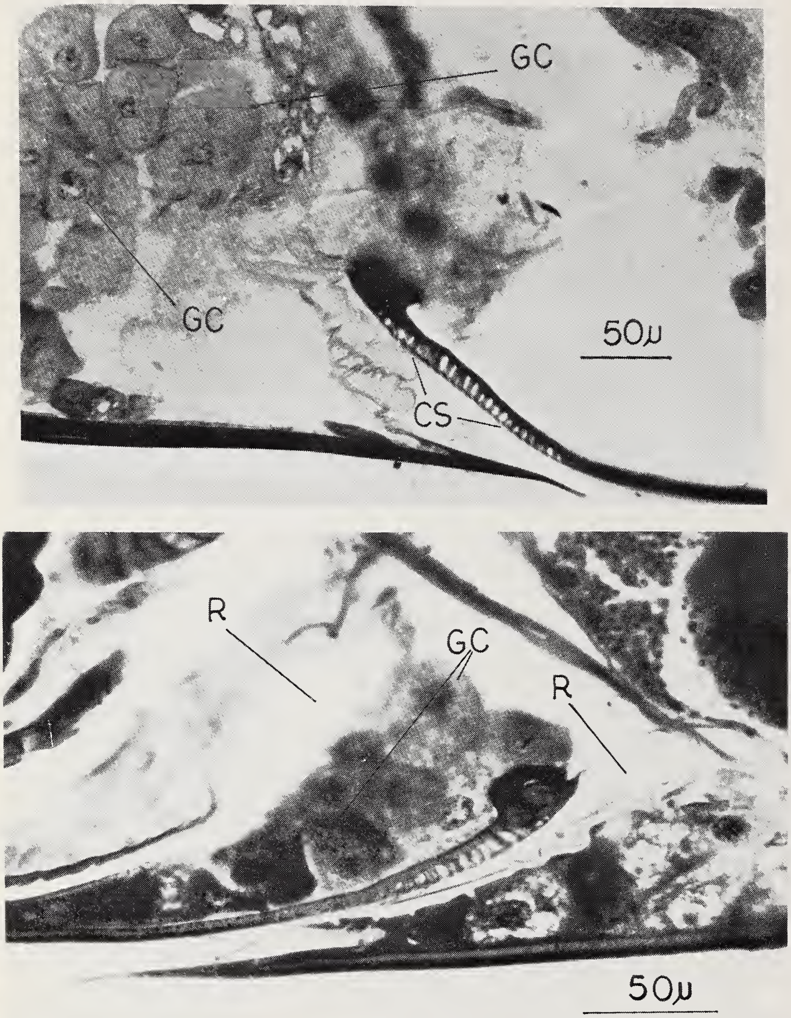

Figure 12. Above: Sagital section through sternal gland between 5th and 6th sterna of *Leptogenys neutralis.* Usually the 6th sternum has a distinct cuticular structure (CS), very similar to that on the 7th tergum. Below: Section through both sternal glands (Between 5th and 6th, and 6th and 7th sterna) of *Leptogenys nitida.* (Lettering as in Fig. 5; R = reservoir).

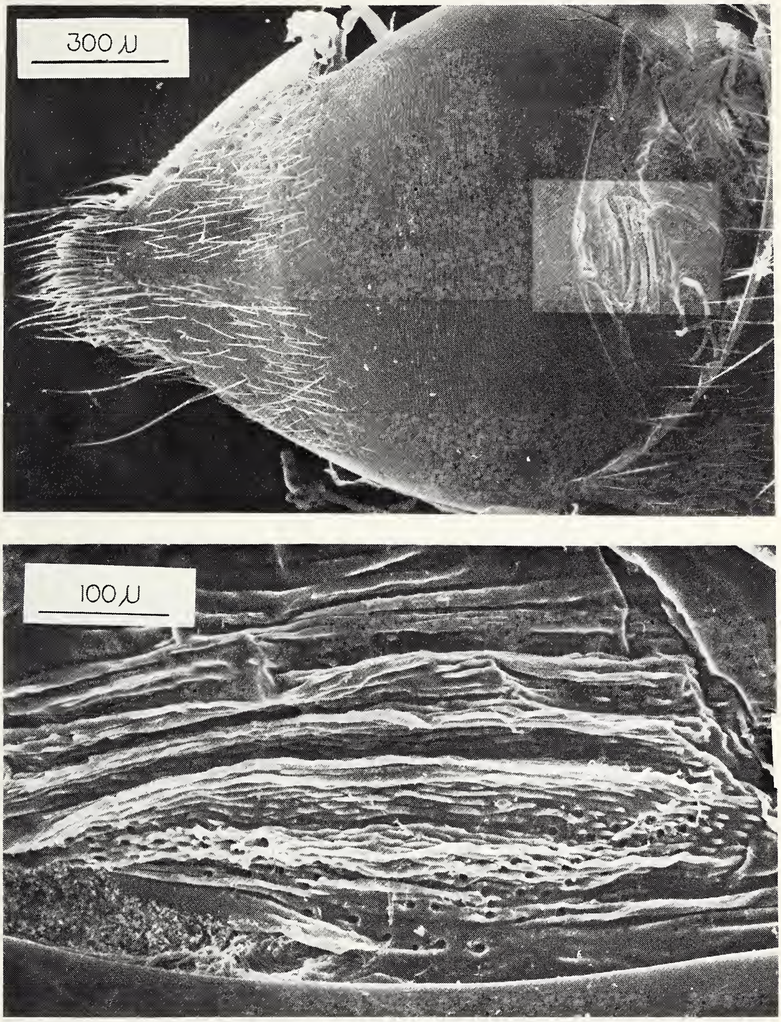

Figure 13. SEM photograph of the sternal gland area between the 6th and 7th sterna of *Paltothyreus tarsatus.* The picture below is an enlargement of the lighter rectangle in the picture above. The openings of the glandular cell channels in the intersegmental membrane are clearly visible.

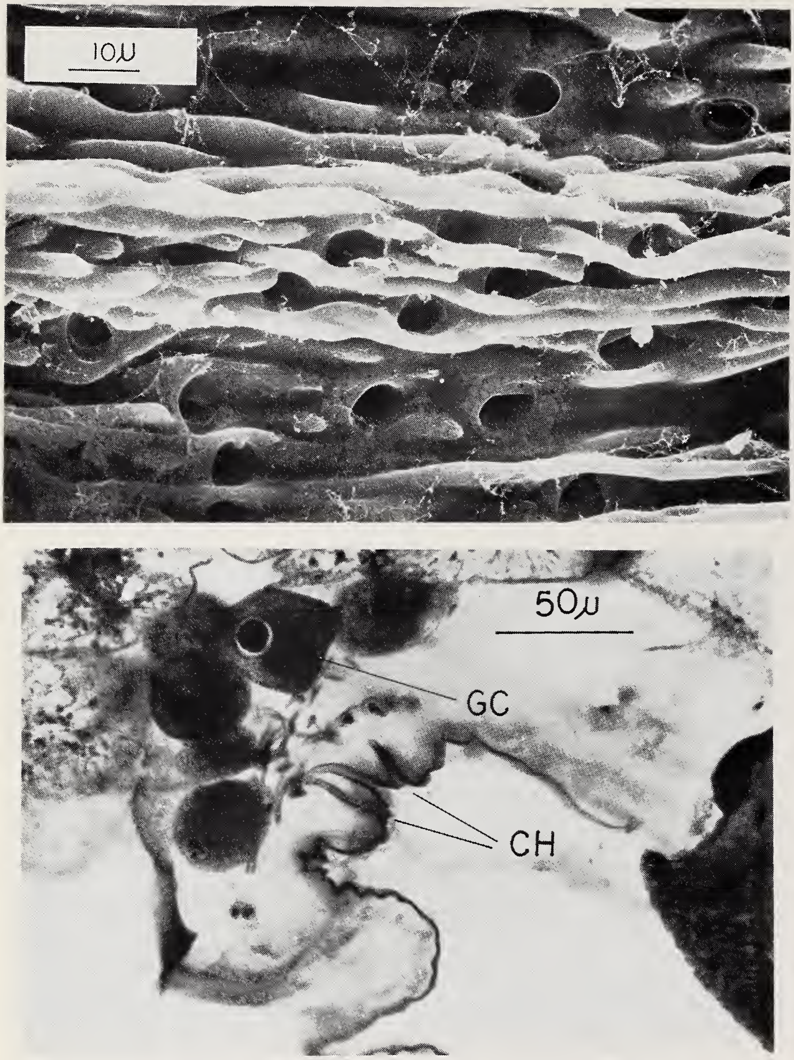

Figure 14. Above: SEM photograph of the glandular cell openings of the sternal gland of *Paltothyreus tarsatus.* Note the filament-like protrusions of the intersegmental membrane. Below: Sagital section through the same area. (Lettering as in Fig. 5).

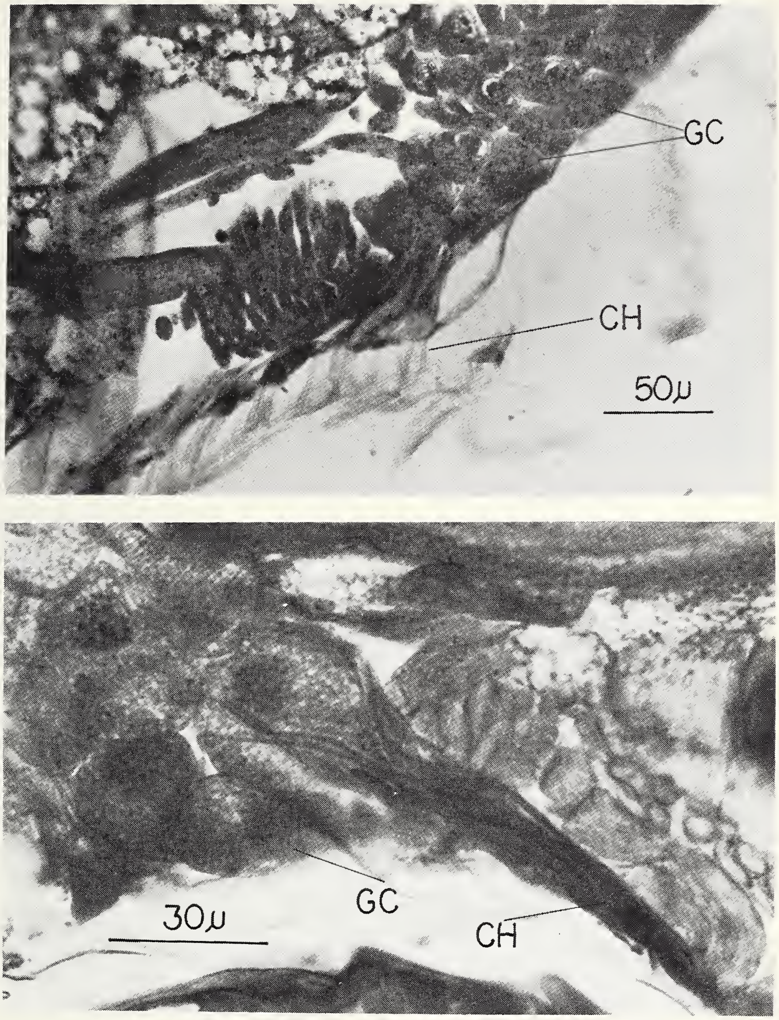

Figure 15. "Sting glands" of *Myrmecia pilosula* (above) and *Amblyopone pallipes* (below). (Lettering as in Fig. 5).

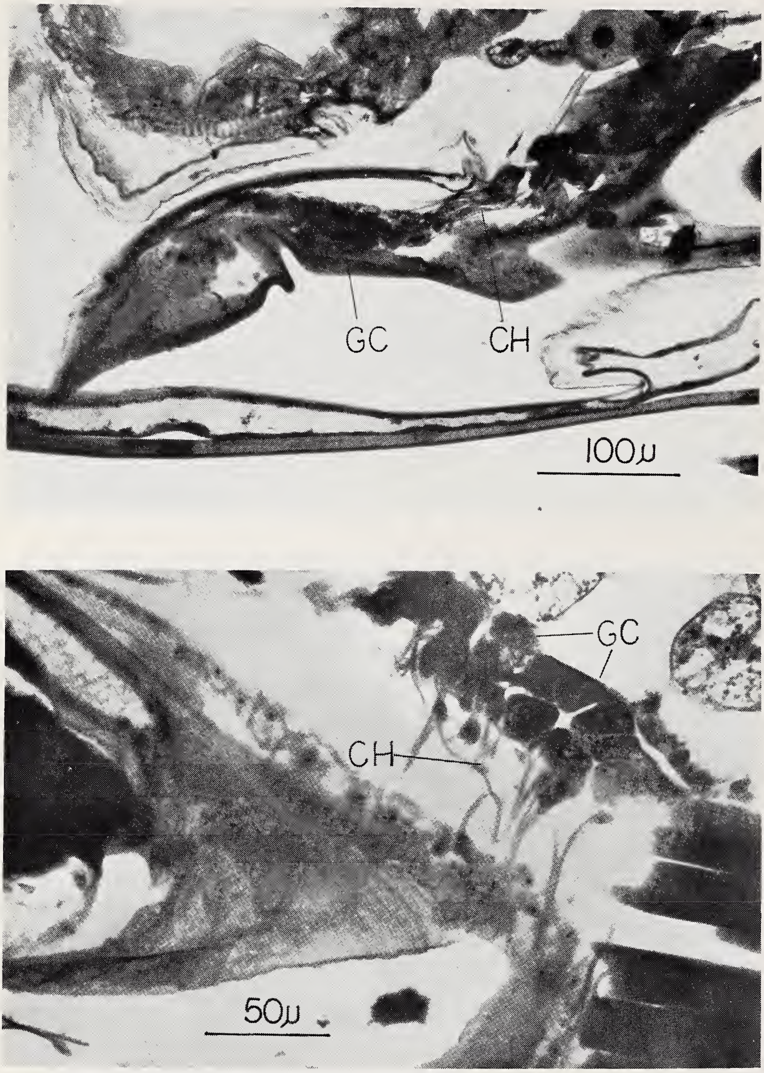

Figure 16. Glands associated with the sting sheath. Above: Sagital section through sheath valve with glandular cluster and channels in *Odontomachus haematoda*. Below: *Myrmecia pilosula*. (Lettering as in Fig. 5).

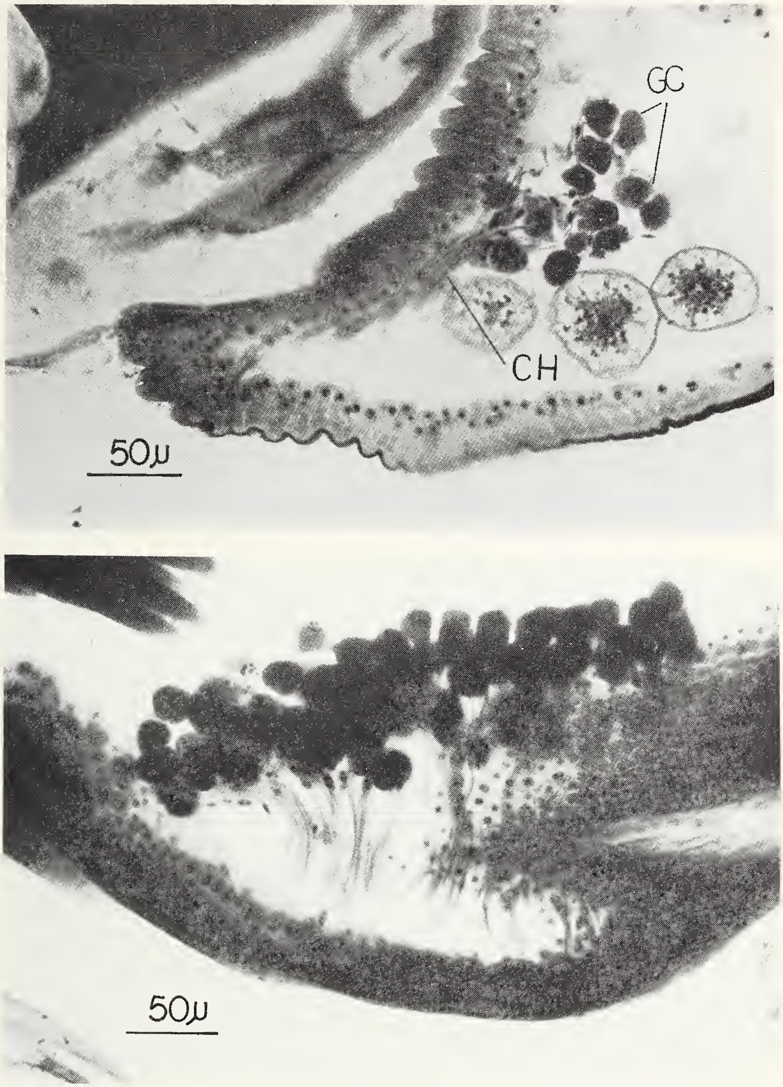

Figure 17. Glands associated with sting sheath in *Paltothryeus tarsatus.* Above: Sagital section through glandular cells with channels. Below: Sagital section through glandular cell cluster with channels. (Lettering as in Fig. 5).

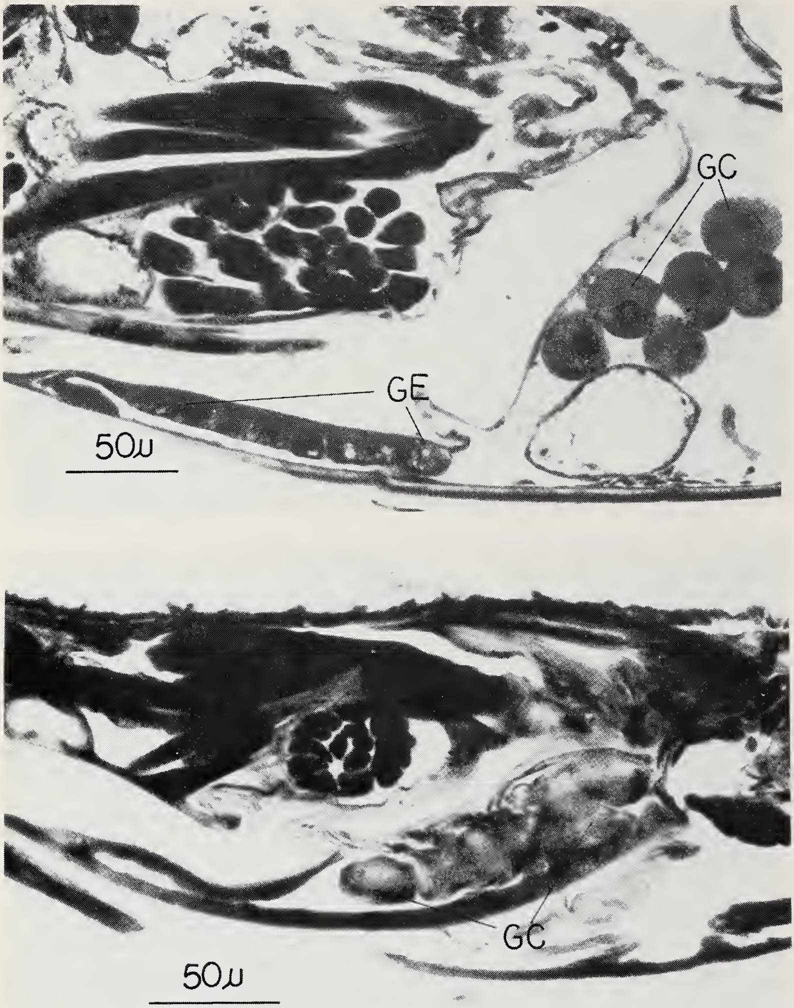

Figure 18. Glandular cell clusters in the 7th abdominal sternum of *Novomessor cockerelli* (above) and *Veromessor pergandei* (below). GE = glandular epithelium in the 7th sternum. (Lettering as in Fig. 5).

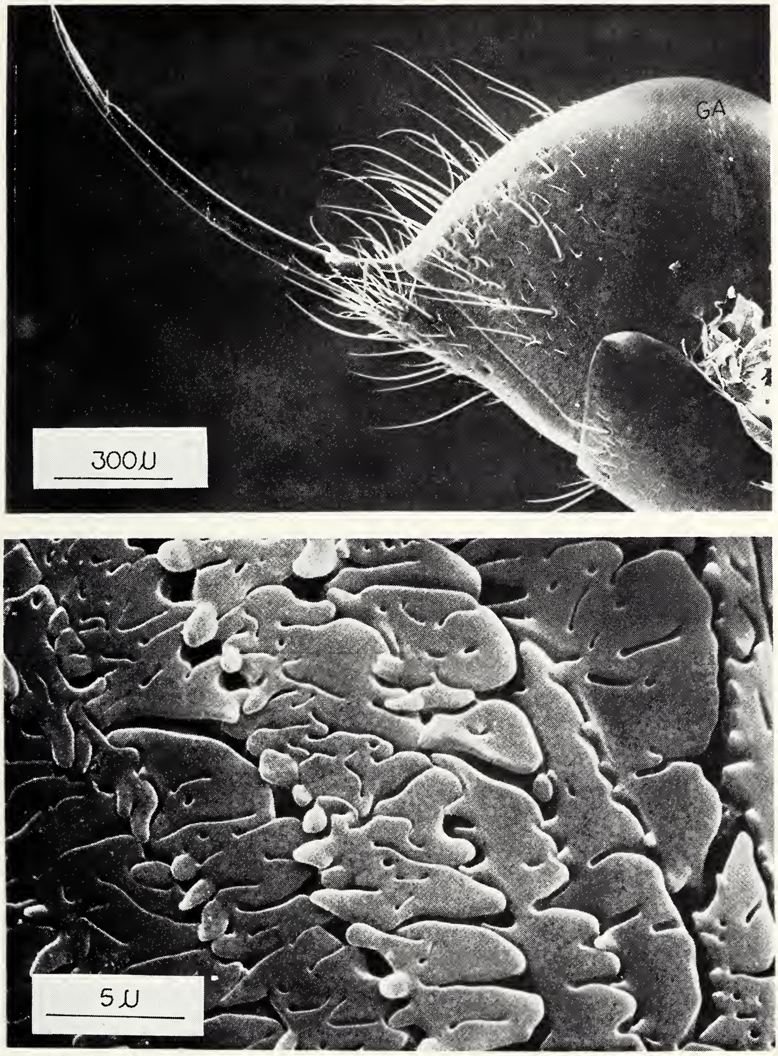

Figure 19. SEM photograph of the 7th tergum of *Pachycondyla* (=*Termitopone*) *laevigata*. Glandular applicator surface (GA) is shown in greater detail in the picture below.

