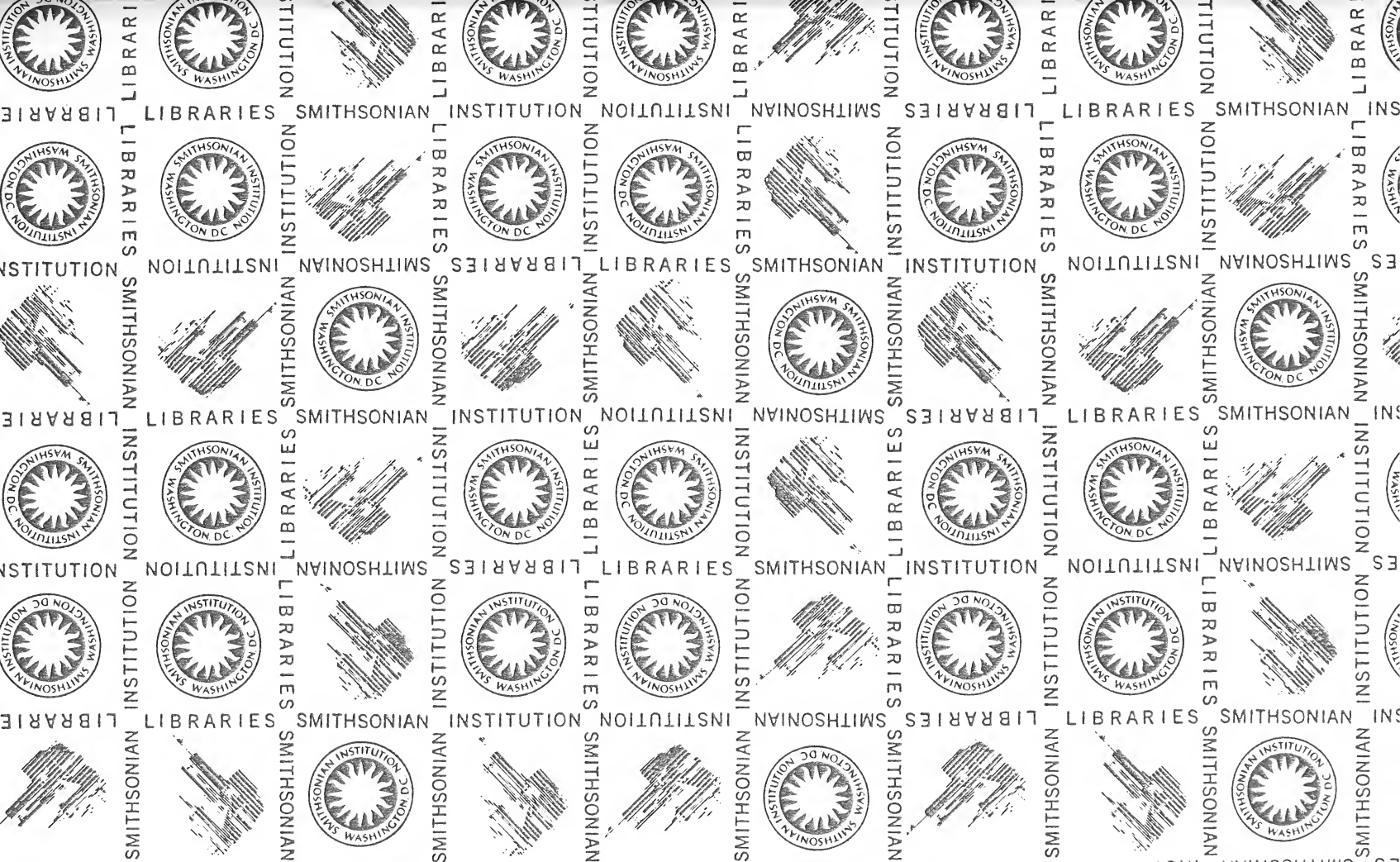
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TRAIL PATTERNS AND MOVEMENT OF WORKERS AMONG NESTS IN THE ANT *FORMICA OBSCURIPES* (HYMENOPTERA: FORMICIDAE)*