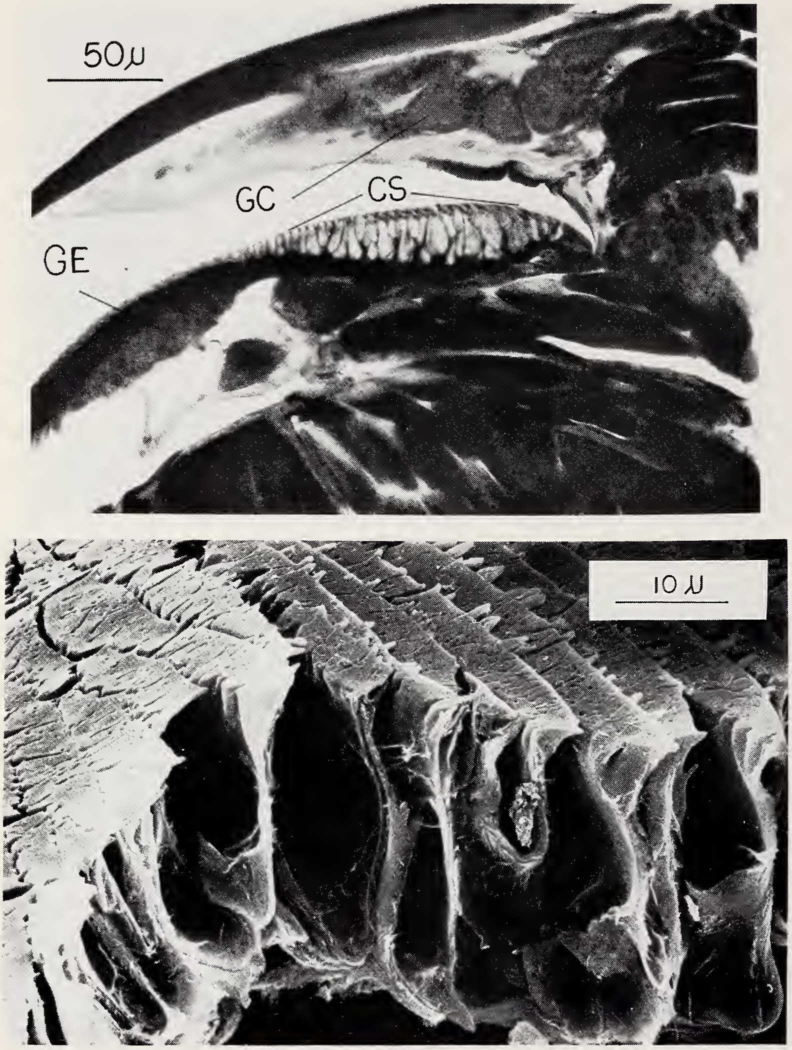

Figure 20. Above: Sagital section through the pygidial gland of *Pachycondyla* (=*Termitopone*) *laevigata.* Below: SEM photograph of the cuticular structure (GA in Fig. 19) on 7th tergum. The cut open area shows the large cavities associated with the structure. (Lettering as in Fig. 5 and Fig. 18).

Figure 21. Sagital section through the gaster of *Odontomachus haematoda,* showing the well developed reservoir of the pygidial gland (PG).

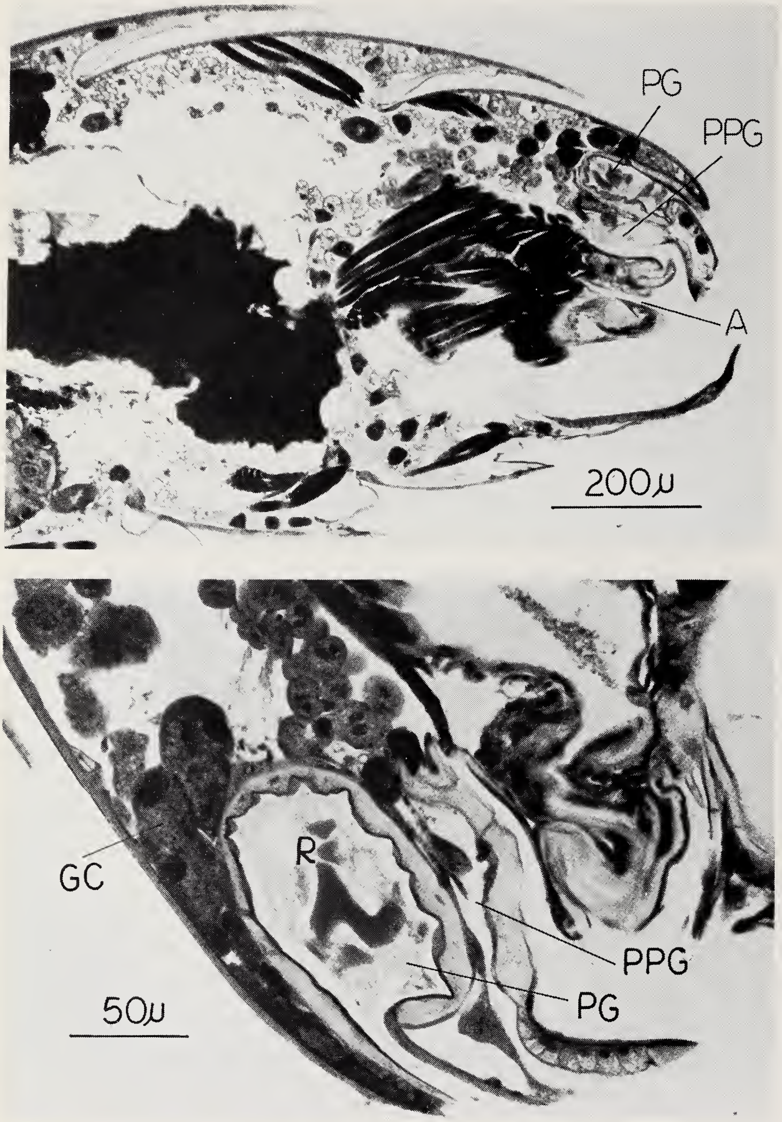

Figure 22. Above: Sagital section through the gaster of *Neivamyrmex nigrescens,* showing the pygidial gland (PG), postpygidial gland (PPG) and anus (A). Below: Close up of sagital section through pygidial gland and postpygidial gland of *N. nigrescens.* (Lettering as in Figs. 5 and 8; R = reservoir).

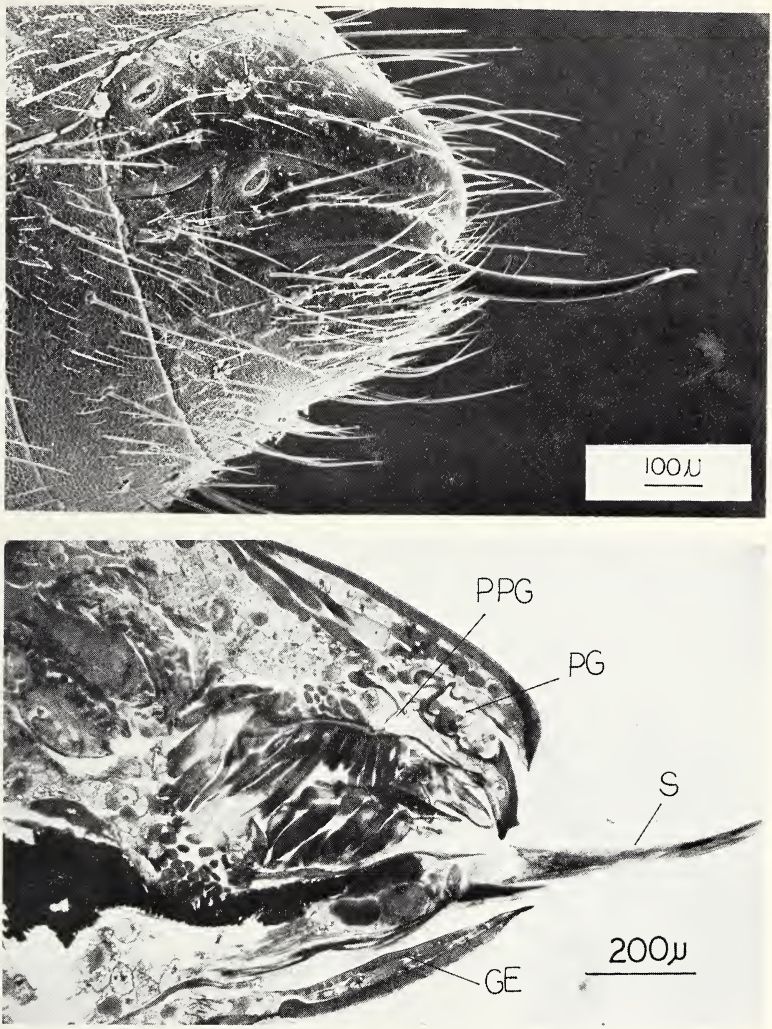

Figure 23. Above: SEM photograph of tip of the gaster of *Eciton hamatum*. Below: Sagital section through the same segments. (Lettering as in Fig. 8; S = sting; GE = glandular epithelium in 7th sternum).

Figure 24. *Eciton hamatum:* SEM photograph of the intersegmental membrane between 6th and 7th terga, where the pygidial glands open. Below: Close up of the brush-like structure.

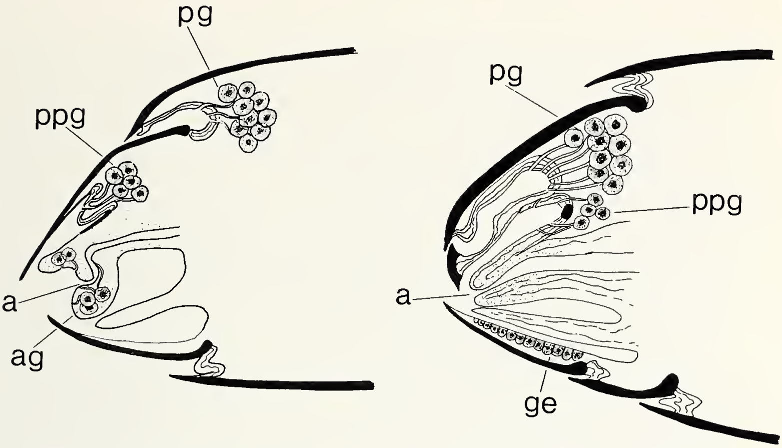

Figure 25. Schematic drawings of sagital sections through the gaster tips of *Dorylus molesta* (left) and *Eciton hamatum* (right). (Lettering as in Fig. 8; a = anus; ag = anus glands).

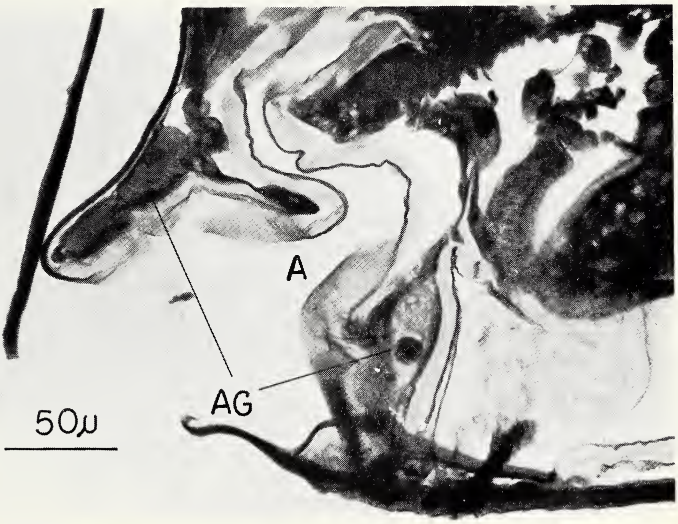

Figure 26. Sagital section through anus of *Dorylus molesta* worker; AG = anus gland; A = anus.

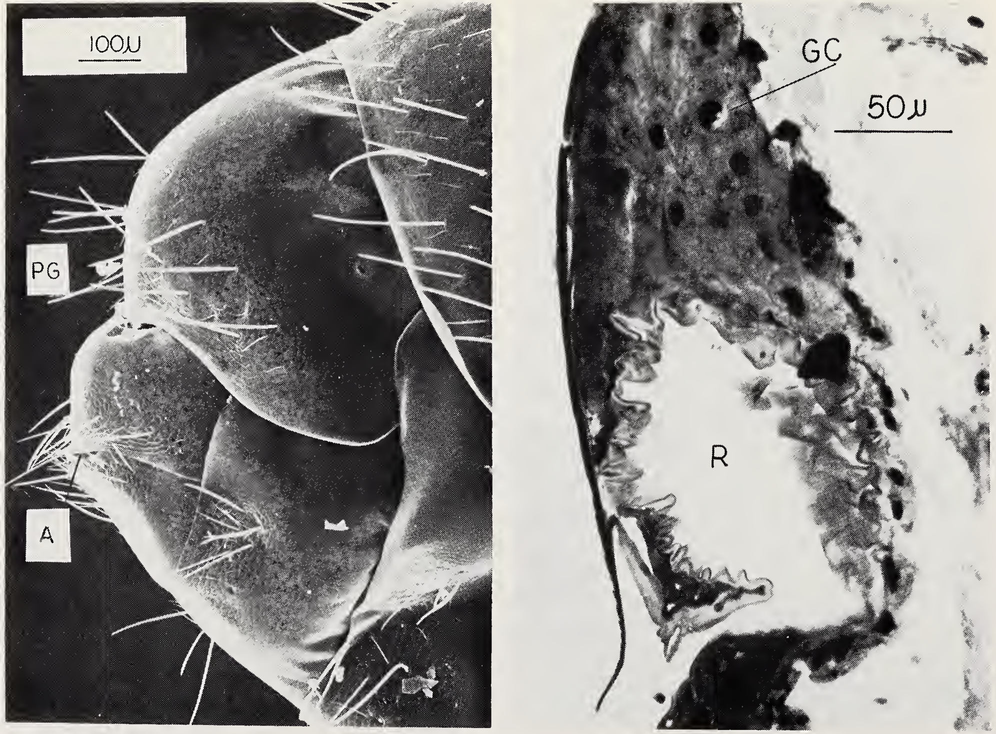

Figure 27. Left: SEM photograph of abdominal tip of *Veromessor pergandei.* "PG" indicates opening of pygidial gland between 6th and 7th terga; "A" indicates opening of anus. Right: Sagital section through pygidial gland of *Veromessor,* which has a large reservoir (R) and each cell cluster contains 50–70 glandular cells (GC).

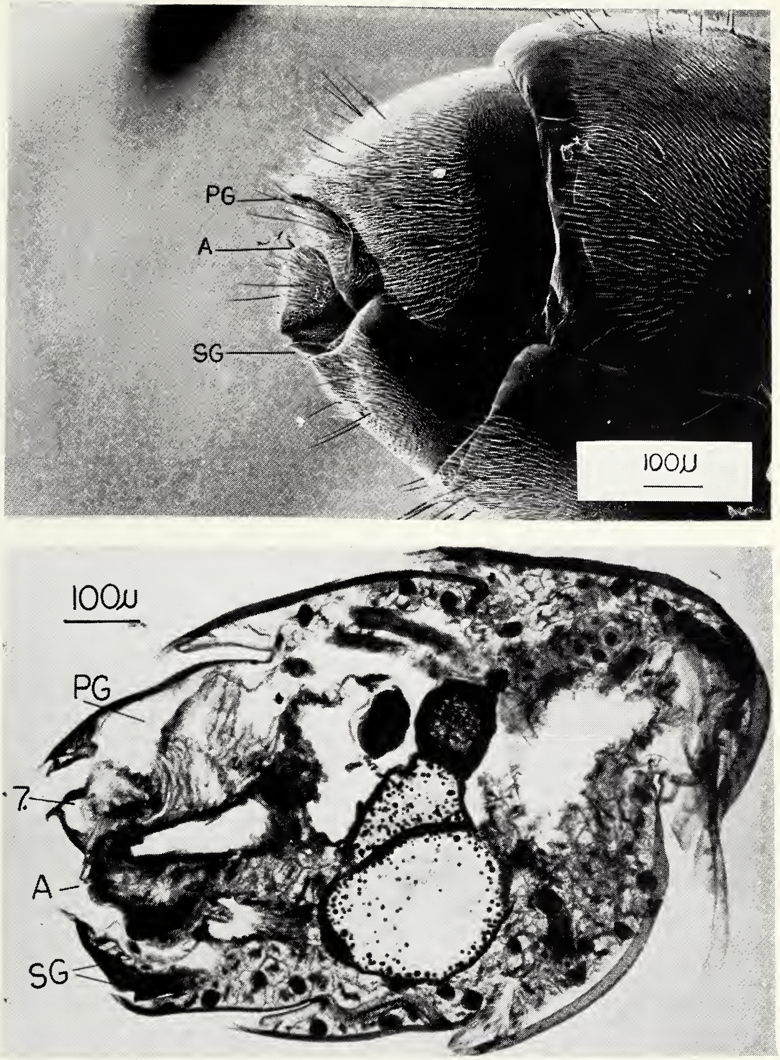

Figure 28. Above: SEM photograph of abdominal tip of *Liometopum apiculatum*. "PG" indicates where the pygidial gland opens between 6th and 7th terga. "A" indicates opening of anus; SG = sternal gland (Pavan's gland). Below: Sagital section through gaster of *L. apiculatum*. PG = reservoir of pygidial gland; 7. = 7th tergum.

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LIFE HISTORY OF *DYNASTOR DARIUS* (LEPIDOPTERA: NYMPHALIDAE: BRASSOLINAE) IN PANAMA

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Dynastor darius (Fabr.) (Figure 1)[1] is a large crepuscular butterfly found from Guatemala south into Brasil (Blandin, 1976; Blandin and Descimon, 1977). The larva is known to feed on various bromeliads. In the interests of amplifying the scattered and fragmentary descriptions of the immature stages by previous workers, and commenting upon certain discrepancies between their findings and our own, we here present data on twelve individuals of *Dynastor darius* reared on Barro Colorado Island (BCI), Panama in 1978.

On 21 June we captured a female of *Dynastor darius,* and over the period 23–25 June obtained twelve eggs (Figure 2). These were spherical, 2.2 mm in diameter, and cream colored with a pattern of anastomosing striae oriented from pole to pole. The first instars emerged eleven days after oviposition and we presented them with leaves of a variety of monocot species: *Musa paradisiaca* (Musaceae), *Heliconia* sp. (Heliconiaceae), *Monstera* sp. (Araceae), *Cocos nucifera* (Palmae), *Zingiber* sp. (Zingiberaceae), *Philodendron tripartitum* (Araceae), *Ananas comosus* (Bromeliaceae), and an unidentified grass (Gramineae). The larvae ate only the pineapple (*Ananas comosus*).

First Instar Larvae

Newly hatched larvae were 7.6–8 mm in length excluding the caudae, which were 2 mm long, orange on the basal half and black apically. At the tip, each cauda bore a 1 mm long seta which was black on the basal half and white apically, plus several appressed setae toward the base. The tip of the body between the caudae was red. The

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[1] Figures 1 and 11 represent the individual in rearing Lot 78–75. Figures 2–10 represent the twelve individuals in rearing Lot 78–84.

Figure 1. *Dynastor darius,* adult male. Left: dorsal; Right: ventral. Scale = 20 mm.

head capsule (Figure 9, A and B) displayed a complex pattern of beige, brown, and black, almost obscured by a dense covering of 1 mm long black, plumose setae. Four pairs of low bumps marked the positions where horns appeared in the second instar.

Before taking their first meal, each larva (Figure 4) had a red-brown dorsal stripe plus four yellow and three red-brown lateral stripes, and an oval red dorsal spot (Figure 7A) between abdominal segments 3 and 4. After feeding and expanding, the larval stripes (Figure 5) became green and yellow, with several extra yellow stripes appearing between old ones. The dorsal spot became black, flanked on the sides with red and orange, and bordered on each end with orange and white (Figure 7B). A second and much smaller dorsal spot, white at the anterior end and black posteriorly, appeared between abdominal segments 5 and 6. The positions of these spots correspond to positions 6–7, and 8–9 of the system used by Burmeister (1873) and Müller (1886) who numbered thoracic and abdominal segments as one series.

A pinkish red eversible gland (Figure 3), located ventrally on the prothorax between the legs and head, became particularly evident in later instars. When disturbed, larvae reared up and waved from side to side, emitting a pineapple-like odor that seemed to come from the large everted gland.

FURTHER LARVAL DEVELOPMENT

Number of instars

Although larvae were reared separately and given food *ad libitum,* the number of instars varied among the ten individuals surviving to pupation. Three reached pupation after completing five instars, six after six instars, and one after seven. Due to this variability in development, larval size could not be used to identify instar number (Figure 6).

Development time

For the eight individuals surviving to adulthood[2], average development time, from oviposition to eclosion, was 80.9 days (range: 73–88 days, s: 6.6 days, N = 8). The amount of time spent in each stage by each individual is shown graphically in Figure 8. The average time

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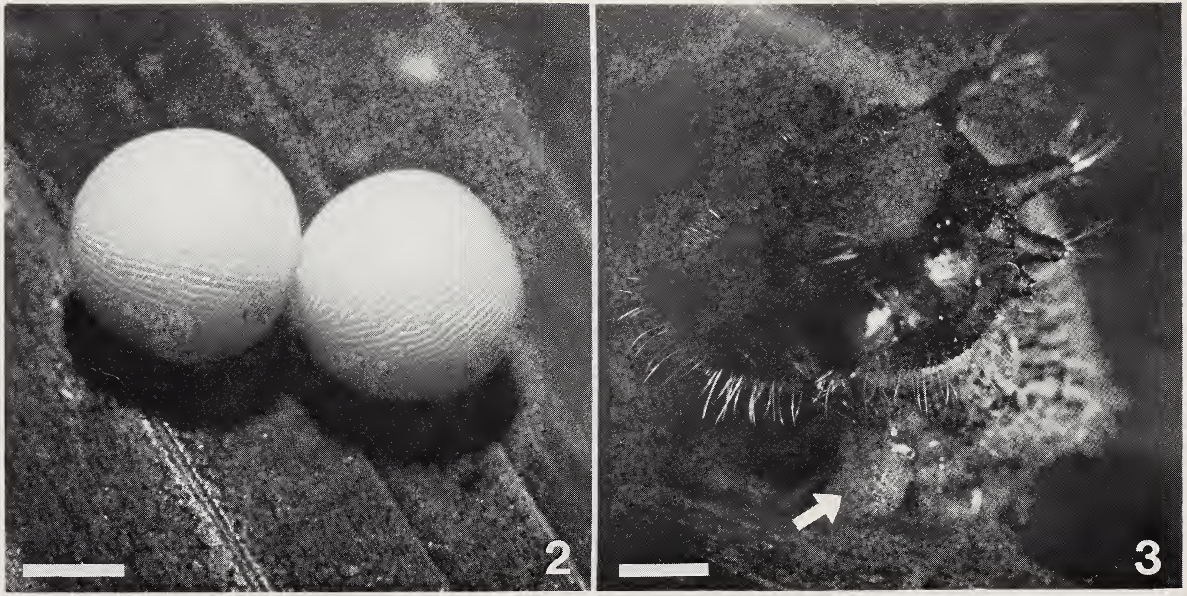
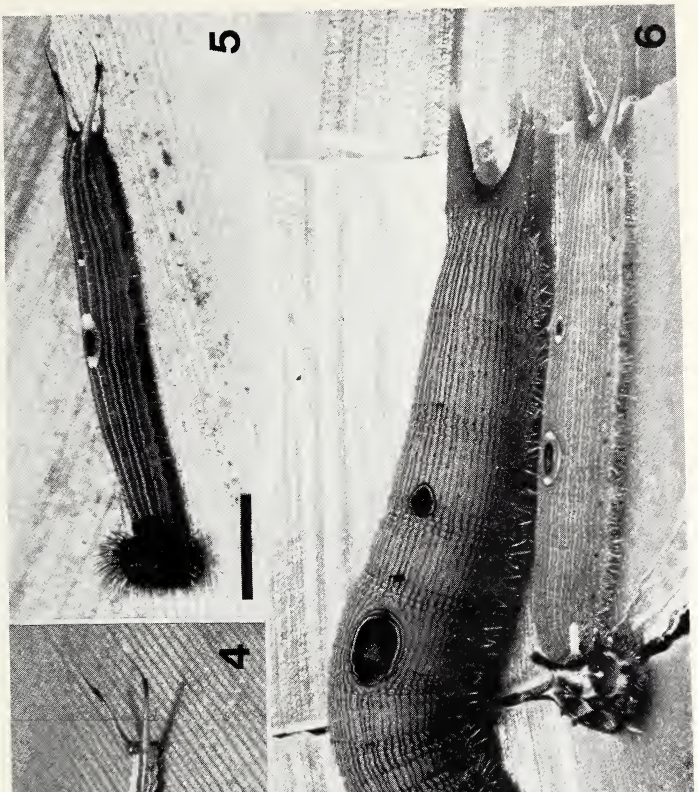
[2] Of the remaining four, one died as a first instar, one sixth instar was killed for preservation, and two underwent poor pupations.