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Introduction

In ants of the genus *Formica,* intraspecific interactions among workers from different nest mounds vary from mutual tolerance to aggression and territoriality. For example, workers of *Formica opaciventris* and *F. ulkei* commonly visited nearby nests without evoking agonistic responses (Scherba, 1964; Talbot, 1961). On the other hand, in a study of a British population of *F. rufa,* workers engaged in aggressive territorial contests with workers from nearby mounds (Skinner, 1980). Both aggressive and non-aggressive interactions have been observed within populations of *F. rufa* in Russia (Marikovsky, 1962) and *F. polyctena* (Mabelis, 1979a, b). This is not surprising, since *Formica* populations may consist of separate colonies, some of which have multiple nests (i.e. polydomous colonies; Pamilo *et al.,* 1978; Wilson, 1971). The elucidation of patterns of interactions among workers from different nest mounds is essential for an understanding of the genetic organization of populations (Pamilo, 1981, 1982; Pamilo *et al.,* 1978), the social structure and spatial dispersion of colonies, and the proximate factors influencing the form of intraspecific interactions among ants. Such interactions are apparently influenced by the recent history of nest founding and

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nest splitting in a population which defines the spatial correlates of relatedness among nests and colonies (Mabelis, 1979a, b; Pamilo, 1981) and may be regulated by the patterns of foraging trails (Hölldobler, 1974, 1976; Hölldobler and Lumsden, 1980; Skinner, 1980; Brian, 1983). Competition among ant colonies for limited resources may also play a role in defining the nest distribution (Levings and Traniello, 1981; Ryti and Case, 1986) and nature of interactions (Mabelis, 1979b; Skinner, 1980).

Formica obscuripes Forel is a common ant of the northcentral and western United States, where it constructs mound nests covered with twigs, grass stems, and other plant material. Nests are connected to foraging areas via a system of permanent trails over which foragers return to nests with honeydew, prey, and carrion (Weber, 1935). This paper reports the results of a study of the pattern of trails among a group of 45 nest mounds and the movement of workers among nests in relation to trail location in *F. obscuripes.* Here, the term "nest" refers simply to a distinct above ground mound, without implying that each mound represents a discrete colony.

Materials and Methods

Formica obscuripes was studied at a site along an unused railroad track near the outskirts of Bozeman, MT from 16 June through 11 September, 1986. There were 45 nests active during the study period. Twenty-nine were chosen for more careful study. A map of the study site was constructed to include the location of all of the nests, trails used by the worker ants, and the major patches of plants visited by the ants. The site was surveyed at least once per week for the presence of new trails and nests. The mounds of plant material constituting the above ground portion of nests of *F. obscuripes* at the research site ranged in height from four to 33 cm (mean = 9.9; SD = 7.8; N = 29) with the maximum width of mounds ranging from 15 to 130 cm (mean = 54.9; SD = 28.8; N = 29). Since there were few plants growing on nests, the mounds were conspicuous. Thus, it is likely that all of the mounds within the research site were located.

To determine the movement patterns of workers, a large number were marked using two different techniques: 1) between 17 July and 18 August, 1300 workers from five nests were marked on the dor-

sum of the abdomen with dots of colored enamel paint; 2) a larger sample of unknown size was marked by spraying the surface of active nests with a fine mist of enamel paint, applying minute spots of paint to the surface of the ants. Workers ants marked in this manner continued to work on the nest surface and forage for the remainder of the season. This indicates that this marking technique did not have an adverse effect upon most workers. At least three of these workers were still present on nests on 15 March, 1987. Ants from nine nests were marked using these methods, allowing me to later determine the distance that many of the ants moved from the original location at which they were observed.

Nest census techniques were modified from those of Scherba (1964). After tapping the surface of the nest to arouse the workers, all marked workers appearing over the next two minutes were counted, removed, and killed. This was done once each day on nine days between 25 August and 11 September. The study was terminated at this time because the railroad company had the tracks removed on 14 September. This destroyed many of the nests and disrupted much of the system of trails between the remaining nests. Censuses were conducted only before 1000 hours or after 1700 hours, since workers did not remain on the nest in the middle of the day when surface temperatures were high (O'Neill and Kemp, unpublished). In the results, a single "crossover" refers to the recapture, on a censused nest, of one or more workers originally marked on another nest. Thus, if five workers marked on nest #6 were later recaptured on nest #11, this is recorded as a single crossover.

To determine whether workers on a nest would tolerate the presence of workers from other nests, an experiment was conducted in which workers were transferred between nests. The experimental group consisted of 40 workers collected on the surface of nests and transferred individually to other nests, not connected via a trail to the nest on which they were captured. As a control, 30 workers were moved between nests connected to one another via a trail system. A second control consisted of 5 workers removed from the surface of a nest and returned to the surface of the same nest. Each ant was handled only with a pair of forceps that had just been washed with ethylene chloride and air dried. After introduction to the surface of the nest, the worker was monitored until ten workers from the nests had made contact with it; during this period I recorded whether or not it was attacked by workers present on the nest surface.

Results

Trail pattern: Trails of *Formica* consisted primarily of permanent pathways used by ants to travel from nests to foraging areas and to other nests. The workers foraged for at least two types of resources. They visited plants in the area that had populations of honeydew-secreting Homoptera. These included several species of aphids (Aphididae) and two species of Membracidae (*Campylenchia latipes* Say and *Publilia modesta* (Uhler)). They also foraged on and near trails for dead and living arthropods. The major items being carried by workers to nests along trails included terrestrial isopods (Crustacea: Oniscoidea), various species of leafhopper (Homoptera: Cicadellidae), Lepidoptera larvae, and workers of other species of ants, especially *Formica neoclara* Emery. Workers of *F. obscuripes* were observed to prey upon workers of *F. neoclara* on at least a dozen occasions. Nests of the latter species were sometimes within a meter of nests of *F. obscuripes.*

The major trails (Figure 1) remained active throughout the study period. The trails coming from the nests led to 1) concentrations of Homoptera on Canada thistle (*Cirsium arvense*), chokecherry (*Prunus virginiana*), and several other species of plants and 2) other nests (Figure 1). Five non-overlapping systems of trails (labelled A through D in Figure 1) that intersected 32 of 45 nests were identified at the study site. The longest trail system (A), consisting of two long parallel trails and branches leading from them, followed an old railway bed and served 23 nests (nest group A). The other trail systems, within nest groups B through E, served two, three, two, and two nests, respectively. Six of the 13 nests for which no trails were observed became inactive by the end of the study period; all other nests remained active throughout. Only two short sections of trail (i.e. one between nests #4 and #6 and another crossing the railway bed near nest #6; Figure 1) disappeared during the course of the study. Both had been abandoned at least one month before the censusing began.

Worker movement: Workers were marked on eight nests from group A. In nine surveys (sampling without replacement) of 29 nests in the area made on nine days between 25 August and 11 September, 1986, ants from these eight nests were found to make 88 (39%) of a possible 224 different crossovers to other nests. A total of 405 workers were recaptured on nests other than those on which they