Figures 2 and 3. 2. Eggs. Scale = 1 mm. 3. Fifth instar larva (individual no. 4) displaying everted prothoracic gland. Scale = 2 mm.



Figures 4–6. 4. Early first instar larva (individual no. 1). 5. Late first instar larva (no. 1). 6. Fifth instar larvae (no. 1 (small) and no. 4 (large)). Note that no, 4 has “final” instar head capsule. All scales = 3 mm.

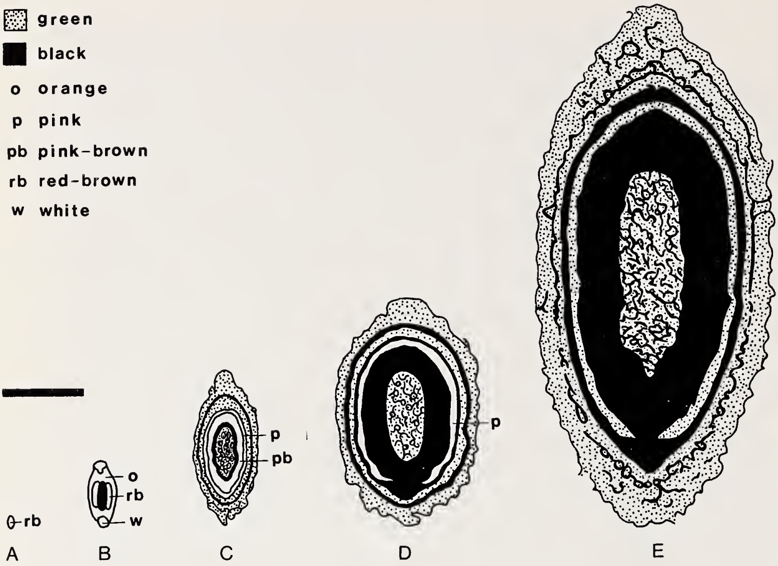


Figure 7. Dorsal spot at junction of abdominal segments 3 and 4. A: early first instar (individual no. 1); B: late first instar (no. 1); C: fourth instar (no. 8); D: early fifth instar (no. 4); E: late fifth instar (no. 12). Scale = 2 mm.

spent in any given instar was 9.6 days (range 6–16 days, s: 2.4 days, N= 63). Every larva spent four days molting from each instar to the next: new cuticle formation occurred during the first two days, ecdysis took place on the thrid day, and by the end of the fourth day the new cuticle had hardened. No feeding took place during these four-day periods. These data reveal that the larvae were engaged in molting-related activities approximately 40% of the time, and feeding and resting 60% of the time.

Head capsule

Beginning with the second instar, the head bore four pairs of horns (Figure 9, C and D) radiating from it in a transverse plane perpendicular to the body axis. The larger and most dorsal two pairs were slightly expanded towards their rounded tips, while the smaller and more lateral two pairs were conical. The fine white simple setae which covered the head did not obscure pattern details. Setae on the horns were longer and projected from their tips.

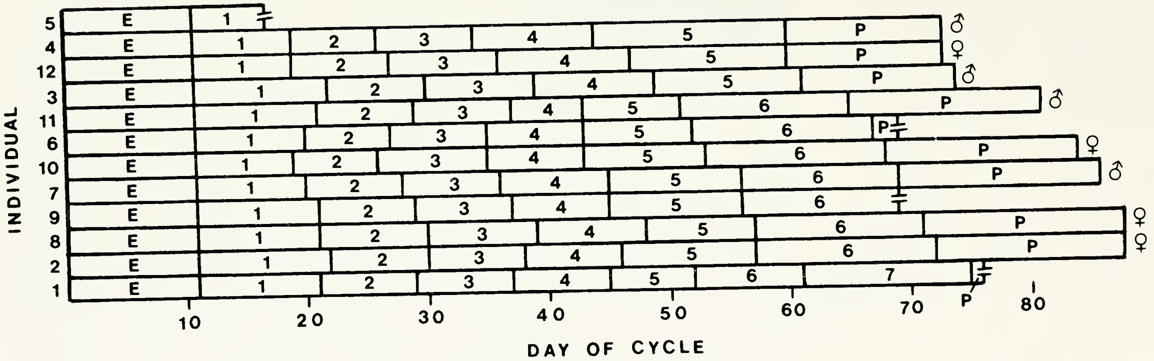


Figure 8. Comparative development of twelve individuals, four of which (1, 5, 6, and 9) did not survive to adult. E = egg; number in rectangles = instar number; P = pupa.

The complex beige, brown, and black head pattern of the second instar persisted through all succeeding instars except the final one. With the final instar, regardless of the number of previous instars, the head capsule took on a new, less complex pattern (Figure 9, E and F) of brown and black. All larvae which attained this new head pattern pupated at their next molt.

Head capsule widths, measured for all instars of each individual, indicate that size variation increased with each succeeding instar (Figure 10). However, the final instar, regardless of number (5th, 6th, 7th), showed slightly less size variation than did the next to last instar, suggesting that once a larva has reached a certain critical size it molts to the final instar, and from there to the pupa.

Body

With growth, the body colors underwent gradual change and additional stripes were added continually. The yellow and green stripes passed through a pale and dark green stage, and finally became dark brown and dark green. In mature larvae they anastomosed slightly.

The large dorsal spot changed from the pattern described for the first instar, to one with a greenish and black center, ringed with black, followed by pink-brown, pink, green, black (narrow), and green (Figure 7C). This pattern gave way to one with a black and green reticulated center, ringed with black (wide), pink (narrow), black (narrow), green (narrow), black (narrow), and green (medium) (Figure 7D). In mature larvae, the central black and green reticulate pattern was surrounded by a wide black ring, followed by rings of green, black, green, black (narrow and irregular), and green (wide) (Figure 7E).

The smaller dorsal spot also changed with growth. Gradually the anterior white portion expanded and encircled the black, and the center became reticulated black and white. By maturity the small spot had become an exact miniature of the larger one.

As larvae reached their full size, four smaller spots appeared, at the junctions of abdominal segments 1–2, 2–3, 4–5, and 6–7. Initially these spots were red-brown, but later changed to black. In addition, the nine pairs of spiracles showed as black spots along the sides of the body (prothorax, abdominal segments 1 through 8).

Caudae

From the second instar on, the caudae lacked apical setae, and

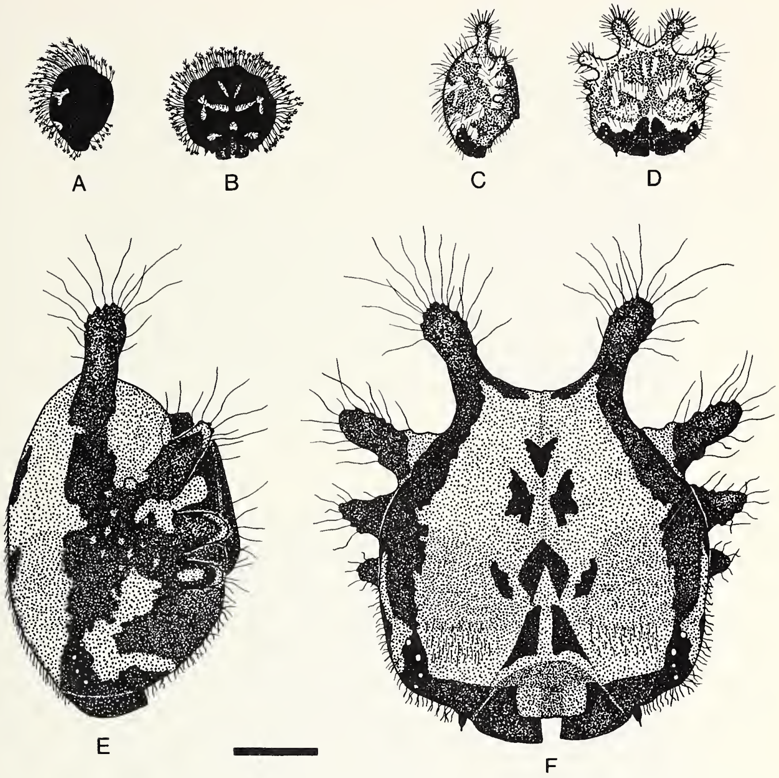


Figure 9. Head capsules of larva no. 3. Lateral (A, C, E) and frontal (B, D, F) views of instars one (A, B), two (C, D), and five (E, F). Scale = 2 mm.

were covered with short appressed setae. With growth the caudae became shorter in proportion to the body, and widened basally, approaching a conical shape in large larvae. Meanwhile, the black portion decreased until only the tips of the caudae were dark. The orange changed to red-brown and at last to dark brown, and the red area disappeared from the tip of the abdomen.

Pupation

Pupation and the processes leading to it took four days. During the first day, the larvae stopped eating, turned dark brown, emptied their guts, and shortened their bodies. The second day was spent crawling upon a support and spinning a silk stalk. During the third day, larvae grasped the stalk with their anal prolegs and hung upside down, and

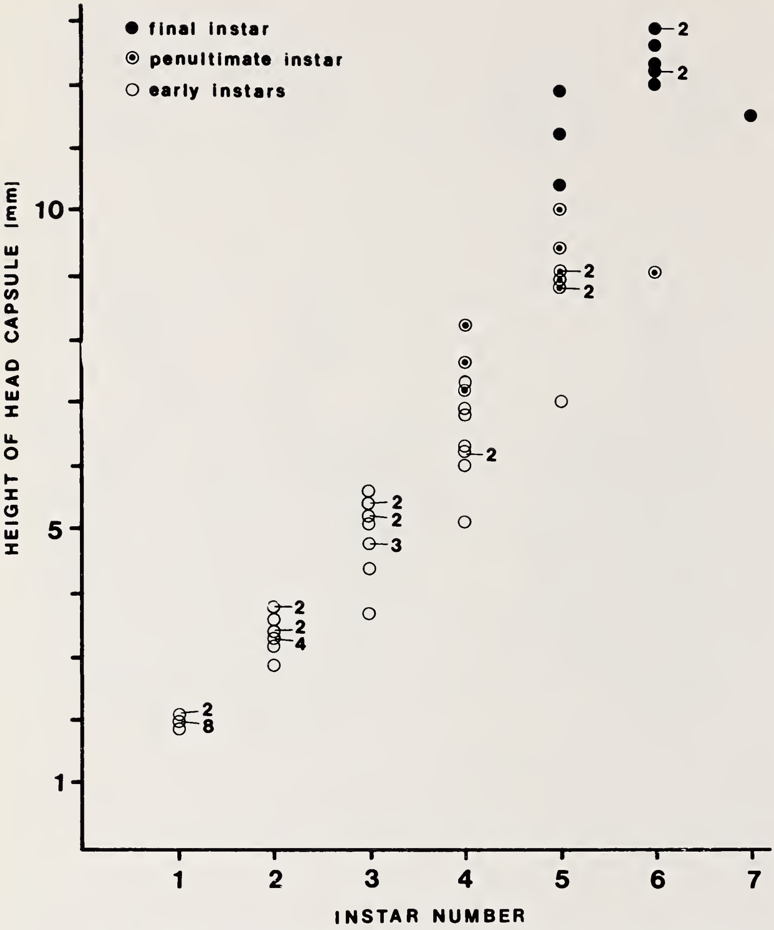


Figure 10. Heights of larval head capsules of each instar. Small numbers indicate frequencies greater than one.

on the morning of the fourth day they shed the last larval skin. By the evening of the fourth day, the pupae were hardened and darkened.

Pupa

Based on the eleven individuals available to us, the pupa (Figure 11) of *Dynastor darius* is about 4 cm long and bears a remarkable resemblance to the head of a snake. Its brown, beige, and whitish

Figure 11. Pupa. Scales = 5 mm.

pattern, coupled with the constriction across the wings, the false scales beneath, the snake-like eyes (located where the true eyes of the adult butterfly will form), and large size give a very convincing illusion of snakeness, despite the fact that the eyes are in the "wrong" position for snake eyes. The question which arises when trying to understand such resemblances, is, "what good does it do to mimic a snake if, during those precious moments when your surprised predator hesitates, you cannot carry through by turning and running?" The answer may be that the predator itself turns and flees after suddenly coming face-to-face with a realistic "snake" that waves violently back and forth, as does the pupa of *Dynastor darius* when disturbed.

Like many brassoline pupae, the pupa of *Dynastor darius* has two lateral pairs of keels. The first begins on the outer margin of the wing very near the tornus, and runs across the wing perpendicular to the outer margin, ending at the edge of the discal cell. The second begins near the midpoint of the inner margin and follows that margin to the base of the wing.

The ground color of the pupa is whitish. The ventral side is irregularly striped with fine brown longitudinal lines which become more dense along a line following the spiracles. These lines fade into pseudo-reptilian scaling toward the anterior end of the pupa. Dorsally, the abdomen bears a complex brown pattern of fine lines and spots, which ends abruptly at its interface with the darker, ventral pattern.

The fore wings (concealing the hind wings) are covered with reticulations, which are beige except at the tornal angle where they are brown. The dark tornal angle lies between the keels and is marked off sharply from the rest of the wing by a dark brown line which begins at the midpoint of the inner margin (beginning of the second keel), runs perpendicular to it until reaching the end of the first keel, then turns sharply, following that keel to the outer margin where it joins the dark line which follows the spiracles.

The eye is beige with tiny black spots and is surrounded by a fine black line.

The pupal stage lasts an average of 15.1 days (range: 13–17 days, s: 1.8 days, $N = 8$). The day before eclosion, the pupa turns dark brown. The dorsal pattern of the fore wings begins to show through the pupal integument several hours before emergence of the adult butterfly.

DISCUSSION

The life cycle

Burmeister's (1873) brief description and figure of a last instar larva of *Dynastor darius* from Rio de Janeiro agrees with our observations in all important respects, differing only slightly in details of the dorsal spots and the color of the head. The dorsal spots of Burmeister's larva were described as "oval eyes, black, with a yellowish pupil, surrounded by a white outer margin, bordered with black." It is not surprising that descriptions of the complex and ever changing dorsal spots would vary. The black and green reticulated center might be interpreted as dull yellow from a distance, the dark green or brown might be seen as black, and the outermost green rings, which blend with the pattern of the rest of the body could easily be overlooked. The head of Burmeister's specimen was "yellow-brown with a large dark maroon spot on each side immediately in front of the horns which are of the same color." His observations may have been made from a newly molted, partially darkened individual, or Brasilian specimens might be paler than Panamanian ones.

During a long visit to southern Brasil, Müller (1886) reared *Dynastor darius* from egg to adult, but did not describe the egg. His larva passed through five instars, the period from hatching to adult lasting 71 days. His detailed description notes changes in the dorsal spots and in the exact number of stripes present on the body. Our larvae showed considerable variation in number of body stripes among individuals of the same size. Müller's first instar was "red-brown and white," in contrast to ours which were red-brown and yellow. As did Burmeister, Müller also described the dorsal spots as having a yellow center. His pupa was "greenish white with very dense, fine, irregular long brown stripes." All eleven of our pupae were brown. Perhaps the pupal color varies geographically, genetically, or depends upon light conditions during or prior to pupation.

Rothschild (1916) briefly described and figured the last instar larva and pupa of *Dynastor darius* from an unpublished sketch by E. Hartgen, in the Tring Museum Library. The larva, as far as can be determined, was essentially the same as ours. Rothschild's figure of the "deep grass-green" pupa is difficult to interpret; the wings appear to cover the dorsal rather than the ventral side of the body. Being a figure from a sketch, perhaps something was lost in translation.

None of these authors made reference to the snake-like appearance of the pupa. The resemblance may not be so obvious in green pupae.

Ontogenetic variability

With respect to the number of instars of *Dynastor darius,* the situation may be similar to that of *Manduca sexta* (Sphingidae). The larvae of *M. sexta* initiate the sequence of events leading to pupation at a critical weight, independent of the rate of growth (Nijhout and Williams, 1974a, 1974b). Like *Manduca, Dynastor* exhibits variability in the number of larval instars, corresponding with variability in growth rate, and it appears that the larvae commit themselves to pupation when a critical size is reached. In contrast to *Manduca* however, commitment in *Dynastor* may take place during the next to last instar, as evidenced by the fact that the final instar always has a head capsule pattern different from that of previous instars. Another possibility is that there may be two commitments: one to the final head capsule pattern, and another to pupation.

Preserved material (head capsules, pupal skins, adults, and larvae in alcohol) of *Dynastor darius,* upon which this study was based, labeled as Lots 78–75 (an individual collected as a pupa) and 78–84 (reared from eggs), has been deposited in the Museum of Comparative Zoology, Harvard University.

We would like to thank the Smithsonian Tropical Research Institute, Panama, for use of their facilities, Mr. Gary Stump for locating a wild pupa of *Dynastor darius* on BCI, Mr. Nigel Franks for assisting with rearing, Mr. Gordon B. Small for identification of the butterfly, and Mr. Norman Woodley for reading the manuscript.

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A CLOSE RELATIONSHIP BETWEEN TWO SPIDERS (ARACHNIDA, ARANEIDAE): *CURIMAGUA BAYANO* SYNECIOUS ON A *DIPLURA* SPECIES*

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Spiders are known to be strictly carnivorous and, moreover, often cannibalistic as well. Yet some animals have achieved a status of close coexistence with several spiders, notably web spinners. Web-building spiders do not change web sites frequently. They are rather sedentary (Turnbull, 1964), which makes their webs a suitable habitat for associates. Some wasps (*Eumenidae,* for example) build their mud nests within the webs of the "social" spider *Anelosimus eximius* (Vollrath, in prep.) whose webs also harbor certain moth larvae (Robinson, 1977a) and Hemiptera (Vollrath, in prep.). The most striking examples of coexistence, however, are the kleptoparasitic spiders of the genus *Argyrodes* (Theridiidae) that inhabit the snares of many web-building spiders (Brignoli, 1966; Robinson and Robinson, 1973; Vollrath, 1977).

In this article I describe some aspects of the biology of another spider that lives in close association with a web-building spider. It is the only spider known so far that is unable to capture its food but has to rely on its host to catch and, even further, to predigest the prey.

CURIMAGUA AND *DIPLURA*

Curimagua bayano (Symphytognathidae; Forster and Platnick, 1977) has only been found riding on the cephalothorax and crawling on the webs of *Diplura* sp. (undescribed species of Mygalomorphae, specimen in the American Museum of Natural History) in Panama. Although the diplurid host is not uncommon in different localities in the monsoon forest at Pipeland Road (Canal Zone), only in the Bayano limestone cliffs (the stream banks of the Río Majé and Río Tigre) did their webs harbor *Curimagua.* On a recent trip to Iquitos,

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Peru, I found a similar association between a *Curimagua* and a *Diplura* in the "white sand forest" of Mishana.

Diplura sp. is a beautifully colored spider that measures up to 4 cm in length and builds sheet- or funnelwebs spreading up to 50 × 50 cm. The spider rests in the entrance of its retreat, a silken tube, waiting for prey to fall onto or crawl over the sheet. The prey is bitten in a sudden lunge and dragged into the retreat for consumption. In a few minutes the prey (e.g., a cricket) will be a mushy and liquified body, due to the combined action of the masticating movements of the relatively large chelicerae and the regurgitated digestive enzymes of the spider. *Diplura's* prey, as judged from the remains, seems to consist mainly of beetles (Coleoptera), crickets (Gryllidae), and ants (Hymenoptera). Millipedes (Diplopoda) and tailless whipscorpions (Amblypygi) were also found, as was a partly digested dendrobatid frog (Anura, *Dendrobatas auratus*).

In contrast to the diplurid host, *Curimagua bayano* is a tiny, mitelike spider. The pale body of the adult female is globular and measures not more than 1.3 mm in length. The male is equally small; for exact measurements, see Forester and Platnick (1977). *Curimagua bayano* was found in the retreats of several webs of *Diplura*. The highest number per host was three females and one male, all in the relatively small web (30 × 30 cm) of a male *Diplura*. An egg case which was also found in the host's retreat, and which was assumed to be of curimaguan origin, consisted of four small eggs incorporated into a transparent and fluffy sphere (diameter 0.8 mm) of loosely spun silk. *Curimagua* crawls about between the silken threads of the host retreat, several centimeters behind the entrance, near the place where the host feeds. Because of its minute size, *Curimagua* has no difficulty in negotiating the fine mesh of silk. Often the animals were observed riding on the diplurid, perched on the center of its cephalothorax, apparently clinging to the fine hairs that cover it. Even their host's violent lunge for prey does not shake them off. I never saw the host react to *Curimagua* crawling about in the web or traversing the body of the host, even when it moved across the host's eyes (Figure 1). *Diplura* collected on Pipeline Road (where *Curimauga* was absent in ten *Diplura* webs inspected) also showed no hostile reaction when *Curimagua* climbed "aboard," suggesting that instead of being ignored the associate may not be perceived by its host.

Figure 1. The mygalomorph spider *Diplura* sp. in its silken retreat, feeding on a grasshopper. Perched on its eyes and on its chelicerae is the symphytognathid associate *Curimagua bayano.*

When I brushed *Curimagua* off the dipluran cephalothorax, they crawled about in the web and, as soon as contact was made with an extremity of the host, they started to climb it to regain their former position. During an experiment, a *Curimagua* female was taken from the back of a *Diplura* and confined to a Petri dish (diameter 5 cm) with another mygalomorph spider of approximately the same size as the diplurid. The *Curimagua* did not attempt to mount this spider.

FOOD OF *CURIMAGUA*

Scanning photographs of a female *Curimagua* taken in frontal view of the "head" region (frontal ridge of cephalothorax: clypeus) show the distinct feature of this group, that is, the pedipalpal coxae lack the palpae (Figure 2). The coxae and the clypeus form a circular depression which is densely covered with fine hairs as well as trichobothria. The chelicerae — which in spiders are normally used to hold and kill prey — are tiny and fused at the bases (see also Forester and Platnick, 1977). Moreover, the chelicerae are located deep inside the mouthlike basin. Therefore, I consider it unlikely that they could be used to hold or tear even the smallest prey, thus restricting *Curimagua* to liquid food. I confined *Curimagua* to Petri dishes (diameter 5 cm) which contained a variety of small arthropods (Collembola, Coleoptera, Ricinulei) found in *Diplura* webs, as well as dead food items, but never did I find the spiders feeding on any of these offerings. *Curimagua bayano* shares fused chelicerae with its congenerics (Forster and Platnick, 1977), some of which construct very finely meshed orbicular webs with a diameter of only several mm (Eberhard, pers. comm.). The prey of these free-living congenerics are unknown. Their nets with a mesh size of approximately 125 μ (Patu saladito) may serve to filter for aerial plankton such as pollen and fungus spores (Vollrath, in prep.).

When a *Diplura* that is carrying *Curimagua bayano* is fed an insect, the *Curimagua* climbs forward from its resting position on the central cephalothorax, over the eyes, and down the mighty chelicerae of its host until it reaches the digestive fluids enveloping the prey item. The abdomen of the pirating associate visibly swells and only a few minutes pass before the *Curimagua* climbs back onto the cephalothorax. Individuals moving about in the silk of the retreat are also attracted to a feeding *Diplura,* perhaps alerted by the vibrations generated by the masticating movements of the host.

OTHER ASSOCIATES OF *DIPLURA*

Curimagua is not the only associate of *Diplura* webs. Other spiders (*Mysmenopsis* ssp.; Platnick and Shadab, 1978) have been found by Kraus (1955) in Guatemala, and three species of *Mysmenopsis* (*M. dipluroamigo, M. ischnamigo,* and *M..gamboa*) were observed by Kirkendall (in prep.) in Panama in the webs of three differently sized diplurid spiders. These associates move about in the sheet region of the diplurid web, approaching and catching small insects that failed to attract the host. Some individuals might also move toward a feeding host, but I rarely saw them sharing its prey. Most often their approach is detected by the *Diplura,* which then turns around in the retreat, spreading silk with its long spinnerets and thus hindering the advance of the would-be pirates. I never observed this behavior of *Diplura* directed toward *Curimagua.* The

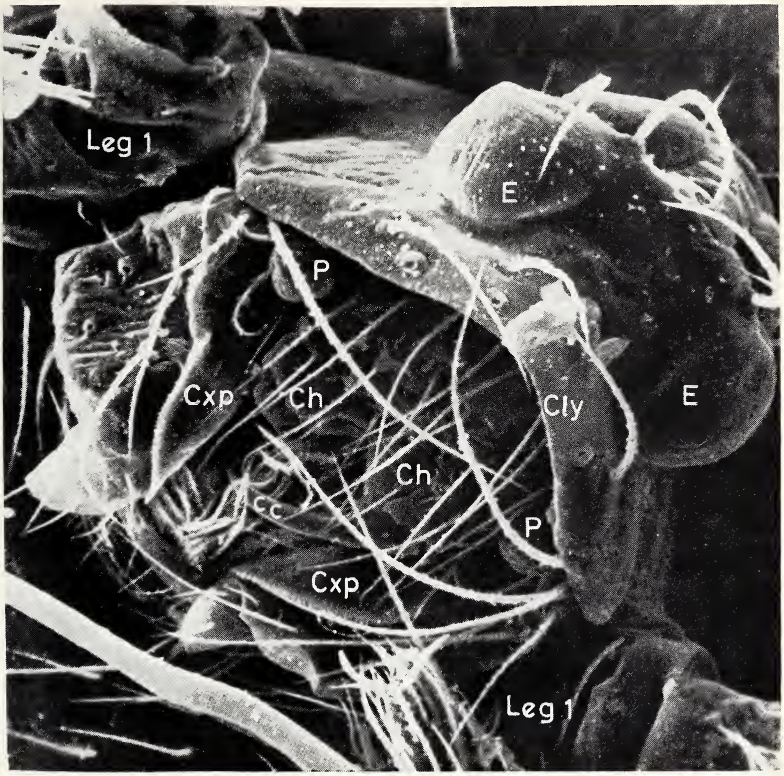

Figure 2. Scanning electron microscope photograph (350×) of the frontal cephalothorax of *Curimagua bayano* showing the two frontal eyes (E), the coxae and trochanter of legs I, the frontal ridge of the cephalothorax (the clypeus = Cly), the coxal processes (Cpx) of the pedipalpae with the reduced pedipalp (P), and, finally, the chelicerae (Ch) with the cheliceral claws (CC).

ability of *Mysmenopsis dipluroamigo* to survive without the "proper" host is shown by the fact that Kirkendall and I found a complex space web in a bush, resembling the web of the "social" spider *Anelosimus eximius* (Simon, 1892). This web (34 × 37 × 27 cm) contained 9 females, 10 subadult females, 16 males, 2 subadult males and 25 juvenile *M. dipluroamigo,* in addition to 2 *Ischnothele guianenesis* (Walck.). Other associates of *Diplura* webs encompass Coleoptera, dipteran larvae (Kirkendall, in prep.), lepidopteran larvae (Robinson, 1977), and therediid spiders of the genus *Argyrodes* (Vollrath, 1977).

DISCUSSION

Curimagua bayano is an extreme case of specialization in spiders. It is the first spider described which is not a predator and not even a carnivore *sensu strictu,* but an ectoparasite or — in the terms of Robinson and Robinson (1977) — a dipsoparasite, resembling, in a way, representatives of another and most successful Arachnid order, the mites (Acarina) which produced many parasite genera (Vollrath, E., 1978). *Curimagua bayano* should not be called a commensal (Gray, 1967) since the fluids imbibed are either the host's costly digestive enzymes (5% protein solution in *Tegenaria 'trica;* Mommsen, 1977) or liquefied prey tissue. In both cases, *Curimagua* deprives its host of nutritive proteins, thus reducing its fitness.

ACKNOWLEDGMEMTS

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SYSTEMATICS AND EVOLUTION OF FOREST LITTER *ADELOPSIS* IN THE SOUTHERN APPALACHIANS* (COLEOPTERA: LEIODIDAE; CATOPINAE)

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The beetle genus *Adelopsis* was described by Portevin in 1907, and was proposed for a microphthalmic soil-inhabiting species from Bolivia. Since then, some 20 additional species have been described, and the genus is known to be distributed through the Neotropics from Mexico to southern Brazil and adjacent Argentina. The species are generally large-eyed and winged, and are probably all scavengers of decaying organic matter in mesic tropical lowland and montane forests. They may occasionally occur in caves. The beetles are seldom represented in collections, but they may be frequently collected by sifting forest litter, or by using dung or carrion-baited pitfall traps. My field program of such collecting in the Neotropics since 1966 shows the genus to be far more diverse, abundant, and widespread than indicated in the present literature (Peck, 1977).

Adelopsis was first found to occur outside the Neotropics when I (Peck, 1973) realized that *Adelops mitchellensis* (Hatch, 1933) from Mt. Mitchell, North Carolina, actually belonged in the genus *Adelopsis*. Some authors had placed the species in the genus *Ptomaphagus*. At that time I noted that I also had material of other species from North Carolina, Georgia, Tennessee, Alabama and West Virginia. My indication that they were also in New Mexico was in error (Peck, 1978). The purpose of this paper is to describe these species which occur in forest litter and soil habitats in the southeastern United States, and to consider their distributional and evolutionary history.

Generic diagnosis. The characters are those of Leiodidae, Catopinae, Ptomaphagini (as given in Peck, 1973). As such they are small beetles with a loose antennal club, with segment 8 always smaller than 7 and 9. They have transverse pronotal and oblique

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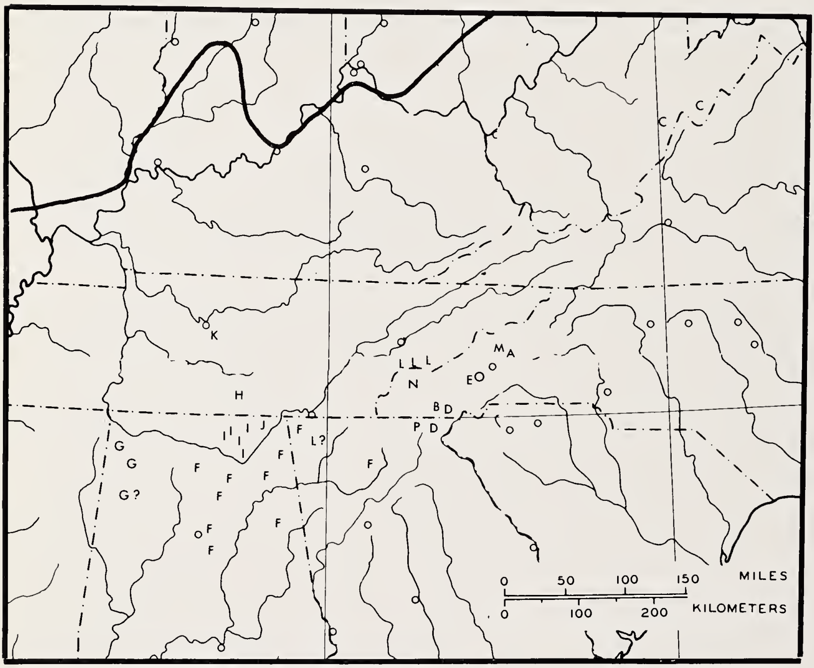
elytral strigae, and the summits of their tibiae are armed with a comb of many short and equal spines, as well as by two longer spurs (see Peck, 1973, 1977 and their cited references).

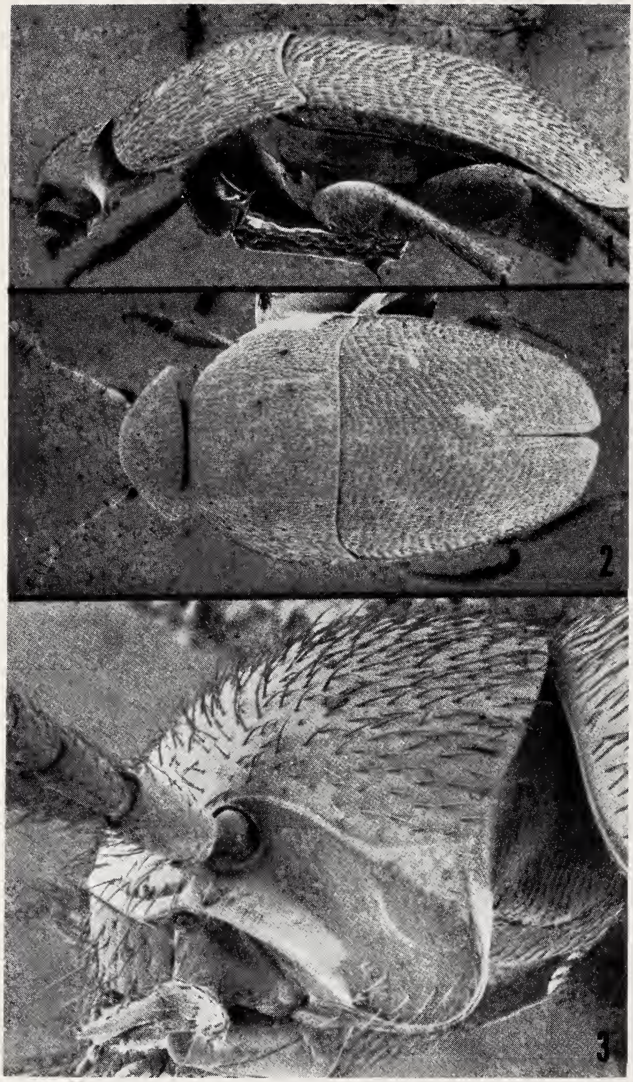
Adelopsis is generally difficult to separate from its nearest neighbor, the genus *Ptomaphagus,* using only external characters. Tropical species of *Adelopsis* (but not those of the U.S.) usually differ by being smaller (length 2.6 mm or under) and in having the antennal club more loosely composed of gradually larger segments, of which the last two are often conspicuously lighter in color. The genera are more reliably separated by the chitinized internal reproductive structures of the aedeagus and spermatheca. In *Adelopsis* the spermatheca (as far as is known) is a more simple curved tube, and the aedeagus has a tip which is more elaborately sculptured, or



Map 1. Distribution of known species of *Adelopsis* in the southeastern United States. Heavy irregular line indicates maximum extent of Pleistocene glaciations. A, *A. mitchellensis.* B, *A. steevesi.* C, *A. alleghenyensis.* D, *A. suteri.* E, *A. richlandensis.* F, *A. appalachiana.* G, *A. jonesi.* H, *A. bedfordensis.* I, *A. cumberlanda.* J, *A. scottsboroensis.* K, *A. nashvillensis.* L, *A. fumosa.* M, *A. alta.* N, *A. joanna.* O, *A. pisgahensis.* P, *A. orichalcum.*

is broader and more blunt. The orifice is dorsally sub-terminal and cuts the left side of the aedeagus as in *Ptomaphagus*. The southeastern U.S. *Adelopsis* species are all forest litter and soil inhabitants. They are all wingless and have eyes reduced to a collection of about 20 pigmented facets. These structural features will help to distinguish them from most *Ptomaphagus,* which are either winged and with larger eyes, or are more subterraneanly adapted (for life in caves) and have more-reduced eyes.

Description. The following applies only to the range of variation known in the species in the southeastern U.S. Additional details on Neotropical species may be found in Jeannel (1936) and Szymczakowski (1964, 1968, 1969, 1975). Length 2.3 to 2.6 mm, width 1.2 to 1.3 mm. Form elongate oval, compact, convex (Figs. 1, 2). Color light to dark reddish brown. Pubescent, with numerous short recumbent hairs. Head finely punctured; eyes reduced to collection of about 20 pigmented facets (Fig. 3); eye width 1/3 width of space from antennal base to head margin across eye. Antennae short, compact; club darker, somewhat flattened; reaching from middle to hind margin of pronotum when laid back; segment 3 shorter than 2, segment 6–10 wider than long; 8 over twice as wide as long (segments usually longer and thinner in upper elevation deep-litter species than in lower elevation litter-soil species). Last article of maxillary palp slightly shorter than preceding; conical, thinner. Pronotum widest 1/3 before base, 1.4 to 1.5 times as wide as long; hind angles acute, hind margin straight; sides arcuate; covered with seta-bearing punctures strongly to faintly organized into striae. Elytra fused, sides gradually tapering to apex in both sexes; external apical angles broadly rounded; sutural angles rounded; apex oblique; strigae distinct, oblique, composed of seta-bearing punctures. Metathoracic (flight) wings reduced to tiny scales. Mesosternal carina low, its notch distinct. Legs not noticeably short and compact (seemingly adapted for running and not digging); protibiae bowed-in, mesotibiae bowed-out, metatibiae straight; comb of spines limited to tibial apex; protibial apex oblique and rounded in both sexes; sexual dimorphism only in protarsi, males with first 4 protarsal segments expanded and spongy-pubescent beneath. Aedeagus curved, stout, blunt, with orifice cutting to dorsal surface through left side; internal sac with curled, short, terminal stylet with surface ridges on one side of tip; about 6 sensory hairs on under



Figures 1–3. SEM photomicrographs of *Adelopsis mitchellensis* (Hatch). 1. Lateral view, left proleg removed. 2. Dorsal view. 3. Lateral view of head showing eye reduced to collection of about 20 poorly defined facets.

surface of each side of tip. Parameres fused to aedeagus at base; with three terminal hairs. Spiculum gastrale short, thick, less than ¼ its length projecting beyond anterior end of genital plates. Spermatheca thin and curved; anterior recurved and often with flattened crest; posterior end often laterally curved-back on itself.

Bionomics. The known United States species are all inhabitants of moist moss, litter, and soil of forests in the Appalachian Mountain Chain, south of the limits of glaciation, from the lowlands inside the Fall-line to the summits of the highest mountains. They are occasionally found in soil-filled rock crevices or under large rocks deeply embedded in forest soils, but are more usually captured by sifting litter and moss and by extracting them with Tulgren-Berlese funnels. The litter at the sides of rotting logs seems to be a favored habitat. They may be locally abundant in association with decomposing fleshy fungi or material richly impregnated with fungal hyphae, but some may be taken at dung or carrion baits in forests, or in caves. The frequency with which they have been collected in caves reflects only that this is a way by which a collector can gain easy access to the faunas of deep soils. In caves, the beetles are found near cave entrances only and not in the deep regions of caves. The beetles are not morphologically adapted for caves as such. This is evident when they are compared to cave-evolved species of *Ptomaphagus* (Peck, 1973), so they should be termed edaphophiles (or endogeans or edaphobites), rather than troglophiles, or troglobites. In litter, they seem to be more frequently encountered in the springtime and early summer, probably because they are more commonly present in the upper layers of litter and soil which are cool and moist at these seasons. They probably retreat downwards with the increasing warmth and dryness of summer. Records do not indicate it, but I think they would be active and accessible to the collector in the late fall and at certain times of the winter as well.

Life cycle characteristics have been determined only from specimens captured on several occasions in Morrison's Cave, Dade County, Georgia, and kept in laboratory culture at 15°C. The techniques are those used in culturing *Ptomaphagus* beetles (Peck, 1973, 1975). Eggs are laid singly by the females on the soil surface of the culture vessel. These hatch in a mean time of 12 days (range 9–15, $n = 7$). There seem to be three larval instars, and these feed for about 20 days before constructing a mud igloo or pre-pupation cell, in which the larvae spend a mean of 14 days (range 12–16, n = 7) before pupating. The total larval duration then has a mean time of 34 days (range 23–40, n = 7). The pupal stage lasts for a mean of 20 days (range 14–24, n = 6), and pupal darkening is evident for the last two days before eclosion. The newly emerged adult remains in the pupal chamber for 5 days (n = 3) before emerging. The cycle is similar to that of several litter and cave species of *Ptomaphagus* at the same temperature (Peck, 1973, 1975, and unpubl.). Total longevity of adults is unknown. Adults of unknown age collected in April lived in culture for up to 10 months. Oviposition frequency could be determined for only one paired female which laid 9 eggs in 30 days at intervals of from 1 to 10 days.

The larvae are very similar to those of *Ptomaphagus* and I am unable to confidently distinguish the two. There is no strong evidence for seasonality in reproduction. In caves (and deep soil?) it may occur whenever moisture and food conditions are suitable and this probably holds for forest litter situations with cool-moist seasons being better than warm-dry ones.

Systematics

Methods and Materials. Specimens were borrowed from the following collections and curators: American Museum of Natural History (AMNH), Lee Herman; Field Museum of Natural History (FMNH), Henry Dybas; Illinois Natural History Survey (INHS), Milton W. Sanderson; United States National Museum (USNM), John Kingsolver; Museum of Natural History, University of Alabama (UANH), Herbert Boschung; Museum of Comparative Zoology (MCZ), John Lawrence and Alfred Newton. Specimens not attributed to these collections are in that of the author. Types are deposited in the Canadian National Collection (CNC) unless otherwise indicated. Initials of collectors who frequently found material are as follows: SBP, Stewart B. Peck, often helped by Alan Fiske, James Peck, and Jarmila Peck; WBJ, the late Walter B. Jones, often helped by A. Flannagan, J. M. Valentine, and others; HRS, Harrison R. Steeves, Jr., often helped by J. Patrick. WRS, Walter R. Suter. All HRS and WRS material is in the FMNH.

My collecting methods are described in sufficient detail elsewhere (1973, 1977, and Newton and Peck, 1975) and need not be repeated. This is also true for the methodology of specimen preparation, with one major exception. A scanning electron microscope (SEM) was found to be of great help in viewing and understanding the three-dimensional structure of the tips of the minute aedeagi. With this understanding, they can be more easily interpreted in the usual slide or glycerine jelly mounts and preparations. SEM photomicrographs were used to make the drawings of the aedeagal tips. A set of three views is usually necessary to interpret and understand the geometry of the aedeagal tip. Although a set of about 6 hairs occurs on each side of the undersurface of the aedeagal tip in all species, these have little value in helping to characterize the species. These hairs have been shown on only a few drawings. Internal sacs were fully seen only in polyvinyl-lactophenol slide mounts.

Variation. Little variation is evident in these species, and little is known of variation within the other species of the genus. Variation over the geographic range of a species is known and illustrated only for *A. simoni* (Portevin), known from Brazil, Venezuela and Mexico (Szymczakowski, 1968) and in *A. brunneus* Jeannel, from cave and forest sites from Columbia through Venezuela to Trinidad (Szymczakowski, 1975). Apparent variation in spermathecae is partly due to the difficulty in preparing these fragile structures. When material is limited and the normal spermathecal shape is not known with certainty, several may be illustrated.

Individual diagnoses are not given in the following species accounts. In all cases it would indicate that the species are characterized by the combination of characters of their geographic ranges, and of the aedeagal tips, and possibly of the spermathecae.

The gender of the genus is treated as feminine, following the use of its author.

The *mitchellensis* species group

This group is probably not a closely related assemblage, and is used as a grouping of convenience. Each of the five species is clearly defined, and each may be as phyletically old as the cluster of 11 species placed in the following *appalachiana* species group.

1. *Adelopsis mitchellensis* (Hatch)

Figs. 1–5, 50

Adelops mitchellensis Hatch, 1933: 208. Synonymy given in Peck 1973: 55.

Material seen. North Carolina. Yancey County. Mt. Mitchell, no other data, holotype male, allotype female, and paratype male 50133, USNM. Mt. Mitchell 4500–6000′ (=1475–1967 m); 17–24.VI.

1939, E. D. Quirsfeld, 1 male, MCZ. Mt. Mitchell, 6400′ (2098 m), 3–10.IV.1967, S. Peck, carrion trap 214 in summit hemlock and moss forest, 1 female. Black Mountains, no other data, 1 female, USNM; 1 female, FMNH. Black Mts., 8.VIII.1911, 2 females, AMNH.

Description. Aedeagus (figs. 4–5) with dorsal section of tip flattened and projecting posteriorly over orifice on upper left side. Ventral section broad with central ogival point. Spermatheca fishhook-like (fig. 50) with simple posterior portion, and prominent crest on anterior end.

Distribution. The species is probably limited to the Black Mountains of Yancey County, containing Mt. Mitchell, the highest point in the eastern United States (2191 m). This is the only locality known to have two species of *Adelopsis,* for here *A. mitchellensis* is sympatric with *A. alta.* Some early collection records confused these two.

Notes. The species is probably most common in the upper elevation forests of spruce-fir or birch-maple. Adults have been collected in April, July, August, and September.

2. **Adelopsis steevesi** n. sp.
Figs. 6, 7

Holotype male and allotype female in CNC. Type data: North Carolina. Macon County. Norton, Coweeta Hydrological Laboratory, 24.X.1965, 4,000′ (1311 m), log-litter, HRS. Paratypes: 17 with same data; 12 with same data but 22.V.1965, 4100′ (1344 m) rot wood debris.

Description. Dorsal section of aedeagus tip (figs. 6–7) incised, upraised as knob on left, and as flattened vertical blade on right. Ventral section deeply emarginate, nearly same length as dorsal section. Spermatheca similar to that of *A. joanna, A. alta, A. fumosa, A. richlandensis,* and *A. suteri.*

Etymology. Named for Mr. Harrison R. Steeves, Jr., of Birmingham, Alabama, in recognition of his extensive field collecting of litter beetles in the southeastern United States (collection deposited in FMNH).

Distribution. The species should be expected in other sites in the vicinity of Highlands, North Carolina.

3. **Adelopsis alleghenyensis** n. sp.
Figs. 8–10, 51, 52

Holotype male and allotype female in CNC. Type data: West Virginia. Pendleton County. 5 mi (8 km) S Witmer, 3000′ (915 m), 16.VII.1971, SBP, litter Ber. 217. Paratypes: 11 with same data; Spruce Knob, 3500′ (1148 m), 8.VI.1967, SBP. Ber. 58, 1 male and 1 female; Pocahontas County, Hills Creek Falls, 19.VI.1971, W. Shear, Berlese, 2 males and 2 females.

Description. Dorsal section of aedeagal tip low and simple (figs. 8–10), with recurved flange on left; ventral section broadly pointed, with tip downcurved, extending far beyond dorsal section. Spermatheca (figs. 51–52) thick and gently curved, anterior crest large.

Etymology. The name refers to the northwestern flank of the Appalachians called the Allegheny Mountains, lying along the border of Virginia and West Virginia and extending into Pennsylvania.

Distribution. The species probably has a wider range than the known 60 mile (100 km) long NE-SW line along the Allegheny Mountains of West Virginia.