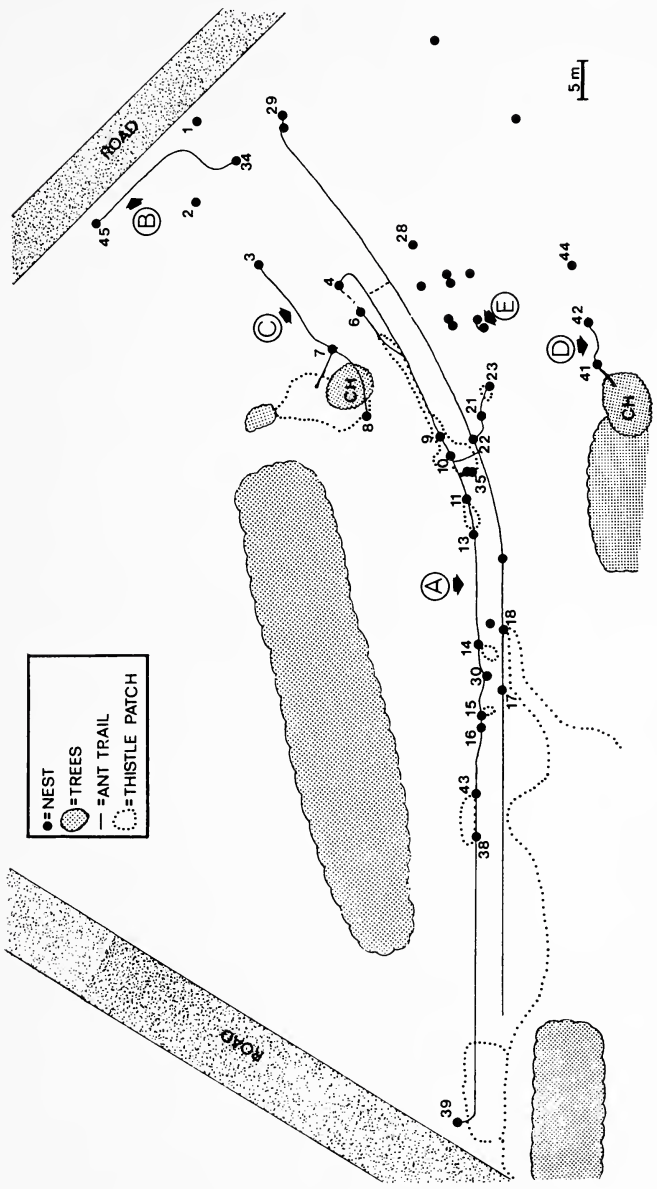

Figure 1. A map of the study site showing ant trail patterns and the position of nests and large patches of vegetation, such as Canada thistle (circumscribed by dotted lines) and chokecherry (shaded CH), harboring honeydew producing Homoptera. Censused nests are numbered and the trail systems connecting nests within groups are labelled A through E. Dashed lined segments of trails are those that disappeared early in the season before censusing of marked workers began.

were marked. Marked ants observed on nests were moving about without interference from other ants present. On five occasions, ants marked on other mounds were observed entering nests. Workers often travelled great distances between nests. For example, the worker from nest #4 found on #39 would have had to traverse over 120 m of trail between the two nests, which were about 112 m apart.

Although there was considerable movement of workers among nests, the pattern of crossovers was non-random. The nest censusing described above included nests that were not connected to each other via trails. While all of the ants were marked on nest group A, only 20 of the surveyed nests were within this group. Of the remaining nine, one (#34) was in group B, three (#3, #7, and #8) were in group C, two (#41 and #42) were in group D, and three (#1, #2, and #28) were not connected by trails to other nests during the course of the study. Ants marked on nests in group A were rarely found on nests of other groups (Table 1). Of the 88 different crossovers noted above, 86 were between nests within group A. The exceptions were an individual from nest #4 found on nests #7 and two from nest #29 found on #28. Thus, fewer than 1% of the 405 marked ants recaptured on nests other than those on which they were marked were found on nests outside of group A. Apparently, workers from nests in group A rarely mingled with those from other trail systems, possibly because they do not travel the distances separating different trail systems or because workers will not tolerate the presence of workers from other colonies.

Crossovers among nests *within* group A were also non-random. The movement of workers among nests was asymmetrical. For example, while only two workers from other nests were seen on nest #29, 142 marked workers from #29 were found on 14 other nests (67% of those censused). The opposite was true of nest #11: 68 workers from seven other nests were found on this nest, while only 13 workers from #11 were found on seven other nests (33% of those censused). In addition, marked workers did not distribute themselves evenly among nests to which they had transferred. For example, of the 142 workers from nest #29 found on 14 other nests, 121 (85%) were found on just five of these mounds.

Out of the total of 1300 ants marked with single dots of paint on the abdomen (described in methods section as marking procedure #1), 313 (42%) were recovered in the nine subsequent surveys. Of

Table 1. The number of different crossovers (i.e. where at least one marked individual from a nest was found on censused nest) and the number of marked workers observed during censuses. All workers were originally marked on one of eight nests in group A. Comparison on different crossovers within group A to those from group A to other censused nests (i.e. row 5 vs. row 6), $\chi^2_1 = 36.0$, $P < 0.001$.

	Different Crossovers			# Workers Crossing Over	
Censused Nest Group (# nests)	Observed	Possible	%	Observed	Mean #/ Nest
Group B (1)	1	8	12.5	1	1.0
Group C (3)	0	24	0	0	0
Group D (2)	0	16	0	0	0
Others not in Groups (3)	1	24	4.2	2	0.7
SUBTOTAL (Non-Group A) (9)	2	72	2.8	3	0.3
Group A (20)	86	152	56.6	402	20.1
Overall Total	88	224	39.3	405	14.0

these, 152 (49%) were found on nests other than those on which they were marked (Table 2).

Lack of tolerance of ants from one nest group for ants of another was demonstrated in experiments in which ants were transferred between nests. Ants taken from distant nests and placed on nests in group A were always vigorously attacked by workers on the surface of nests (rows 1 and 2 of Table 3). Attacking ants attempted to bite and seize the intruder with their mandibles and often succeeded in dragging the intruder into the nest. This was essentially the same type of aggressive response to alien workers reported for *Formica fusca* (Wallis, 1962). Intruders were sometimes attacked within several seconds, with as many as six attackers eventually surrounding them. A similar result was found when ants from groups A and C were switched between groups (row 3). On the other hand, ants in control manipulations were not attacked (rows 4–6).

Observations on a section of the trail near nest #6 (Figure 1) showed that ants marked on other nests in the same nest group (A) brought dead arthropods and honeydew to this nest. In 51 ten minute censuses on 14 days between 21 July and 20 August, 52 marked ants were carrying liquid (probably honeydew) to the nest (i.e. they had extremely distended abdomens and regurgitated liquid when

Table 2. A comparison of the number of marked workers from five nests that were recaptured on the nest on which they were marked with the number found on other nests.

Nest that ant was marked on (total released)	Number recaptured on nest on which ant was marked	Number recaptured on other nests	Total recaptured
Number 4 (200)	8	22	30
Number 7 (250)	29	18	47
Number 11 (200)	10	13	23
Number 15 (300)	75	66	141
Number 21 (350)	39	33	72
Total (1300)	161	152	313

squeezed slightly) and seven carried dead arthropods. Of these, 20 (34%) had been originally marked on other nests of group A (i.e. nests 4, 9, 10, and 11). During the same censuses, none of the 72 marked ants (including 31 from other nests) moving away from nest #6 were obviously replete with honeydew or were carrying arthropod carrion or prey. Thus, traffic of successful foragers occurred in only one direction along this trail (i.e. towards nest #6) and included foragers originally seen on other nests. However, workers transporting live ant larvae were seen travelling along trails in both directions near nest #6 and elsewhere in the manner described for *F. polyctena* (Mabelis, 1979a).

The data above support the conclusion that nests of group A form a group of physically inter-connected (i.e. by trails) and, possibly, functionally integrated nests. Workers were rarely found on nests of other groups and did not tolerate the presence of workers from distant nests. However, an absolute barrier did not exist between nests not connected by trails. As noted above, one worker from nest #4 was active on the surface of nest #7 and two from nest #29 were on #28, apparently being tolerated by other workers. Furthermore, some of the 250 workers marked on nest #7 (group C) were recaptured either on nests of group A (11 observations during the nine censuses) or on the trail system of group A (3 observations during the censuses of trail near nest #6). Most (36) of the recaptured workers from nest #7, were found on nests of group C.

Discussion

The data reported here indicate that movement of workers among nest mounds in the local population *F. obscuripes* was non-random,

Table 3. Results of introduction of worker ants to the surface of nests. Each was handled only with a pair of clean forceps and was watched for 30 s after being in introduced.

Manipulation	# ants tolerated	# ants attacked	Total	% Attacked
Moved from site 15 km away to nests of group A	0	10	10	100
Moved from site 1 km away to nests of group A	0	10	10	100
Moved between nests of group A and group D	4	16	20	80
Within nest group switches: group A	20	0	20	0
Within nest group switches: group D	10	0	10	0
Sham switches (ant picked up and returned to same nest)	5	0	5	0

both within and between nest groups. The vast majority of workers found to move to other nests were recaptured within the same nest group: 99% of workers from group A that were recaptured and 77% of workers from group C that were recaptured. This occurred even though the absolute distance *between* nest groups was often much less than the distance between given nest pairs that exchanged workers within a group. For example, while the distance moved by workers within group A was often greater than 50 meters, they were rarely found to leave the nest group and join nests of other groups that were sometimes just several meters away from the trail system. Within nest groups, a mound did not always receive the same number of marked workers that were found to move from it to other nests. Furthermore, marked workers moving off of a nest did not distribute themselves evenly among other nests within a nest group. As indicated by occasional recapture of marked ants on nests outside of their "home" nest group (Table 1) and the results of experiments transferring workers between nests in groups A and D (Table 3, row 3), the barrier between nest groups was not absolute. This suggests, perhaps, that territoriality in these ants is expressed as a graded effect, with tolerance for conspecifics from other colonies decreasing with distance or the duration of time passed since two

mounds had a common ancestor (Mabelis, 1979b). However, further data are needed to confirm this for *F. obscuripes.*