4. **Adelopsis suteri** n. sp.
Figs. 11, 12, 53, 54

Holotype male and allotype female in CNC. Type data. Georgia. Rabun County. Mountain City, Black Rock Mountain State Park, 15.VI.1973, W. R. Suter, litter at log under *Rhododendron.* Paratypes: 1 with same data; Black Rock Mountain State Park, 3000′ (915 m), 21.VII.1967, 2 males. North Carolina. Macon County. 5 mi (8 km) NE Highlands, 27.X.1969, W. Shear, *Rhododendron* litter, 1 male. Jackson County, 7 mi (11 km) S Cashiers, 11.VI.1973, Whitewater Falls, elm-maple pseudofork, WRS, 1 female.

Description. Dorsal section of aedeagal tip (figs. 11–12) inflated, upturned, with broad and shallow depression in middle, equal in length to uniformly emarginate ventral section. Spermatheca (figs. 53–54) with sharp bend in posterior end, which projects strongly above plane of central curved section, anterior crest high.

Etymology. Named for Dr. Walter R. Suter of Carthage College, Kenosha, Wisconsin, in recognition of his extensive collecting

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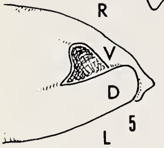

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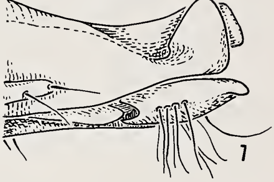

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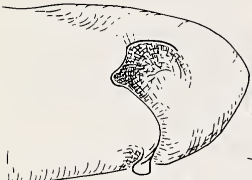

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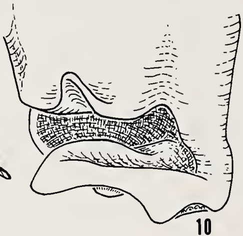

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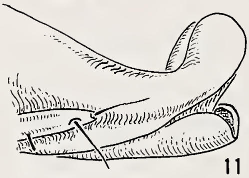

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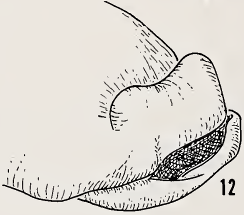

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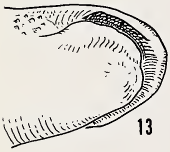

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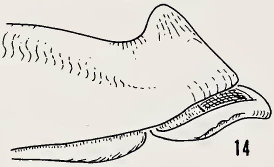

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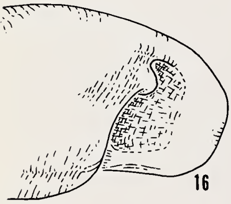

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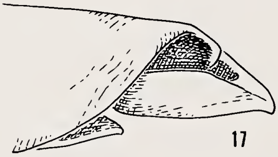

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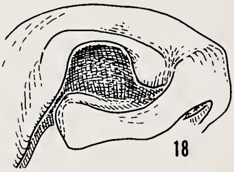

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of litter beetles in the southeastern United States (collections deposited in FMNH).

Distribution. The species is to be expected in other localities in the Coweea Mountains in the vicinity of Highlands, North Carolina, which has been found to be a region rich in species of ground dwelling beetles.

5. **Adelopsis richlandensis** n. sp.

Figs. 13, 14, 55, 56

Holotype male and allotype female in CNC. Type data. North Carolina. Haywood County. Richland Balsam, 6000′ (1967 m), 7–26.VIII.1965, S. & J. Peck, carrion trap. Paratypes; three females with same data; and 1 female, Haywood-Jackson Counties, Rinehart Knob, 6000′ (1967 m), 1.VIII.1960, T. C. Barr.

Description. Dorsal section of aedeagal tip (figs. 13–14) uniformly rounded, but with slight emargination; sloping downwards from high crest on right to low and flat left side, ventral section uniformly rounded and projecting beyond dorsal section. Spermatheca as in figs. 55–56, characteristic form not known with certainty.

Etymology. The name refers to Richland Balsam, the type locality, and highest point on the Blue Ridge Parkway.

Distribution. There seems little reason to expect only this species on Richland Balsam. Mt. Pisgah, with *A. pisgahensis,* is on the same mountain ridge and there are no intervening lowland barriers to dispersal of these flightless beetles. Soco Gap and Balsam Gap to the northwest, each above 3000′ (1000 m) separate Richland Balsam from the Plott Balsams and Balsam Mountains, but these also seem inadequate barriers to isolate Richland Balsam from species inhabiting these other mountain regions. Intensive collecting should resolve the questions of how these species are distributed with regards to each other.

Figs. 4–18. Structures of *Adelopsis.* 4. Left lateral view of entire aedeagus of *A. mitchellensis,* with internal sac (IS), ventral blade of tegmen (VBT), and dorsal (D) and ventral (V) sections of aedeagal tip. 5. Dorsal view of aedeagal tip of *A. mitchellensis* indicating right (R) and left (L) sides, and dorsal (D) and ventral (V) sections of the tip. 6–7. Dorsal and lateral views, aedeagal tip, *A. steevesi.* 8–10. Dorsal, lateral, and posterior view, aedeagus, *A. alleghenyensis.* 11–12. Aedeagal tip. *A. suteri.* 13–14. *A. richlandensis* aedeagal tip. 15. Internal sac *A. appalachiana.* 16–18. *A. appalachiana,* note that parameres and hairs on ventral surface of ventral section of aedeagus are not shown in most drawings.

The *appalachiana* species group

This group is seen as a naturally based and closely related phyletic unit. It is based on *A. appalachiana,* the most widespread species in both lowland and montane regions. Progressive modification of the relatively simple aedeagus (assumed to be generalized and pleisotypic) in the nominate species could readily produce the other aedeagal types known in the group.

6. **Adelopsis appalachiana** n. sp.

Figs. 15–18, 57–60

Holotype male and allotype female in CNC. Type data: Alabama. DeKalb County. Fort Payne, Manitou Cave, 1937, W. B. Jones, trap. Paratypes: 49 with same data; 8 with same data except 1939; and the following: *Alabama.* DeKalb County. Kelly Girls Cave, 1 mi (1.6 km) SE Collinsville, 25.VIII.1965, SBP, 2; Cook Cave (Ala 253), 13.VIII.1958, WBJ, 2; Lykes Cave, 27.VIII.1965, SBP, fungus on entrance talus, 22; Cherokee Cave, 4.5 mi (6.5 km) NE Ft. Payne, 15.VIII.1967, SBP, 1. Blount County. Blount Springs, 19.III.1966, SBP, litter in limestone crevice, 1; 7 mi (11 km) S Cleveland, outside Horseshoe-Crump Cave, 28.VI.1967, SBP, litter Ber. 70, 2; outside Bangor Cave, 19.III.1966, SBP, rotten tree roots, 4; outside Bangor Cave, 5.IV.1967, SBP, 1; inside Bangor Cave, 20.XII.1965, SBP, 1; near Inland Lake, 28.IX.1958, HRS, forest floor debris, 4. Shelby County. Helena, 3.I.1959, HRS, treehole, 1. Jefferson County. Near Purdy Cave #1, 13.IX.1958, HRS, forest debris in rock crevice, 1. Morgan County. 3½ mi (6 km) SE Fayette, 21.V.1972, SBP, Ber 241, litter outside cave entrance, 14. *Georgia.* Dade County. Morrisons Cave 13.VII.1967, SBP, 6; 16.IX.1968, SBP, 1; 16–23.VI. 1972, SBP, 3; 4 mi (6.5 km) NE Rising Fawn, 15.VII.1967, SBP, forest litter Ber 78, 4; Johnson Crook Cave #2, 4 mi (6.5 km) NE Rising Fawn, 14.VII.1967, SBP, 2 in cave entrance; outside Johnson Crook Cave #2, 14.VII.1967, SBP, 6 in litter.

Tentatively associated material. *Alabama.* Etowah County. Wright Cave, 11.VII.1958, WBJ, 1 male, 1 female. Morgan County, Inge Cave, 2.V.1959, T. C. Barr and HRS, under debris, 2 males. Cleburne County, Cheaha Mountain State Park, 330 m, 13.VI.1967, SBP, litter Ber 59, 2. Marshall County. Guntersville, near Griffith Cave, 30.IV.1960, HRS, 1 female; Kelly Ridge Cave, near Warrentown, 23.VIII.1958, HRS, 1 female. *Georgia.* Walker County.

McLemore Cove, 9 mi (15 km) SW LaFayette, 14.VII.1967, forest log litter Ber 79, SBP, 3. Dawson County. Mt. Oglethorpe, 2000′ (610 m), 20.VIII.1967, SBP, litter Ber 80, 1 damaged male.

Description. Dorsal section of aedeagus tip (figs. 16–18) regularly curved, unadorned, shortest on left side and longest on right; ventral section regularly curved with downturned tip; posterior view with dorsal section forming a uniformly arched genital orifice, with a uniform border; setae on ventral surface lying in groove rather than separated depressions. Internal sac thick, not narrowed into curved tube at apex (fig. 15). Spermatheca (figs. 57–60) smoothly curved, anterior part broadened and without crest, posterior part recurved off structural plane.

Variation. The Morgan County, Alabama, sample has a lower arch, with a flattened middle to the genital orifice when seen from behind. This opening is most highly arched in the Cheaha Mountain, Alabama, male which also has a differing left margin to the ventral section.

Etymology. The name refers to the Appalachian Mountains, around the southern end of which this species is distributed.

Distribution. This is the most widely distributed species, ranging from north-central Alabama, south of the Tennessee River, eastwards into northwestern Georgia.

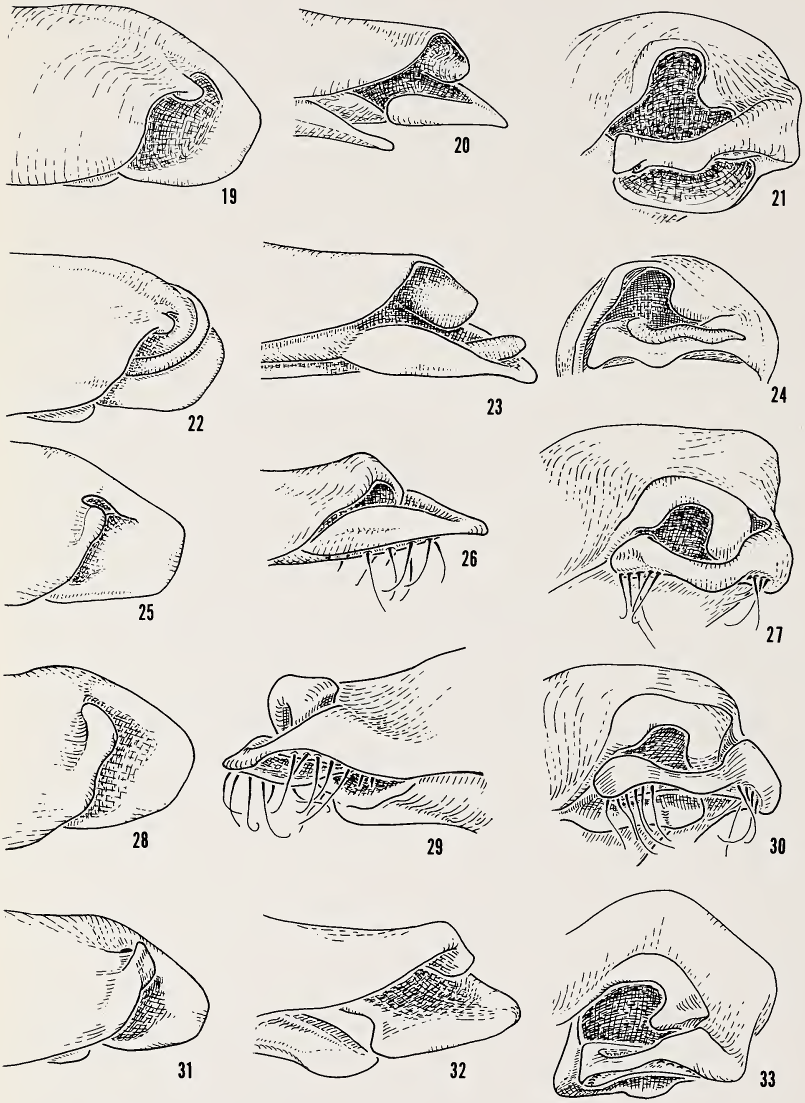
Field Notes. This is the most frequently collected species because it has a wide range, and occurs in a region which has received much collecting attention. It has been found in forest litter and in the entrance zone of caves, in the months of January, March, May, June, July, August and September. It is probably active throughout the year.

7. **Adelopsis jonesi** n. sp.

Figs. 19–21

Holotype male in CNC. Type data. Alabama. Colbert County. Wolf Den Cave (Ala. 83), near Maude, 25.IX.1940, W. B. Jones.

Tentatively associated material. Alabama. Colbert County. McClusky Cave, near Maude, 15.IX.1940, WBJ, 1 male missing aedeagus; Gist Cave, 13.V.1940, WBJ, 2 females. Franklin County, The Dismals, 30.VIII.1958, HRS, forest floor debris, 1 female. Hale County. Moundville State Park, 7.VII.1967, SBP, log litter Ber 75, 3 females. Tuscaloosa County. No other locality, VI, Alabama Museum Expedition, 1 female (UANH).



Figs. 19–33. Views of aedeagal tips of *Adelopsis*. 19–21. *A. jonesi*. 22–24. *A. bedfordensis*. 25–27. *A. cumberlanda*. 28–30. *A. scottsboroensis*. 31–33. *A. nashvillensis*. Scale of aedeagal tips approximately equal.

Description. Dorsal section of aedeagal tip with highly raised edge forming large arch over genital orifice (figs. 19–21); ventral section smoothly rounded. Spermatheca of tentatively associated females indistinguishable from those of *A. appalachiana.*

Relationships. This species is easily derived in aedeagal type from *A. appalachiana* by an increased arching of the dorsal section of the genital orifice. It probably represents an isolated and now differentiated peripheral population of the latter.

Etymology. The species is named for the late Dr. Walter B. Jones, of Huntsville and Tuscaloosa, Alabama, who, as former State Geologist and Director of the Alabama State Museum of Natural History, did so much to promote studies of the natural history of the southeast.

8. **Adelopsis bedfordensis** n. sp.

Figs. 22–24

Holotype male in FMNH. Type data. Tennessee. Bedford County. Campbell Cave, 17.I.1960, H. R. Steeves, Jr., under rock in dark zone.

Description. Aedeagal tip (figs. 22–24) with uniformly arching dorsal section without upturned flange in dorsal and lateral views. Genital orifice moderately arched in posterior view and asymmetrical. Internal sac long, thin, and curved.

The aedeagus is difficult to distinguish from that of *A. appalachiana,* except for the striking differences in their internal sacs.

Etymology. The name refers to the county in which the type was collected (and to which it may be approximately restricted in distribution), located in the eastern Highland Rim of south-central Tennessee.

9. **Adelopsis cumberlanda** n. sp.

Figs. 25–27, 61

Holotype male and allotype female in CNC. Type data: Alabama, Jackson County. 5 mi (8 km) N Garth, 19.V.1972, S. Peck, leaf litter Ber 239. Paratypes: 65 with same data; 2 with same date but in dung baited pit traps; and the following: *Alabama.* Jackson County. Paint Rock, Nat Mountain, 15.III.1966, SBP, 3 under log; Keel Cave, Sharp Mt., 11.VI.1940, WBJ, 1; Clemons Cave, Sharp Mt., 9.VI.1940, WBJ, 1; Rousseau Cave, July, 1968, R. Graham, 1; Rousseau Cave, 12.VII.1973, SBP, 4 baited near entrance; Paint Rock, near Crossing (Stewart) Cave, 5.VII.1958, HRS, 2 in rock crevice debris; 5 mi (8 km) NW Princeton, 19.V.1972, SBP, forest litter Ber 240, 1. Madison County. Monte Sano State Park, 17.V.1972, SBP, log litter Ber 238, 5; Monte Sano, Huntsville, 1936, R. Hopping, 2 (UANH). Monte Sano, VI.1937, Ala. Mus. Exped., 1 (UANH); Tumbling Gap (NE ridge of Monte Sano), June 3–8, 1911, H. P. Loding, 2 (UANH); Sharps Cove, 5.VII.1965, SBP, leaf Ber., 1. Marshall County. Grant, Guffey Cave, 25.V.1958, 1 in floor debris in entrance light zone, HRS; Grant, near River Cave, 25.V.1958, 4 under debris at entrance light zone, HRS; Creek Cave, 25.V.1958, HRS, 1 in cave debris; 1 mi N Guntersville Dam, 26.VI.1967, litter Ber 68, SBP; Hampton Cave, Guntersville, 11.VII. 1973, SBP, 1.

Description. Dorsal section of aedeagal tip short (figs. 25–27) thickened and upcurved, especially at right side where small broad tooth exists (best seen from right side); ventral section projecting, tip truncate; posterior view with uniformly broad arch over orifice. Internal sac thick and slightly curved. Spermatheca similar to that in *A. scottsboroensis* (fig. 62) but with more bend in posterior part when seen from right, and with a lower crest on the anterior part.

Etymology. The name refers to the Cumberland Plateau, flanking the NW face of the Appalachian Mountains.

Distribution. The species range is in the forested slopes and valleys of the southern end of the Cumberland Plateau, in northeastern Alabama, north and west of the Tennessee River. This river is a natural boundary of the species range, separating it from that of *A. appalachiana* south of the river.

Notes. The species has been found in moist forest litter and cave entrances in the months of March, April, May, June, July and August.

Relationships. The species is derivable from *A. appalachiana* by an increased arching of the genital orifice, a thickening of the dorsal orifice lip, and an increase in the length of the ventral section.

10. **Adelopsis scottsboroensis** n. sp.
Figs. 28–30, 62, 63

Holotype male and allotype female in CNC. Type data: Alabama. Jackson County. 10 mi (16 km) N Scottsboro, 16.V.1972, SBP, forest litter Ber 237 (from limestone crevices near Tumbling Rock Cave). Paratypes: 6 with same data.

Description. Dorsal section of aedeagal tip short (figs. 28–30) and upturned, with right side free and reflexed; in posterior view right margin of arch above orifice projecting and deflexed to right. Spermatheca thin and uniformly curved as in figs. 62–63.

Etymology. Named for the city of Scottsboro, which sits at the base of a spur of the Cumberland Plateau, near the margin of the drainage basin probably containing the species range.

Distribution. The species should be expected to occur in additional sites below the Plateau escarpment in the headwaters of Mud and Coon Creeks, Jackson County. Some beetles and other invertebrates are known to be endemic to this area, so some general mechanism may have worked to isolate them in this section of the Cumberland Plateau escarpment. How the species range overlaps or intergrades with that of *A. cumberlanda* (occurring a short distance to the west and south along the same general face of the Plateau, and in the drainage of the Paint Rock River) is not known.

Relationships. The species can be considered a local isolate of *A. cumberlanda,* from which the aedeagal tip is easily derived.

11. **Adelopsis nashvillensis** n. sp.

Figs. 31–33

Holotype male in USNM. Type data: Tennessee. Davidson County near Nashville, 3 November 1937, S. F. Austin, "elm-maple, 562". Tentatively associated material; one female, Tennessee, Warren County, Hubbard Cave at Irving College, 16.X.1948, W. B. Jones and J. M. Valentine.

Description. Aedeagus with dorsal section of tip (figs. 31–33) upturned, and recurved on right side; in posterior view genital orifice deflected up and to the right.

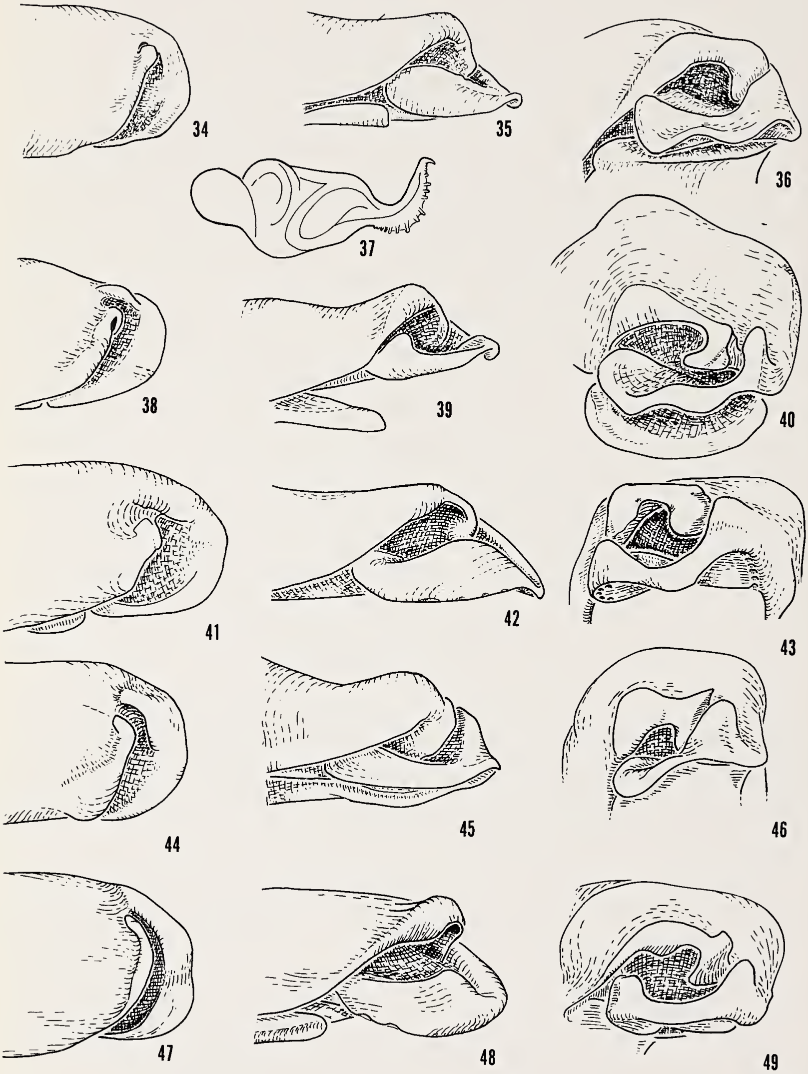
Etymology. The name refers to the city near where the species was collected.

Relationships. The species seems to be closest to *A. cumberlanda,* from which the aedeagal tip can be easily derived.

12. **Adelopsis fumosa** n. sp.

Figs. 34–37, 64, 65

Holotype male and allotype female in FMNH. Type data. Tennessee. Sevier County. Great Smoky Mountains National Park,



Figs. 34–49. Aedeagal structures of *Adelopsis*. 34–36. *A. fumosa*. 37. Internal sac, *A. fumosa*. 38–40. *A. alta*. 41–43. *A. joanna*. 44–46. *A. pisgahensis*. 47–49. *A. orichalcum*.

16.IX.1953, 2.5 road miles (4 km) above Chimney Campground, 3600 ft. alt. (1180 m), H. S. Dybas, leaf litter Berlese. Paratypes: 7 with same data; and the following from Great Smoky Mountains National Park. Cherokee Orchard, 2–3000 ft (610–910 m), 15.IX. 1953, H. S. Dybas, 2 in *Tilia* treehole; 3 in forest floor litter; 4 in flood debris (all in FMNH). State road to Newfound Gap, 3500 ft (1147 m), 16.IX.1953, H. S. Dybas, litter, 8 (FMNH). Chimney Campground, 1.IX.1948, Ross and Stannard, 3, (INHS). Gatlinburg, 14.IX.1948, Quirsfeld, 5 (MCZ). Clingman's Dome Summit, 6640 ft (2177 m), 6–26.VIII.1965, SBP, carrion trap; 8 mi (13 km) S Gatlinburg, 3100 ft, 17.V.1972, A. F. Newton, 2 in carrion trap; Buckeye Nature trail, 10.VIII.1974, J. L. Bengtson, maple litter. *Georgia.* Walker County. Bible Spring Cave, 2 mi (3 km) NE Lookout, 20.VI.1967, SBP), male.