Discussion of several limitations of the data are in order. First, as noted by Scherba (1964) the census techniques used produced only minimum estimates of crossover of marked workers among nests, since only a limited number of censuses were conducted. Second, workers captured from a nest for marking did not necessarily develop within that nest. The data reported here provide evidence for worker movement among mounds, but not an absolute picture of the pattern of switching among nests. For example, if all workers marked on nest #6 did not originate in that nest, their recapture on nest #11 does not indicate the exact proportion of workers making the switch from nest #6 to nest #11. In fact, we could reverse our interpretation of the mark-recapture data: perhaps workers captured on a nest for marking developed in the mound on which they were subsequently recaptured. This also means that the data do not allow us to determine whether workers originating in one nest eventually acted as foragers for other nests. Finally, since the majority of the workers marked were probably foragers rather nest workers, the percentage of ants found to cross over is probably an overestimate, since the latter are probably more philopatric.

In the absence of such information as the recent history of nest splitting (Mabelis, 1979a, b) and degrees of relatedness among nests and colonies (Pamilo, 1981, 1982), the pattern of worker movement observed remains descriptive. However, the data indicate that, in this population, some colonies of *F. obscuripes* are polydomous. This matches observations from an earlier study of this species in which Weber (1935) found "secondary nests...generally connected by a well-defined runway to the main nest". Since the history of the population in the present study is unknown, the parent ("main") nest within a group cannot be determined. Although the nest mounds varied markedly in size, it is known for *F. ulkei* that there is not a simple linear correlation between nest size and age (Dreyer, 1942).

Colonies with multiple nest mounds connected via trail systems have been noted within other species of *Formica* (Mabelis, 1979a; Marikovsky, 1962; Skinner, 1980) and within species of other ant genera, such as *Lasius* and *Iridomyrmex* (e.g. Greenslade and Halliday, 1983; Yamauchi *et al.,* 1981). However, the existence of permanent trails is not a prerequisite for exchange of workers among mounds. Crossover of workers among mounds occurs in the

absence of trails in *F. opaciventris* (Scherba, 1964) and at times when apparently temporary trails are formed in *F. ulkei* (Talbot, 1961). When trails do exist in polydomous colonies they seem to function both as pathways for worker movement among nests and to foraging areas. Trail patterns may also be correlated with the shape of a colony's territory both in *Formica* (Mabelis, 1979b; Skinner, 1980) and other ants (Hölldobler, 1974, 1976) and, thus, be a product of both resource distribution and interactions among neighboring colonies. Habitat heterogeneity influences trail pattern, when the workers construct trails to avoid or cross unused areas of habitat (Reyes, 1986) and when features, such as roads or railway beds, define the pattern of usable habitat. The trail patterns observed in the present study suggest that habitat heterogeneity and the distribution of nests and Homoptera bearing plants influence trail location.

Summary

Workers of the ant *Formica obscuripes* Forel, at a site in southwestern Montana, used a system of trails to travel between different nest mounds and between nests and foraging areas (primarily patches of plants bearing honeydew secreting Membracidae and Aphididae). Different groups of nests, served by non-overlapping systems of trails, apparently constituted polydomous colonies. Movement of workers among mounds was non-random both within and between nest groups. In a mark-recapture study, 97% of the workers recaptured on nests other than those on which they were marked were found on mounds within the same trail system. Experiments in which workers were transferred between mounds demonstrated that ants tolerated workers from mounds within their own nest group, but usually acted aggressively towards workers from other nest groups. The trail patterns remained stable during the three-month study and connected nests up to 135 m apart. The results are compared to those obtained in other studies of *Formica*.

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mined the Membracidae. Ruth O'Neill, Daniel Bartell, Howard E. Evans, Michael Ivie, William P. Kemp, Wendell Morrill, and Randall Ryti provided comments on the manuscript. Contribution No. J-2086 from Montana Agric. Exp. Sta.