Description. Dorsal section of aedeagal tip (figs. 34–36) uniformly rounded and arched; ventral section on right enlarged to enclose right dorsal section. Internal sac as in fig. 37. Spermatheca (figs. 64–65) with prominent crest.

Variation. The single male from the summit of Clingman's Dome seems to show differences that, with adequate material, could prove to be specifically distinct. The aedeagal tip seems more bilobed on the dorsal section and with a more prominent recurved flange on the right. The internal sac seems more elongate and less curved in its distal half.

Etymology. The name is derived from the Latin for smoke, referring to the species range in the Great Smoky Mountains. However, the Georgia population is a disjunct some 200 km to the southwest.

Relationships. The aedeagal tip shows the closest similarity to, and is most easily derived from that of *A. appalachiana.*

13. **Adelopsis alta** n. sp.

Figs. 38–40, 66

Holotype male in USNM. Type data: North Carolina. Yancey County. Mt. Mitchell, 6500 ft (2131 m), 25.VI.1937, E. Shoemaker. Paratypes: Mt. Mitchell, 4–6000 ft. (1311–1967 m) 17–24.VI.1939, Quirsfeld, 4 (INHS); Mt. Mitchell, 12.VI.1973, litter under *Rhododendron,* WRS, 1.

Description. Dorsal section of aedeagal tip (figs. 38–40) higher and thicker on left, right side with downturned process curving into genital orifice; ventral section thickened and upturned at base on both right and left sides. Spermatheca (fig. 66) with central piece curved inwards like grip of an archer's bow.

Etymology. The name is the Latin adjective for "high" and refers to the species' high elevation habitats in the Black Mountains and Mt. Mitchell.

Notes. This species is sympatric with *A. mitchellensis,* with which it has been confused, but to which it is not at all closely related judging from the dissimilarity of the aedeagal tips.

Relationships. The species is most easily derived from a generalized ancestor like *A. appalachiana* by modification of the aedeagal tip through stages similar to *A. alta, A. cumberlanda,* and *A. nashvillensis,* though these may not be direct ancestors.

14. **Adelopsis joanna** n. sp.

Figs. 41–43, 67, 68

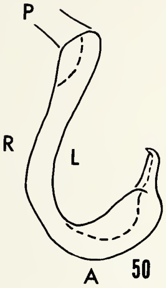
Holotype male and allotype female in CNC. Type data: North Carolina. Cherokee County. Joanna Bald, near Andrews, 4700 ft (1540 m), 26.VII.1967, S. B. Peck, litter Ber. 96. One paratype female with same data.

Description. Dorsal section of aedeagal tip (figs. 41–43) not smoothly curved, but more angular and forming offset arch over genital orifice; ventral section upcurved on left but more so on right, forming prominent notch between it and the dorsal section. Spermatheca thin, irregularly curved (figs. 67, 68).

Etymology. The name refers to the type locality, and is used as a feminine noun in apposition.

Relationships. The species seems to be derived from a *cumberlanda*-like ancestor through a form like that in *A. alta,* and may be an isolate of the ancestor of this species.

Figs. 50–68. Spermathecae of *Adelopsis.* 50. *A. mitchellensis* indicating anterior (A), posterior (P), right (R), and left (L) sides as oriented in the beetle. 51–52. *A. alleghenyensis.* 53–54. *A. suteri.* 55–56. *A. richlandensis.* 57–58. *A. appalachiana,* Morrison Cave, Georgia. 59–60. *A. appalachiana,* outside Bangor Cave, Alabama. 61. *A. cumberlanda,* paratype. 62–63. *A. scottsboroensis.* 64. *A. fumosa,* 8 mi S Gatlinburg, Tennessee. 65. *A. fumosa,* Clingman's Dome, Tennessee. 66. *A. alta.* 67–68. *A. joanna.* All drawn to same scale.



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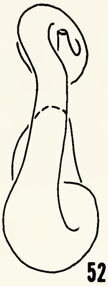

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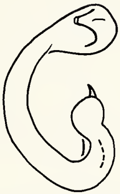

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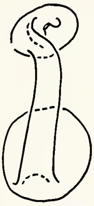

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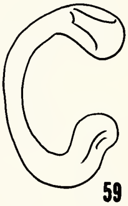

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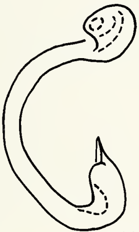

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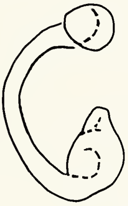

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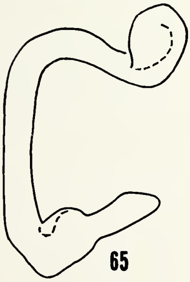

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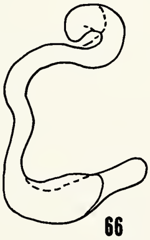

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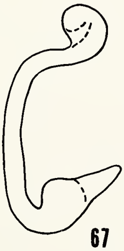

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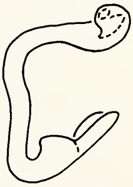

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15. **Adelopsis pisgahensis** n. sp.

Figs. 44–46

Holotype male, allotype female, and paratype male in MCZ. Type data: North Carolina. Haywood-Transylvania County line, Mt. Pisgah, about 1475 m (on Blue Ridge Parkway), 11–12.IX.1934, Quirsfeld.

Description. Aedeagal tip (figs. 44–46) with dorsal section broadly swollen on left and with sharp point on right; ventral section low and regular on left but on right broadly expanded and upraised along notch between it and dorsal section.

Etymology. The name refers to the type locality. Mt. Pisgah is a section of the mountain ridge continuous with Richland Balsam, inhabited by *A. richlandensis.* There is no evident barrier to dispersal between the two and they must be assumed to be parapatric or sympatric.

Relationship. The species has a highly derived type of aedeagal tip and may be descendant from an ancestor similar to *A. alta.*

16. **Adelopsis orichalcum** n. sp.

Figs. 47–49

Holotype male in CNC. Type data: Georgia. Union County. Brasstown Bald, el. 2415 ft (790 m), 24.X.1966, H. R. Steeves, forest debris.

Description. Dorsal section of aedeagal tip (figs. 47–49) uniformly thicker from left to right, ending in upcurved spur; ventral section upcurved on left, depressed and emarginate in middle, and more upcurved on right.

Etymology. The name is Latin for brass, is used as a noun in apposition, and refers to Brasstown Bald, the highest point in Georgia, in the vicinity of which the species is probably restricted.

Relationships. The species is derivable from a generalized stock like *A. appalachiana* through intermediates that were probably also ancestral to *A. pisgahensis, A. joanna,* and *A. alta.*

Evolutionary and Distributional History

Jeannel (1936, 1964) considered the evolutionary center of the genus (and the tribe) to be in Colombia and Venezuela. Species here have an aedeagus with a copulatory orifice displaced onto a nearly sagital plane. This condition was judged to be a form from which all other aedeagal tips could be derived. He also saw this genus as ancestral to *Ptomaphagus,* which developed a more "successful and harmonious" and less variable aedeagal type, and then spread through North America, and across the proto-Atlantic to Europe in the Eocene. He also saw an earlier connection from South America in the Jurassic to southeast Asia, where another derivative genus, *Ptomaphaginus,* now occurs. Szymczakowski (1964, 1969) agrees with the idea of an American evolutionary origin, but sees little evidence to support arguments for specific despersal routes. The survival of *Proptomaphaginus* in relictual species in the Caribbean and Mexico supports the idea of an American origin for the stock that became *Ptomaphaginus* in the Oriental Region.

I do not yet have a suitable overview of the genus as a whole to elaborate on or offer alternative hypotheses to those of Jeannel and Szymczakowski. This is best postponed until after my now massive tropical American collections are studied. However, some ideas can be proposed for the collection of species limited to the southeastern United States.

The genus probably originated in tropical America in the late Mesozoic. Whether this was in what we now know as South, Central or North America probably cannot be known with certainty. However, the greatest present generic diversity in the tribe is now known to be in or adjacent to Mexico. This area (and Central America) has been an important evolutionary center in its own right. Savage (1966) suggested that broad, terrestrial, forested connections united these three regions in the Paleocene and permitted north-south faunal movements, so that mesic tropical climates and forests were continuous through South America up to what is now the central United States. The patterns of distribution of forest litter reptiles and amphibians may be informative and related because they occupy environments similar to Catopinae, though their dispersal abilities are probably very different. However, Savage (1974) has reconsidered the evidence and now finds less substantial support for such broad connections, and now thinks there was a significant water gap separating South America from "nuclear Central America" and North America from the Cretaceous up to the Pliocene. This is more consistent with other current ideas of plate tectonic biogeography (Raven and Axelrod, 1975). This gap, however, could have been crossed by island hopping and waif dispersal, of which winged *Adelopsis* (and *Ptomaphagus*) should have been capable.

These considerations then suggest an origin of *Adelopsis* in "tropical" North or Central America perhaps in the late Cretaceous or early Tertiary, and a movement through forests in the early Tertiary into the Appalachian Region. The continuous distribution of the genus was then broken with the developing xeric climates of the Miocene, forming an effective non-forested barrier across what is now northern Mexico (Axelrod, 1960, Graham, 1973). This disjunction is observed in many groups (see Rosen, 1978). Since this disjunction the assumed large-eyed and winged ancestral stocks have vanished from what became the United States, leaving only the small-eyed and wingless soil species of the Appalachians. Past workers have suggested that the mesic forests of the Appalachians and Mexico were rejoined in Pleistocene glacials, but most recent analyses do not tend to support this (Graham, 1973; Martin and Harrell, 1957; Rosen, 1978).

The comparative uniformity of overall morphology and aedeagal types in the Appalachian species suggests that a single ancestral species became an inhabitant of soil and deep litter. Subsequent (late Tertiary?) isolations perhaps produced the set of less-similar species in the *mitchellensis* species group. Differentiation of these species may have been reinforced by Pleistocene climatic fluctuations and distributional displacements. One of these species may have become something like *A. appalachiana* and it experienced speciation by range expansion, contraction, and population isolation in response to Pleistocene climatic fluctuations. The more cool and wet conditions accompanying glacials (Watts, 1970, 1975; Whitehead, 1965) would allow their spread through the lowlands. Warmer and drier conditions of interglacials would separate populations of these seemingly poorly mobile beetles as they retreated to favorable and more isolated sites at higher elevations or in mesic forest refugia of canyons, gorges, and protected spots below topographic escarpments. By this process, an *A. appalachiana*-like ancestor differentiated into the species of this more closely knit group.

The production of 16 species from one ancestor seems only a modest amount of differentiation if the southeastern *Adelopsis* have truly been isolated from their Neotropical congeners for some 35–40 million years, especially when compared to some examples of "explosive" species production on islands in 10 million years or less. However, the fossil record shows that other groups with the same Appalachian-Mexican disjunction have undergone very little differentation in the same time, especially in certain tree genera (Axelrod, 1960, p. 269; Rosen, 1978). It should also be noted that these papers deal more with examples that seem to be northern in origin and which have moved into Mexico and southwards rather than the opposite (Graham, 1973).

It might at first seem puzzling that a Neotropical genus, characteristic of lowland mesic tropical forests should have species isolated on the highest peaks of the southern Appalachians. However, it is not difficult to see the origin of the situation. When they were first colonized the Appalachians seem to have had a tropical or subtropical climate, and to have had a more gentle relief, sometimes called the "Schooley Peneplain". Their present relief is due to later Tertiary uplift and erosional rejuvenation, a process to which the beetles could undoubtedly adapt as their populations either were slowly elevated, or slowly moved into higher sites.

The broad patterns of species distribution seem similar to those of other flightless beetles inhabiting deep litter and/or soil in the Appalachians (see Darlington, 1943). Close comparisons can be made with the eyeless *Anillinus* carabids (Barr, 1969; pers. comm.), *Arianops* pselaphids (Barr, 1974), and more distant ones with *Trechus* carabids (Barr, 1962, 1969), and *Catopocerus* leiodids (Peck, 1974). These show species to be generally confined to upland areas or in deeper soil (collected in caves) or protected gorges in the lowlands. Some of these groups have species which may be more widespread in the northern end of the unglaciated Appalachians, but most contain more species, but with not much more sympatry, in the vicinity of the junction of North and South Carolina and Georgia (the vicinity of Highlands, North Carolina). The mechanism that acted to generate and then preserve the diversity near Highlands might have worked in a relatively similar manner on these and many other groups of forest litter-inhabiting insects and other arthropods.

Conclusion

The genus *Adelopsis,* otherwise Neotropical in distribution, is found to have 16 species in the southern part of the Appalachian region of the United States. All these species are small-eyed and wingless, are inhabitants of forest soil and deep litter, and must have limited dispersal abilities. Higher elevation Appalachian localities seem generally to be occupied by distinct, more distantly related, and very localized species. Lower elevation sites are more often occupied by more similar species which are more often of a wider distribution. This last generalization is reflected in the *appalachiana* species group which may have resulted from a more recent series of speciation events. There is not enough evidence to suggest how ranges may have been affected and populations isolated with the changed climatic conditions of the Pleistocene, but these are known to have markedly lowered vegetational zones in the southern Appalachians in the last glacial. Since most of the material reported on in this paper was incidentally gathered by persons in persuit of other beetles, many more species undoubtedly remain to be discovered. These may possibly more than double those already known, particularly in the poorly collected regions extending for some 260 km (160 mi) along the Appalachian and Blue Ridge crests between the NE corner of North Carolina, through Virginia, to Spruce Knob, West Virginia. A more firmly based interpretation of the evolutionary history of the genus in the southeastern United States will be possible when these taxa and additional distributional data become known. Because of inadequate material, this paper is only a preliminary report. This is a reflection of the still inadequate status of knowledge of the soil and litter faunas of North America in general.

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EXTERNAL SEX BRAND MORPHOLOGY OF THREE SULPHUR BUTTERFLIES (LEPIDOPTERA:PIERIDAE)*

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Introduction

Males of many pierid butterflies have specialized scales, in patches or scattered over the wing surface, that are thought to be involved in the dissemination of a chemical signal (Chapman, 1971). Recent experiments with two sulphurs, *Eurema lisa* Boisduval and Leconte and *Colias philodice* Latreille, have borne out this assumption (Rutowski 1977, 1979). In these species, the male has a patch of cells and scales in the friction area of either the ventral forewing (*E. lisa*) or the dorsal hindwing (*C. philodice*) that produces a chemical signal used to seduce females during successful courtship. Females respond to the chemical signal by extending the abdomen ventrally out from between the hindwings, thereby permitting copulation.

In many sulphur butterflies the males' sex brands are much more distinctive than those found in *E. lisa* and *C. philodice*. It is the purpose of this report to document the external morphology of the male sex brands of three species of pierids, *Nathalis iole* Boisduval, *Eurema nicippe* Cramer, and *Colias cesonia* Stoll, (Figure 1A). These species were chosen for two reasons: 1) they appear to represent a range of sex brand morphologies typical of that found in the pierid tribe, Coliadini (sulphurs), and 2) they have close affinities to species for which the function of the sex brand is well-documented. A special effort will be made to understand the possible adaptive significance of this variation in sex brand structure.

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METHODS AND MATERIALS

All specimens were collected in Arizona between 17 July and 16 September 1978. The dainty sulphur, *N. iole,* was collected at Clint's Well, the sleepy orange, *E. nicippe,* near Rye, and the dog face, *C. cesonia,* near Tortilla Flat. In addition, *N. iole* was reared through several generations in a greenhouse on the Arizona State University campus, Tempe, Arizona, on their natural foodplant, the tickseed (*Coreopsis cardaminefolia* Torrey and Gray or *C. atkinsonia* Douglas). To assess the effect of age on sex brand color or condition in *N. iole* and *E. nicippe,* individual males were assigned to one of three age classes on the basis of wing condition and scale loss: 1) fresh — no noticeable scale loss or wing tattering, 2) slightly worn — visible scale loss and some tattering, especially along wing margins, and 3) worn — substantial scale loss and/or wings with deep nicks and tears. The categories used to describe sex brand color variation are presented in the results. Sex brand condition in *N. iole* was also a function of scale number and morphology. Scales in the sex brand were scored for whether or not they were present and, if so, whether they were flat, withered, or between these two extremes (half withered). Lab-reared males were examined on the day they eclosed; wild males were examined either alive or within 6 hours after they had died.

Changes in sex brand color with time since death were documented for *N. iole.* The wings of 16 freezer-killed males were stored in glassine envelopes at room temperature and the coloration of their sex brands scored at weekly intervals until all attained the final pale yellow color.

Wings of all three species were mounted on aluminium pegs with Dag^{R}, coated with gold in a D. C. sputterer for 3 minutes, and examined with an AMR-1000A scanning electron microscope at 20 KeV accelerating voltage. In some cases severe charging of the specimens necessitated longer coating times or low accelerating voltages (5 KeV). All sex brands viewed with the SEM were from either freshly-killed males, live males, or males killed and stored at −5° C. To minimize the effects of desiccation at high vacuum some *N. iole* wings were dehydrated in ethanol, and passed through Freon-113 before critical point drying using Freon-13 as the transition fluid.

Scale densities were estimated for the sex brand and discal areas of the wings from scanning electron micrographs of wings whose

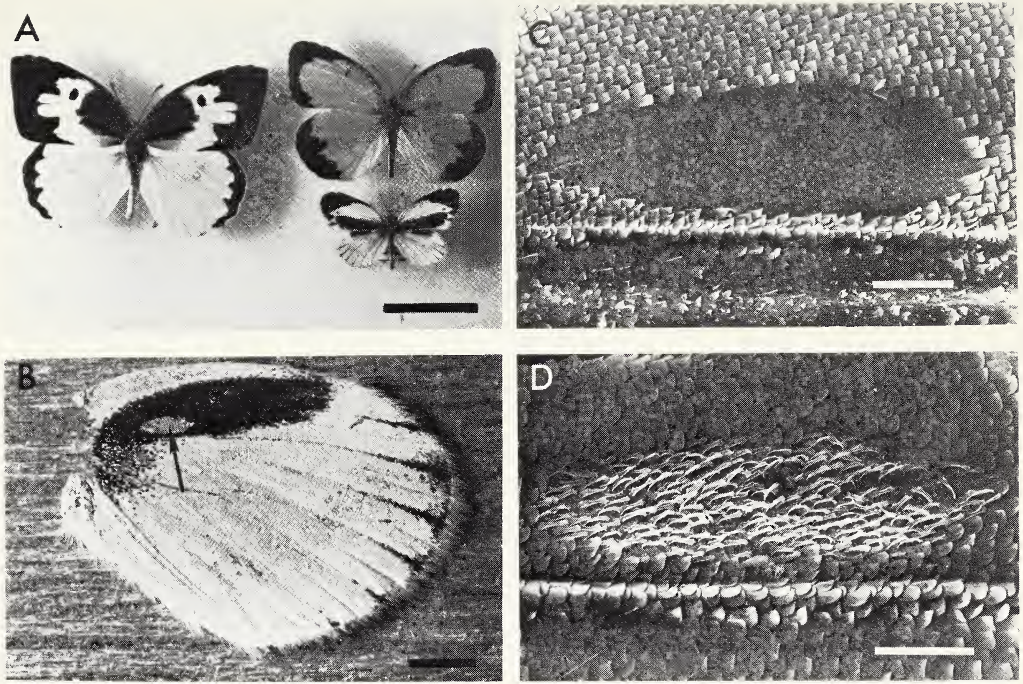

Figure 1. A, males of *C. cesonia* (left), *E. nicippe* (upper right), and *N. iole* (lower right); B, dorsal hindwing of male *N. iole* (note sex brand under tip of arrow); scanning electron micrographs of *N. iole* sex brand without (C) and with (D) scales. Scale lines: A, 3 cm; B, 2 mm; C, 300 μ; D, 200 μ.

Table 1. The relationship between sex brand color in *N. iole* and several variables.

	% of observations				
Variable	Dark orange	Light orange	Mottled	Pale yellow	No. of males
Days since death					
3	88	0	6	6	16
10	38	50	6	6	16
17	6	56	25	13	16
24	6	44	31	19	16
31	0	6	31	62	16
38	0	0	0	100	16
	$\chi^2 = 107.6$, $p < 0.0001$				
Wing condition/age					
fresh	94	4	2	0	48
worn	71	29	0	0	17
very worn	57	21	11	11	28
	$\chi^2 = 21.42$, $p < 0.005$				
Scales in sex brand					
present	82	13	3	1	76.5[a]
absent	61	18	9	12	16.5[a]
	$\chi^2 = 7.06$, $p < 0.05$				
Condition of scales in sex brand					
shrivelled	82	13	5	0	38
half-shrivelled	81	11	0	7	13.5[a]
flat	86	14	0	0	25.5[a]
	$\chi^2 = 6.85$, $p > 0.3$				

[a] Fractional values indicates a male whose sex brands differed with respect to this variable.

scales had been removed with a small brush. The area of the wing represented in each micrograph was corrected for the fact that all specimens were photographed from an angle of 45°. Scale attachments intersecting the bottom and left hand borders of each micrograph were tallied while those intersecting the top and right hand borders were not. This procedure reduced the possibility of inflated density estimates.

RESULTS

The sex brand of *N. iole*

Males of *N. iole* have an orange, ovoid sex brand (about 0.5 × 1.5 mm) on each hindwing between the subcostal and the radius veins near the wing base (Figure 1B). The brand is surrounded by a bar of melanic scales that runs along the leading edge of the hindwing from the wing base to the outer margin. The most unique aspect of the sex brand in *N. iole* is that it is frequently devoid of scales (Table 1, Figure 1C). This condition is not a result of wear as it occurs in many newly-emerged lab-reared males (Table 2). When scales are present in the sex brand (Figure 1D) they may cover up to 100% of the brand and vary in form from a scale that is tan, flat, and similar to other scales on the wing to one that is black, shrivelled, and contorted (Figure 2A-C; Table 2). Within an individual male the form of the sex brand scales and the extent to which they cover each sex brand is usually uniform.

Scale attachments in the sex brand differ from those on other areas of the wing in appearance and in density. Unlike those in other areas, a typical sex brand scale attachment has fewer ridges running up its side, is more rounded, and has a pronounced swelling or bulge immediately behind the opening of the attachment (compare Figure 2C and D). This bulge is distinctly collapsed in air dried specimens compared with those that are critical point dried. The density of scale attachments in the sex brand is almost twice that of scale attachments in the immediately adjacent discal cell of the wing (Table 3; $t = 40.4$, $p < 0.001$; $df = 7$).

Examination of descaled wings or wings whose scales had been cleared in a dilute solution of sodium hypochlorite reveals that the color of the sex brand in live males is due to an orange pigment in the integument of the wing. This orange pigment typically extends little if at all beyond the edges of the sex brand. The pigment is visible under the light microscope in the space between the dorsal and ventral surfaces of wings that were crudely sectioned with a razor blade. Scanning electron microscopy of these same preparations reveals an ill-defined matrix of material, probably pigment, in this space that is restricted to the sex brand (Figures 2E and F).

As pointed out by Clench (1976) the orange color changes to pale yellow after the death of the butterfly. The complete transition takes about 6 weeks (Table 1) and does not occur at a uniform rate throughout the sex brand. Splotches of orange pigment remain in some areas while others have changed to yellow ("mottled"). We also made the unexpected observation that sex brand color changes with male age (Table 1). All newly-emerged, lab-reared males ($n = 52$) have dark orange sex brands while older males, as evidenced by wing condition, have significantly higher frequencies of mottled and yellow sex brands (Table 1).

Table 2. Differences between lab-reared and wild males of *N. iole* with respect to the presence and condition of scales in the sex brand.

	Lab-reared		Wild	
Scales in sex brand	%	No. observed	%	No. observed
present	67	52	82	95
absent	33		18	
		$\chi^2 = 3.81, p > 0.05$		
withered	53	35	49	77
half-withered	23		18	
flat	24		33	
		$\chi^2 = 1.03, p > 0.4$		

The sex brand of *E. nicippe*

In *E. nicippe,* the sex brand appears as an orange, triangular patch of scales about 3 mm across on the ventral surface of each forewing between the second branch of the cubitus and the second anal vein (Figure 3A). The scales in the brand are typically brilliant orange in color in contrast with the white to light-orange scales that surround the brand. Orange pigment extends through the base of each scale in the wing integument where it can be seen as an amorphous blob underlying each scale attachment in the sex brand. Unlike that of *N. iole,* the sex brand of *E. nicippe* is always covered with scales that occur at about twice the density of scales in the discal cell of the ventral forewing (Table 3; $t = 78.4$, $p < 0.001$, $df = 7$).

The scales in the sex brand and their attachments are quite different in form from those found on other areas of the wings (Figures 3B and C). The scales are shorter (60 μm as compared to 80 μm for scales in discal cell) and they extend from the wing surface at a greater angle. Other differences in scale shape are evident in Figures 3B and C. The sex brand scale attachments are much larger than those in the discal area of the wing and as in *N. iole* have a pronounced bulge or swelling behind the opening.

The orange color of the sex brand is not constant in all specimens (Table 4). Older specimens, as measured by wing wear, typically have a bright white sex brand. In males in intermediate ages, one often finds an intermediate coloration, with the upper half of the sex brand white in color and the lower half a light orange. The sex brand color does not change with death.

The sex brand of *Colias cesonia*

Colias cesonia males have a sex brand on the dorsal hindwing between the subcosta and radius veins near the wing base (Figure 3D). The color of the brand ranges from lemon yellow to a light yellow with no consistent changes with age or death that we have observed. The color is solely attributible to the scales as the

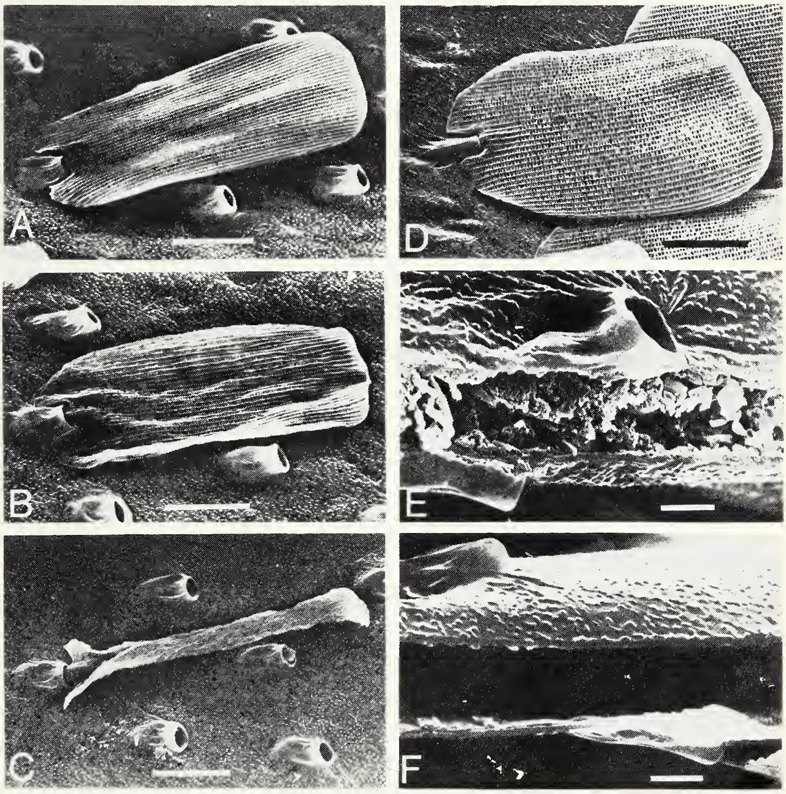

Figure 2. Scanning electron micrographs of *N. iole* wings. A-C, variation in the structure of sex brand scales; D, a scale from the discal cell; E, crude cross section through the sex brand showing pigment between the dorsal and ventral wing surfaces; F, crude cross section of the wings in the discal cell. See text for details. Scale lines: A-D, 20μ; E and F, 5μ.

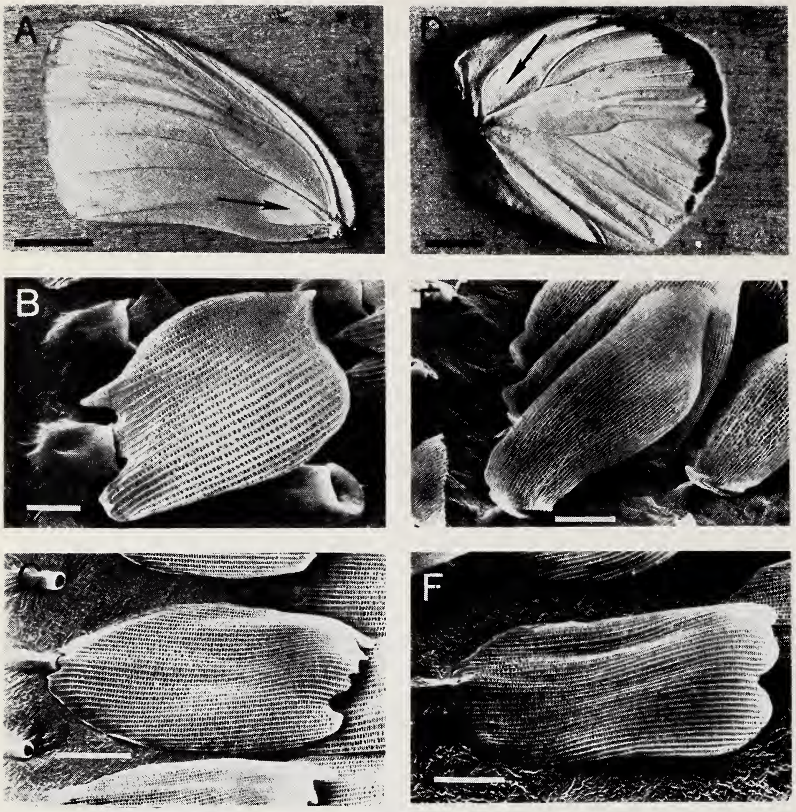

Figure 3. *Eurema nicippe:* A, male ventral forewing (note sex brand under tip of arrow); scanning electron micrographs of male scales from the sex brand (B) and the discal cell (C). *Colias cesonia:* D, male dorsal hindwing (note sex brand under tip of arrow); scanning electron micrographs of male scales from the sex brand (E) and the discal cell (F). Scale lines: A and C, 5mm; B, 10μ; C and F, 20μ; E, 30μ.

integument of the wing under the scales is clear. The scales surrounding the sex brand are of a color similar to that of the brand. However the sex brand is still distinct from the rest of the wing in that the density of scales is twice as high (Table 3; $t = 42.9$, $p < 0.001$, $df = 4$). In fact, the scales in the brand are almost perpendicular to the wing surface.

The scales are also unique in form (Figures 3E and F). In particular, the pedicel of each scale arises from the surface of the scale against the wing rather than projecting from the base in the same plane as the scale. The base of each scale in the sex brand extends beyond the point where the pedicel emerges and partially overlies the scale socket on the wing surface. The spacing of the longitudinal and transverse ridges on these scales also appears more variable than it is on other types of scales.

DISCUSSION

Detailed information is now available about the sex brand morphology of five species of sulphur butterflies in the pierid tribe, Coliadini. They include *Eurema lisa* (Rutowski, 1977) and *Colias philodice* (Rutowski, 1979) as well as the three species discussed in this report. Several generalizations have appeared.

1) All male sex brands are located in the friction areas of the wings, that is, the area of overlap between the forewings and hindwings. Rutowski (1979) has suggested that this placement of the sex brand helps to minimize evaporation from an otherwise exposed and non-eversible scent producing structure.
2) The scales observed in the sex brand are not greatly differentiated from those found in other areas of the wings. This contrasts with the scent scales found in many eversible scent-producing organs that are very hair-like (e.g. danaids (Pliske and Salpeter, 1971), noctuids (Birch, 1970)) and with the presumed scent scales on the wings of some pierids and nymphalids which have fringed distal borders (Barth, 1950; Bergström and Lundgren 1973; Tinbergen et al., 1942).
3) The scales are associated with cells in the integument of the wing that reside in a swelling in the wing immediately behind the scale socket. Presumably these cells are secretory trichogen cells like those found in scent-producing structures that are histologically better known, (e.g. danaids (Pliske and Salpeter, 1971)).

These similarities reflect not only the phylogenetic affinities of these species but also the action of similar selection pressures. The behavior of the male during courtship is similar in all five species. The male buffets the female with his wings while she flies or perches on vegetation (Rutowski, 1978; Silberglied and Taylor, 1978; pers. obs.). Selection has not acted to favor any divergence from this pattern among these species and hence there have been no major

Table 3. Scale attachment densities for the wings of three pierid butterflies.

Species	Area	Attachments/mm² $\bar{X}$	Attachments/mm² SD	Area/sample (mm²) $\bar{X}$	Area/sample (mm²) SD	Sample size
N. iole	sex brand	662.9	156.9	0.050	0.003	5
	discal cell	393.1	22.4	0.144	0.106	4
E. nicippe	sex brand	974.3	142.2	0.048	0.003	5
	discal cell	427.2	63.2	0.234	0.031	4
C. cesonia	sex brand	411.3	40.5	0.231	0.012	3
	discal cell	216.3	21.1	0.216	0.016	3

changes in the basic structure of the sex brands. Still, there are some striking differences in their fine structure for which there is no ready explanation. These differences include: 1) placement of sex brand (forewing vs. hindwing), 2) scale density (some species have sex brands in which there is no apparent increase in sex scale density compared to surrounding areas), 3) presence or absence of scales in the sex brand, and 4) changes in color with male age or death. The biological rationale for these differences will have to await more detailed information on the chemistry and cellular structure of these sex brands.

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Table 4. The relationship between sex brand color and wing condition in *E. nicippe*.

Wing Condition	Sex brand color (no. of males) Orange	Half orange, Half white	White
Fresh	6	14	3
Worn	0	3	9
Very worn	0	0	5

$\chi^2 = 20.8,\ p < 0.0005$

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INTRASEXUAL AGGRESSION IN THE STICK INSECTS *DIAPHEROMERA VELIEI* AND *D. COVILLEAE* AND SEXUAL DIMORPHISM IN THE PHASMATODEA*

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Introduction

Pairing[1] in the Phasmatodea is notable for its duration. The Indian stick insect *Necroscia sparaxes* may remain coupled for up to 79 days (a record for insects) and accounts of matings lasting days or weeks are commonplace (LeFeuvre 1939; Korboot 1961; Gangrade 1963; Gustafson 1966; Clark 1974). Intromission may occur only initially or intermittently. In either case, a substantial proportion of male time-investment is not spent in ejaculate transfer. In captivity, *Diapheromera veliei* and *D. covilleae* pair for 3 to 136 hours and the penis may be inserted and removed up to 9 times. The genitalia are not in contact for ca. 40% of this period, and attachment is maintained by a male clasping organ.

According to the best current explanation, males remain with females when not actively engaged in insemination to guard against the introduction of rival ejaculates and so avoid sperm competition (the competition of sperm from 2 or more males for the fertilization of an ovum; Parker 1971, 1974). Male aggression for possession of mating females has been described in a variety of insects (Parker 1970). In the only account known to me of attempted mate theft by a stick insect, an intruding male *Orxines macklotti* made several futile efforts to engage his genitalia, climbed off and walked away (Robinson 1965). Also indicative of a passive defense was a congregation of *Carausius alluaudi* collected in the Seychelles Islands consisting of 6 males clasping a female's abdomen at various points (a seventh male was nearby) (Bolivar and Ferriero 1912). While sedentary guarding of the female might be typical, lack of any

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[1] The vocabulary describing attachment between male and female is often inadequate for insects. In this paper mating, coupling, and pairing imply continuous attachment and not constant intromission.

observed aggression may result from a paucity of observers, a consequence of the Phasmatodea being ". . . less studied than any other order of the Orthopteroidea . . ." (Bradley and Galil 1977).

This paper describes conflict between males in the walkingsticks *Diapheromera veliei* and *D. covilleae.* Results of an experiment are presented relating male size to ability to monopolize females. Data on sex-related size-dimorphism in the 2 species are compared to published values for other members of the order to reach tentative correlations between population structure, mating strategies and the relative size of males.

MATERIALS

Adult *Diapheromera veliei* were obtained in Bernalillo Co., New Mexico, from the legume *Dalea scoparia,* and specimens of *D. covilleae* from creosote bush (*Larrea tridentata*) in Dona Ana Co., New Mexico. Observations were made on insects contained with the appropriate host plant in 10-gallon aquaria. Densities within aquaria varied from 3 to 10 adults. These densities, while high, were not unnatural. Up to 7 adult males and a single female have been found on a bush whose greatest dimension was 1.5 meters. Insects are often unevenly distributed in nature, and it was not unusual to see several adult males within 30 cm. of a mating pair.

The effect of size on the ability of male *D. veliei* to maintain attachment to females was examined by keeping a small ($\bar{x} = 67$ mm.) and a large ($\bar{x} = 87$ mm.) male with a female in each of ten 10-gallon aquaria. Tandem duration was recorded by checks at 2-hour intervals between 8:00 A.M. and 8:00 P.M.

To determine the distribution of sexual size-dimorphism within the Phasmatodea, body lengths of 155 species were obtained and a male-over-female ratio calculated for each (data from material deposited in the Florida State Collection of Arthropods, Gainesville, Florida; random selections in Brunner Von Wattenwyl and Redtenbacker 1908; the whole of the relevant material in Leigh 1909; Hebard 1923; Rehn and Rehn 1939; Gurney 1947; Salmon 1955; Korboot 1961; Bedford and Chinnick 1966; Gustafson 1966; Stroheker 1966; Paine 1968; Moxey 1971; Clark 1974). Many of the specimens were dried, and the possibility of differential shrinkage of the sexes was examined with specimens of *D. veliei.* Shrinkage in both sexes was 0 to 3% of live length after a drying period of 2 weeks. The sexual dimorphism of *D. veliei* and *D.*

covilleae was determined by measurement of freshly killed specimens (*D. veliei* — 48 males and 34 females; *D. covilleae* — 20 males and 19 females).

RESULTS AND DISCUSSION

Mating in both species is initiated by the male mounting the female dorsally and gripping her body and legs with his tarsi. Females seldom attempted to dislodge a suitor, and were never successful. The male abdomen curves underneath the female and his clasping organ attaches just anterior to the vulva (sometimes attachment is initially well above the vulva). The resulting position is typical of the order (Key 1970; Bedford 1978). Some male copulatory postures may aid in avoiding takeovers. Alexander's (1964) phylogenetic scheme of orthopteroid mating positions initiates with female above which then radiates to include a number of male above or end to end arrangements. These derived postures are conceivably more effective for male control of the area around the mating pair. In *Diapheromera* the dorsal position blocks the length of the female abdomen and facilitates additional means of preventing attachment by a second male.

At the approach of another walkingstick the consort almost invariably bends the tip of the female abdomen down upon itself with his clasping organ. The angle is sometimes sufficiently acute to bring the ventral surfaces of the female abdomen on both sides of the claspers into contact. A large part of the typical site of attachment is thereby denied to competitors. Less frequently, mating males strike out at approaching males with their forelegs.

Striking motions and manipulation of the abdomen are effective defenses and most attempts of intruding males to attach to a mating female were futile. Occasionally second males clasped the female abdomen and sometimes succeeded in inserting their genitalia into the vulva. This usually occurred when the consort was no longer in a dorsal position but had moved to the side of the female to feed. For periods of a few minutes to an hour, such *"menages a trois"* were maintained with incident. In 6 of over a score of double couplings and combats observed in *D. veliei* the entire sequence was recorded from approach of the second male to resolution of the competition. On one occasion the intruder left in less than an hour without harassment. In all other cases, fights occurred which followed a similar pattern.

The males lean backwards, pulling at each other and often anchoring themselves by grasping foliage. Eventually, both become freely suspended, held only by their clasping organs. They then direct rapid sweeping blows against their opponent (Fig. 1). The forelegs are used in a boxing manner. After a few seconds to several minutes, one of the antagonists releases his grip and the victor shortly regains the dorsal position. Once attachment of the second male to the female is accomplished, takeover attempts are often successful. In the 5 fights in which the original male was known, he was displaced 3 times.

In *D. veliei* and *D. covilleae,* a spine is present on the mid femora of both sexes. Those of the male are enlarged and hooked. In *D. covilleae* combats, the opponent's thorax is held in the joint of the mid tibia and femur. By flexing the legs, the spine is brought against the body, and it was once seen to puncture the integument, drawing blood. Spines used in defense by stick insects are invariably more highly developed in males (Lea 1916; Robinson 1968; Bedford 1975) possibly because of their significance in male fighting.

Well-developed male clasping organs (as in *Diapheromera* spp.) are not universally present in the order. In reviewing the Australian Phasmatodea, Key (1970) found male cerci only occasionally modified into claspers. Perhaps varied cercal design is due to differing probabilities of takeover.

The mean male over female length ratio of a sample of 155 phasmid species (approximately 8% of described species) is .727. The average male *D. veliei* is .922 of the mean female length. This is an unusually slight difference in body lengths (see Fig. 2), with 94% of the sample having relatively smaller males (*D. covilleae* has a similar male/female ratio: .916). It might be generally expected that males would be smaller than females when fecundity is dependent on size. By spending less time in development or consuming less food, males take fewer risks in reaching maturity. Even tiny males in species with internal fertilization are capable of producing an adequate ejaculate. Given that the niches of the sexes are similar, the degree of sexual dimorphism is apt to result from a balance of reproductive pressures acting on the male. These forces might include maximizing female encounter rates (mobility, material reserves affecting life span), the ability to invest materially in the success of progeny, and maintaining copulations by aggression.

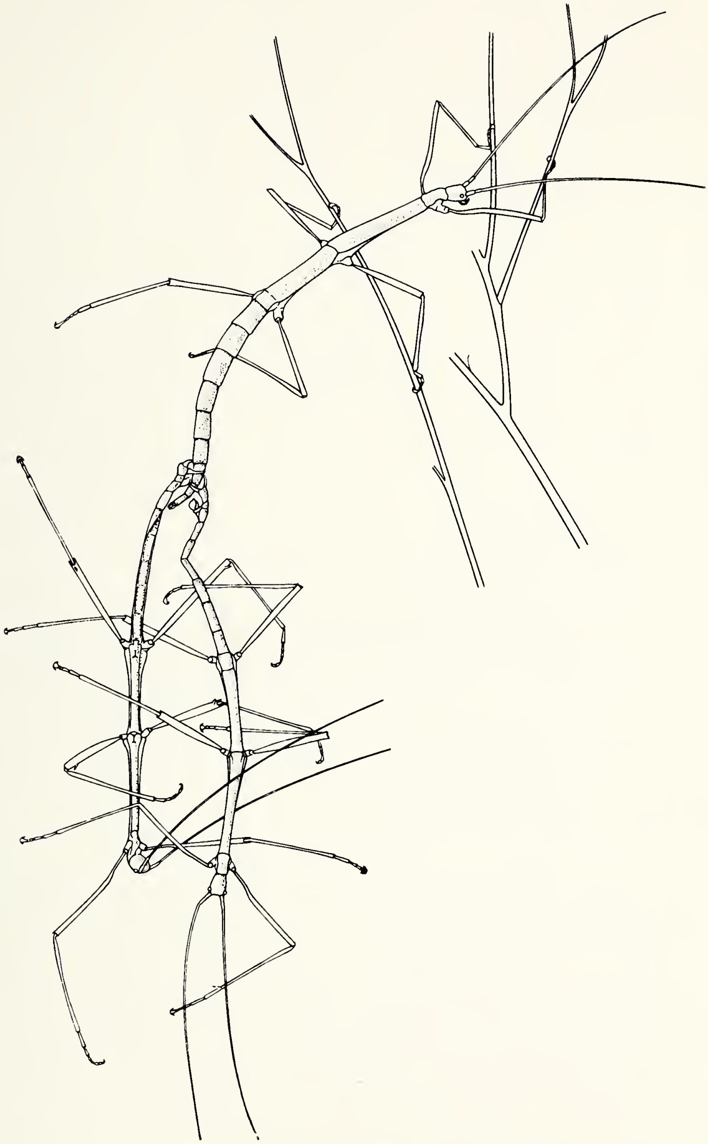

Figure 1. The combat of two male *D. veliei* both attached to a female by their clasping organs (drawing from 35 mm prints of captive specimens).

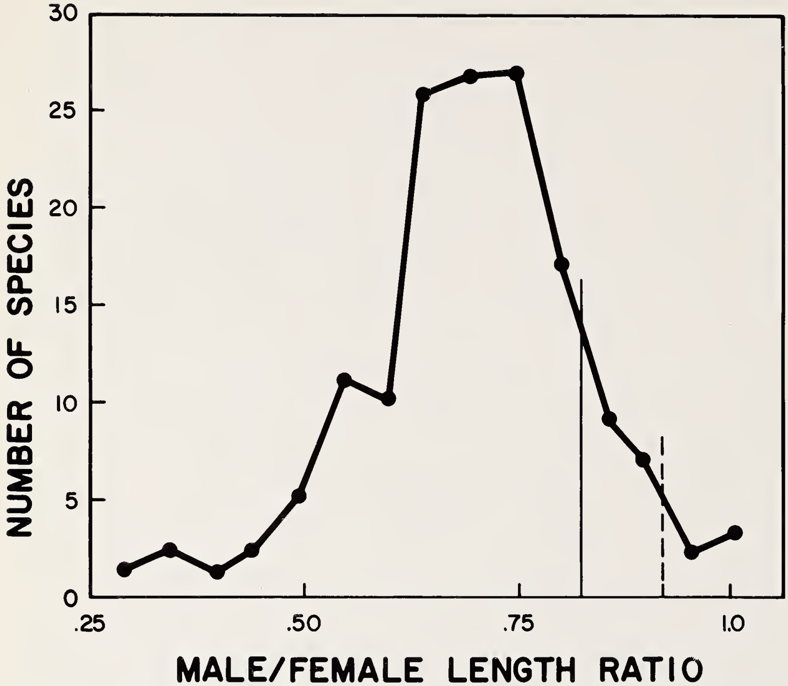

Figure 2. Male length/female length frequency distribution for the order Phasmatodea (generated from citations in materials section). Dots along the curve represent midpoints of categories spanning 5% on the male/female length axis and the number of species occupying these categories. The dashed vertical line represents the position of *D. veliei* (.922), the solid vertical line the mean dimorphism of high density species (.814, see text).

The positive relationship between copulatory success and size is well established for some polygynous vertebrates (citations in Trivers 1972). The great male bulk and armature of the dynastine scarab beetles are agonistic adaptations (Beebe 1944; Eberhard 1977). Larger males of the bibionid fly *Plecia nearctica* are more often found copulating than smaller males (Thornhill 1976). Potter *et al* (1976) showed size to be a critical factor in the outcome of combats between male mites.

In the 2 observed fights between male *D. veliei* of markedly disparate size, the larger won. Two males from the extremes of the size continuum were placed in 10 aquaria with single females and 924 hours of coupling were recorded. Large males accounted for 608 hours (62%). The difference in the mating durations between the size classes borders on significance ($.10 > p > .05$).

Density and sex ratio are major components of the sexual environment and affect the extent of intrasexual competition (Parker 1974). Unlike the majority of walkingsticks, which are uncommon and widely dispersed (Key 1970; Craddock 1972), *D. veliei* and *D. covilleae* are locally abundant (as many as 22 individuals in a 1.5^3 meter bush). Strongly male-biased adult sex ratios (up to 4:1) persist until late in the season, and are perhaps due to a combination of earlier male maturation and selective predation by birds during the early summer nesting period (Sivinski 1977).

In 9 other phasmids known to exist consistently or occasionally at high densities (numerous enough to cause defoliation of trees or at least 5 individuals occupying a bush or refuge), the mean male length/female length ratio is .814 (Wattenwyl and Redtenbacher 1908; Bedford 1975; Lea 1916; Gurney 1947; Wegner 1956; Stockard 1908; Hetrick 1949; Severin 1911; Key 1970; Paine 1968; Wilkins and Breland 1951). Over ¾ of the complete sample is more sexually dimorphic ($p = .2201$) (see Fig. 2). Kentromorphic phases, morphologically distinct forms existing at different densities, exist in several stick insects. As in locusts with density phases, dimorphism usually declines as populations reach their greatest concentrations (Key 1957; Uvarov 1966).

Individuals of *Eurycantha* spp. and *Dryococelus australis* are found in the closest spatial proximity of all known stick insects. Both congregate in tree hollows during the day (Gurney 1947). Aggregation sex ratios vary enormously and as many as 68 phasmids have been found in a single cavity (Lea 1916; Bedford 1975). Length dimorphism is minimal (.908) and males have massive hind femora studded with spines of sufficient magnitude to have been used as fishhooks (Balfour 1915).

Sexual dimorphism in some phasmids is exaggerated in comparison to other orthopteroid taxa. Species with below average dimorphism engage in the longest matings recorded in the order (*Acrophylla tessellata,* male/female = .493, duration 11 days, Korboot 1961; *Anisomorpha buprestoides,* .612, 3 weeks; Clark 1974; *N. sparaxes,* .700, 1–79 days, Gangrade 1963; *Timema californica,* .700, 5 weeks, Gustafson, 1966). Protracted couplings might contribute to selection for male diminution. Disruption of crypticity may be lessened and male maintenance cost kept to a minimum. Since the mating female bears much of the male's weight, a dwarfed male may be more fit in two additional contexts:

1) By allowing the female greater activity, the rate at which additional females are encountered is increased. A potentially polygynous male can search for mates while *in copulo* (blocking the female genitalia until the opportunity for another copulation arises). Mating durations in *D. veliei* are shorter when unmated females are present (Sivinski 1977). 2) By relieving the female's copulatory burden resources could be invested in ova the consort might fertilize. The longer the pairing the more likely this circumstance.

SUMMARY

Intrasexual combats, while common in the Orthopteroidea, have apparently not been previously recorded in the Phasmatodea. Fights between males in *Diapheromera veliei* and *D. covilleae* are described. The minimal sexual size-dimorphism of the two species in comparison to other walkingsticks may be due to a high level of intrasexual competition brought about by atypical population parameters (high density, male-biased sex ratios). It is suggested that extreme dimorphism in the order relieves the burden an attached male places upon female resources during lengthy copulations.

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SEXUAL CALLING BEHAVIOR IN HIGHLY PRIMITIVE ANTS*

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In recent years an interesting mating pattern has been discovered in a number of socially parasitic and dulotic Myrmicine ants, including the related genera *Leptothorax, Doronomyrmex,* and *Harpagoxenus,* and in the guest ant *Formicoxenus nitidulus* (Buschinger, 1968, 1971a, 1971b, 1974; 1975). Typically the alate or ergatoid young female leaves the parent colony, crawls to a prominent position, and settles there motionless for a long period — sometimes amounting to hours — with gaster raised, legs extended, and sting extruded. Sooner or later males assemble about the "calling" female, and mating takes place. Buschinger, who first observed it in these genera, has described the pattern in detail for the slave-making *Harpagoxenus sublaevis* (1968), and in the permanently socially parasitic *Doronomyrmex pacis, Leptothorax kutteri,* and *L. goesswaldi* (1975). He also observed the pattern in fine detail in populations of *F. nitidulus* (1975) maintained in the laboratory as guests of *Leptothorax acervorum,* and found it generally similar to the others, though differing in detail in ways to which we will later allude. Buschinger was able to demonstrate that in all these forms a sex-attractant pheromone was released from the poison gland, as Hölldobler (1971) had been the first to demonstrate in the Myrmicine ant *Xenomyrmex floridanus.*

Recently Möglich, Maschwitz, and Hölldobler (1974), in a particularly provocative study, have presented the results of detailed analyses of "tandem-calling" behavior in the independently-living *Leptothorax acervorum, L. muscorum,* and *L. nylanderi,* a pattern by which workers of these independently-living species recruit sisters to newly discovered food sources, one recruiter guiding only one follower to the source at a time. A component of the initial behavior of the recruiting worker is described as essentially identical with the "calling" behavior in *Harpagoxenus* females, and the authors call attention to the interesting hypothesis posited earlier by Hölldobler (1971) that, in at least some Myrmicine ants, sex

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attractants and recruitment pheromones may have had a common evolutionary origin.

In view of these findings and this challenging suggestion, it becomes unusually interesting to query how early in Formicid evolution the "calling" behavior may have originated. For this reason we are led to put on record some observations of a similar behavior pattern made several years ago in the highly archaic Ponerine genus *Amblyopone,* and also to elaborate some further observations of the same kind in the genus *Rhytidoponera,* a part but not all of which has been noted priviously (Haskins and Whelden, 1965), but without particular reference to this context.

The Genus *Amblyopone*

The Ponerine genus *Amblyopone* includes a rather large group of species widely distributed over the world. In anatomy, colony structure, and behavior patterns they must certainly rank among the most archaic of surviving ants, rivalling or even exceeding in their primitiveness, the very different but also immensely archaic genus *Myrmecia,* as Wilson (1975) has recently emphasized. It was thus of interest to observe what clearly seems to be "calling" behavior in virgin females of two species — the North American *A. pallipes* and the Australian *A. australis,* both widely distributed and fairly common forms in their respective habitats.

Amblyopone pallipes: From 1924 to 1927 an extensive and continuous series of observations was undertaken in the laboratory and field in an attempt to elucidate the nuptial flight and colony-founding behavior patterns in *A. pallipes.* This species appears to be ordinarily completely hypogeaic in habit, foraging entirely underground to satisfy its wholly entomophagous and highly specialized dietary requirements, normally if not invariably confined to a very limited range of Myriopoda. During late summer in the regions of New York State and Massachusetts where the work was done the galleries and chambers of the colonies are concentrated near the surface of the soil, commonly under logs or stones, and are characteristically crammed with cocoons of both sexes and castes. The alate females and males eclose there, and shortly escape aboveground, singly or in small groups. The males, fully pigmented, fly off at once. The females, still of the red callow coloration, climb prominent objects in the vicinity. They may or may not make short flights from these vantage points before coming to rest. They then adopt a posture closely similar to that described for the Leptothoracine ants, resting motionless with legs and antennae extended, gaster arched, and sting protruded or slowly alternately exserted and withdrawn. Characteristically, the arched gaster is rubbed by the tibia of one or the other of the third pair of legs. At the height of the flight season in the localities investigated (typically shady woodlands) numbers of low-flying males soon appeared, landed on vegetation near the female in a high state of arousal, and after some running, one quickly copulated. Often, as in cases described by Buschinger, males attempted to mount one another. Following copulation, females characteristically exhibited reversed phototropism and geotropism and promptly retired underground. This behavior was observed repeatedly both with alate females naturally emerging from wild colonies, and with females reared in the laboratory and subsequently released in appropriate localities. Unfortunately, no determinations were made of the source of the pheromone. The prominence of the sting movements suggest that the source may well, as in *Leptothorax,* have been the sting gland, but the Dufours gland has not been experimentally ruled out at this time, as the source.

Amblyopone australis: A. australis, widely distributed in Australia and in the Pacific Islands as far as New Zealand, is larger and "bolder" in demeanor and habitus than *A. pallipes,* but in general resembles it quite closely. It is, however, partly epigeaic and a much more generalized Arthropod feeder. In this species colony foundation by isolated dealated females has been demonstrated (Haskins and Haskins, 1951). During this period the foundresses forage episodically from their frequently-opened cells in the general pattern of colony-founding females of *Myrmecia.* In the course of work designed to delineate the details of this pattern, alate young females eclosing from pupae collected in the wild were released under observation in appropriate locations. Some of these released females flew briefly, but all soon adopted the "calling" pattern, although, on the occasions of the experiments, no males appeared.

The Genus *Rhytidoponera*

Rhytidoponera is a generalized Ectatommine genus widely distributed in Australia (its apparent headquarters), but extending to

TABLE I

Colony no.	*Date of Observation*	*Time of Observation*	*Number of Workers Involved*
1	4/29/68		1
2	4/ 8/75	7:45 a.m.	15
		8:45 a.m.	11
		8:55 a.m.	2
	4/12/75	7:00 a.m.	11
	4/16/75	5:30 a.m.	10
	4/21/75	7:25 a.m.	6
	4/29/75	7:05 a.m.	2
	4/30/75	7:05 a.m.	1
	5/ 2/75	7:00 a.m.	2
	5/ 6/75	7:10 a.m.	6
	5/ 7/75	7:10 a.m.	2
	5/ 8/75	6:30 a.m.	3
	5/13/75	7:40 a.m.	2
	5/14/75	5:50 a.m.	5
	5/15/75	6:55 a.m.	9
	5/16/75	7:00 a.m.	2
	5/22/75	8:00 a.m.	2
	6/ 3/75	6:45 a.m.	2
	6/ 7/75	6:45 a.m.	2
	7/22/75	6:30 a.m.	9
	10/ 1/75	7:50 a.m.	1
	1/17/76	7:00 a.m.	6
	3/22/76	7:25 a.m.	3
	3/23/76	5:55 a.m.	2
	3/25/76	6:25 a.m.	3

Colony no.	*Date of Observation*	*Time of Observation*	*Number of Workers Involved*
3	5/22/75	8:10 a.m.	1
(Male flights in this colony *only*)	4/16/75	5:30 a.m.	
	5/14/75	5:50 a.m.	

Table 1 (*continued*)

Colony no.	*Date of Observation*	*Time of Observation*	*Number of Workers Involved*
4	4/ 8/75	7:45 a.m.	3
		8:45 a.m.	2
		8:55 a.m.	3
	4/12/75	7:25 a.m.	3
	4/29/75	7:05 a.m.	1
	4/30/75	7:05 a.m.	3
	5/ 6/75	7:10 a.m.	4
	5/ 8/75	6:35 a.m.	2
	5/13/75	7:40 a.m.	2
	5/14/75	5:50 a.m.	1
	5/15/75	6:40 a.m.	5
	6/ 3/75	6:45 a.m.	3

New Guinea, to neighboring regions of Melanesia, and to Timor, the Moluccas, the Solomon Islands, and the Philippines (Brown, 1958; Wilson, 1958; 1959). The genus is a large one, and ranges from tropical rain-forest environments at one latitudinal extreme of its range to temperate and relatively wet habitats in southern Victoria and Tasmania and the extreme Australian southwest, while one group within the genus has invaded highly xerophytic environments in the Australian inland. A large number of species are particularly interesting in that normal alate females are either absent or rare and apparently do not take a normal part in colony functions. Instead a proportion of workers, externally morphologically indistinguishable from their fellows, possess functional spermathecae, are fertilized by the active, low-flying males, and serve as multiple worker-producing reproductives in the colony (Whelden, 1957; 1960; Haskins and Whelden, 1965).

Rhytidoponera is a fairly dominant genus where it occurs, and, as Brown (1958) has pointed out, its more abundant members appear to occupy in Australia the ecological niche of such relatively primitive general-feeding Myrmicines as the genus *Myrmica* in palearctic and nearctic environments. Indeed, it has been suggested that the primitive Ectatommines may be fairly close to the ancestral stirp of the Myrmicinae.

The commonest and best-known member of the genus *Rhytidoponera* is *R. metallica,* the Australian "greenhead" ant. It is fairly ubiquitous in eastern Australia, even commonly invading parks and gardens. It is readily obtainable, easy of culture, and in general a nearly ideal laboratory animal for the study of behavioral patterns in that section of the genus in which normal alate females are usually lacking.

In the course of a ten-year study of this species in the laboratory and the field, particular attention was paid to the mode of mating of the fertilized workers, and of the founding of new colonies. In the course of this investigation, numerous observations have been made of worker behavior closely resembling the "calling" pattern in *Leptothorax*. The earliest of these observations were recorded several years ago (Haskins and Whelden, 1965) but as they have been considerably expanded since, and as they seem to "fit" so accurately the pattern described for *Leptothorax* and its congeners, it has seemed appropriate to expand the record.

In *R. metallica* males are produced irregularly throughout the year, both in the laboratory and in the field. They are characteristically low-flying, and W. L. Brown, Jr. some years ago observed them coursing closely over the ground, and entering the nests of other colonies (unpublished observations).

In laboratory colonies, as earlier described (Haskins and Whelden, 1965) groups of workers were observed in September, 1952, to emerge from the artificial nests and rest quietly grouped near their entrances, with head and thorax closely appressed to the substrate and gaster raised and arched. At the same time, the sting was characteristically exserted. This immobile "pose" was usually main-tained only briefly, but in the longest interval recorded, for over twelve minutes. It was commonly interrupted eventually by other foraging or recently "calling" workers nearby. During this process, copulations might occur with recently emerged males, although there was no clearly exhibited preference of males for "calling" workers over those that were wandering or foraging normally.[1]

Since these observations were published, this pattern has been observed repeatedly in further colonies of *R. metallica* housed in laboratory nests. The sets of observations shown below are typical. They involved three colonies in all, originally collected at Nam-

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[1] See Hölldobler, B. and C. P. Haskins (*Science* 195, 793–794) for illustrations of this behavior.

bours, Northern Queensland, in December of 1963, and maintained under constant conditions in the laboratory since that time.

Several details of interest emerged from this range of observations. The first was the virtually seasonally-independent nature of the events. In 1952 "calling" workers were seen in September and October, in 1953 in July and November, in 1975 in April, May, June, July, and October, in 1976 in January and March. Thus every month was represented except February, August, and December. This is particularly noteworthy since the observations of 1952 and 1953 were made on colonies from a population taken near Sutherland, N.S.W. in essentially a temperate location, while those for 1975–76 were derived from a population in the vicinity of Nambours, Queensland, many miles to the north and in essentially a tropical rain forest area.

Flights of males, as noted both by Brown (1958) and ourselves (1965), are likewise highly non-specific with respect to season. Worker "calling" and male flights both appear to take place predominantly during early to mid-morning hours. It is of interest, also, that the presence of males in the nest, much less their emergence, is not a prerequisite for worker "calling". During the observations of "calling" made in January, 1957 and May 1975 males were present in the nests, and in at least one case there was simultaneous male emergence. However, worker "calling" took place in the absence of male flights in October, 1952 and July 1953 (involving the same colonies in which males were present during "calling" in 1957) and in all of the 34 instances recorded for Colonies 1 and 3. In both those colonies males had long been absent, and examination of samples of pupae present in Colony #1 (3) made during the height of the "calling" period in that small community revealed only workers to be present in the brood.

The length of time of the "calling" behavior of workers of *R. metallica* is typically brief, averaging 1–2 minutes (although one record period of more than 12 minutes has been noted). Usually, however, workers moved about after a short period, commonly resuming the behavior at another location. In this respect, the pattern resembled that observed by Buschinger for *Formicoxenus nitidulus*.

It seems probable that this behavior in *R. metallica* (observed also in three other species of the genus: *R. tasmaniensis; R. inornata,* and *R. violacea*) does indeed correspond quite closely with the typical "calling" pattern in *Leptothorax* and the related Myrmicine genera where it has been observed. As in those cases, the sting is clearly exserted during the "calling" process, but Hölldobler (Hölldobler and Haskins, 1977) has clearly demonstrated that here the newly-described tergal gland, strongly developed in *Rhytidoponera* is an important, if not the sole, source of the pheromone.[2]

With *Rhytidoponera,* as with *Amblyopone,* the behavior is evidently only of sexual significance. No evidence of any worker-worker recruiting has been obtained for either genus.

It seems of real interest that the "calling" behavior seems to be well established, entirely in a sexual context, at so primitive a grade of Formicid evolution. It is particularly interesting that it should be so clearly demonstrated within the Ectatommini, a division of the Ponerinae which, on morphological grounds, is thought to be fairly close to the main evolutionary stem leading from the Ponerinae to the Myrmicinae. Finally, the nature of the colonies and the nuptial flights of both *Amblyopone* and *Rhytidoponera* emphasizes a reflection of Buschinger, who has suggested (1975) that there may well be a correlation between the "use" of male mandibular-gland-derived sex pheromones in the mediation of highly coordinated massive mating swarms and of female sex pheromones, derived from sting or Dufours glands, in smaller, poorly coordinated "straggling" colony flights. The former are characteristic of ant species forming large closely-knit communities, the latter of those existing in smaller, more diffuse, less highly integrated communities of species which are often more rare. Though none of the species considered here is especially rare, all do form typically scattered, rather feebly integrated communities having inconspicuous and essentially uncoordinated nuptial flights.

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[2] An extensive paper by B. Hölldobler and H. Engel on tergal and sternal glands in ants is included in this issue of Psyche.

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A RESTUDY OF TWO ANTS FROM THE SICILIAN AMBER

By William L. Brown, Jr.[1] and Frank M. Carpenter[2]

Introduction

The ants of the (presumably Miocene) Sicilian Amber were monographed by Emery (1891), and, except for corrections published by Emery himself (1913), this faunule has not again been subjected to critical study. Since 1891, of course, formicid taxonomy has undergone radical changes, some of them affecting genera found in this amber. *Ectatomma gracile,* for example, was described from a male specimen that would not today be placed in *Ectatomma,* but instead, as based on Emery's description (1891:571) and figures (Pl. 1, fig. 1, 2) is assignable to *Gnamptogenys* (Kugler and Brown, in prep.).

It is not our purpose here, however, to review all of Emery's Sicilian Amber ants. Rather, we want to present the results of our study of just two of his type specimens that are particularly significant for ant taxonomy. The specimens, in two separate pieces of amber belonging to the Museo Mineralogico dell'Universitá degli Studi, Bologna, Italy, were lent through the kindness of Prof. Gianfranco Simboli, Director of the Museo Mineralogico, who has our thanks. The new preparation of the specimens and their photographs were done by FMC, while WLB is responsible for the taxonomic interpretation of the material.

Hypopomyrmex bombiccii

Emery, 1891:574–575, pl. 1, fig. 10, 11, alate queen.

This specimen (figs. 1, 2) is a badly collapsed winged queen closely involved in the same piece of amber with a worker specimen of *Cataulacus planiceps.* Emery, in his fig. 10, and especially fig. 11, portrays the *H. bombiccii* specimen as a *Strumigenys*-like individ-

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Figure 1. *Hypopomyrmex bombiccii*, type queen viewed from left side. Dark mass below queen is the curled type of *Cataulacus planiceps*. The view is essentially the same as portrayed by Emery (1891: pl. 1, fig. 10). Length of fore wing, 3.7 mm.

Figure 2. *Hypopomyrmex bombiccii*, type queen viewed from right side. Length of fore wing, 3.7 mm.

Figure 3. *Sicilomyrmex corniger*, type worker viewed from right side. Length of body, 4.7 mm.

Figure 4. *Sicilomyrmex corniger*, type worker, dorsal (facial) view of head, tilted slightly forward.

ual; a small eye is shown arising from beneath a scrobe-like head groove, and elongate mandibles are suggested in vague outline. The 10-segmented antenna is depicted by Emery with a clearly 2-merous club and an apically thickened and sharply bent scape.

The amber piece has now been cleaned, partly re-ground, and somewhat cleared by injection of a small amount of Canada balsam. Figures 1 and 2 are photographs of the *Hypopomyrmex bombiccii* type, a winged queen, in the new preparation. The specimen is badly shrivelled and compressed, especially from side to side, and the petiolar and postpetiolar nodes are strongly compressed anteroposteriorly. It can now be seen that the *Strumigenys*-like cranial shape portrayed by Emery is really only his free interpretation of the crumpled head; the deformed left eye protrudes from the dorsolateral margin of the head, not from any scrobe, and the mandibles do not extend as Emery's figure 11 vaguely suggests they do. The right side view (fig. 2) of the head now available shows the right compound eye also distorted, but larger, more elliptical and less protruding than the left eye. The right antennal scape has its apex flattened, but not sharply bent like that of the left scape, indicating that the latter was distorted after death.

Hypopomyrmex is clearly not a member of tribe *Dacetini.* Habitus, wing venation and the form of the waist do place it in the subfamily Myrmicinae. The 10-merous antennae with 2-merous club, the forewing venation and the propodeal teeth make it most likely a member of the group of genera near *Pheidologeton,* and it may be regarded as a doubtful synonym of *Oligomyrmex.* The taxonomy of the living forms of this group is still so poorly known, and the fossil is in such poor condition that formal synonymy here would be premature.

It may be noted, however, that *Oligomyrmex sophiae* (=*Aeromyrma sophiae*), based on male specimens, was described by Emery from the Sicilian Amber in the same (1891) paper.

With the removal of *Hypopomyrmex* from the Dacetini, that tribe loses its entire known fossil history.

Sicilomyrmex corniger

Gesomyrmex corniger Emery 1891:581, pl. 3, fig. 33–35, worker.

This extraordinary formicine is portrayed in the photographs (figs. 3 and 4). Emery originally assigned it to *Gesomyrmex,* but the bicornuate head and two-spined propodeum clearly put it into a separate genus, as W.M. Wheeler realized in 1915, when he applied a new generic name in the combination *Sicelomyrmex corniger.* Unfortunately, the new genus name was one of several misspelled in this German wartime publication, which Wheeler apparently did not see in proof. He published the name in the emended form *Sicilomyrmex* in 1926, and again in 1928, but by 1929 he had reverted, perhaps absent-mindedly, to the spelling *Sicelomyrmex,* and even suggested for it a new tribe, Sicelomyrmicini. The tribal name was in any case improperly coined, since the stem involved is *myrmec-*, not *myrmic-*.

It would seem proper to recognize the emended spelling *Sicilomyrmex* of 1926 and 1928, since it is clear that Wheeler in 1915 was alluding to the provenience of the specimen from the Sicilian Amber, and that the original spelling *Sicelomyrmex* was therefore either a *lapsus calami* or a printer's error, according to Article 33(a)(ii) of the International Code of Zoological Nomenclature. The necessary emendation of the tribal name thus results in Sicilomyrmecini. Whether this tribe is worth retaining can only be decided after full revisionary study of the tribal classification of subfamily Formicinae.

Emery's original drawings of *S. corniger* were good ones, but we think that the first photographs of the type specimen (figs. 3 and 4) give an excellent idea of its habitus.

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The illustration on the front cover of this issue of Psyche is a reproduction of the published figure of the minute diapriid, *Solenopsia americana* (1.3 mm. long), described by C. T. Brues in Psyche (1936, vol. 43, p. 17). The insect was taken in the nest of an ant, *Paratrechina parvula,* in eastern Tennessee.

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