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A CHRYSOPID LARVA THAT CLOAKS ITSELF IN MEALYBUG WAX[1]

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While doing field work on Lignumvitae Key, Monroe County, Florida, on May 18–20, 1974, we noted a widespread mealybug infestation, on the underside of leaves of a shrub of the genus *Eugenia* (family Myrtaceae). The colonies, which sometimes extended over entire branches of the plant, were easily detectable from a distance by the white waxy covering of the mealybugs. Close inspection showed the mealybugs to be of unusual appearance, and to be associated with a chrysopid predator that seemed itself to be cloaked in wax.

The mealybug turned out to be undescribed. Discovered independently by Miller and Denno (1977), it was assigned to a new genus by these authors and named *Plotococcus eugeniae*. The holotype is from a series we collected at our Lignumvitae site. The main features of *P. eugeniae* are evident from Figure 1A. Most conspicuous are the long lateral wax filaments, present in mature and developing females, which impart upon these forms a distinct stellate appearance. Younger individuals, including "crawlers," which have fewer and shorter filaments, are often partly hidden beneath the overlapping filaments of females. Microscopic examination of filaments showed these to consist of central shafts, densely beset with powdery wax (Fig. 2). The surface of infested leaves typically bore a loose coating of this wax.

The chrysopid, camouflaged by the wax packet on its back (Fig. 1B, C), had initially escaped our detection. We eventually learned to spot it at close range, by the oval shape of its packet, and its occasional mobility. It proved surprisingly abundant. We located dozens of individuals amidst the mealybugs in a few hours of observation.

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[1]Paper no. 85 of the series *Defense Mechanisms of Arthropods.*

[2]Deceased, January 13, 1982.

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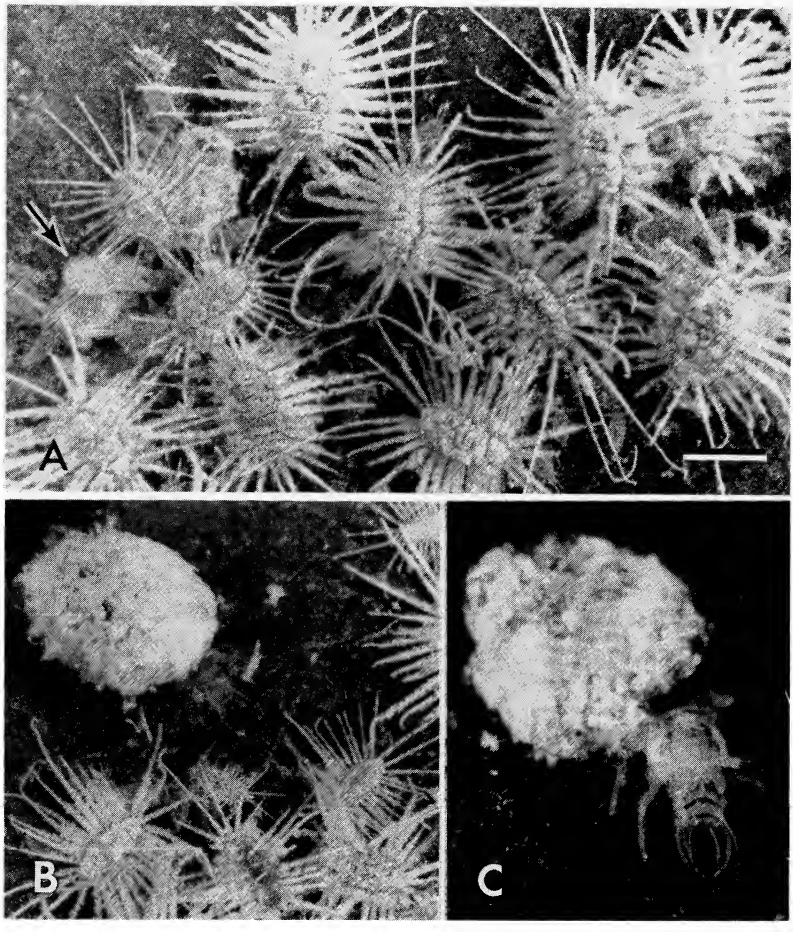

Fig. 1. A, Detail of colony of *Plotococcus eugeniae*. The large stellate individuals are females. A winged male is denoted by the arrow. B, Last instar larva of *Ceraeochrysa cincta* amidst its prey. C, Same, enlarged view (Bar in A = 1 mm).

Pupal cocoons were present as well, as were typical stalked chrysopid eggs, on or near the infested leaves. The cocoons were themselves white from wax incorporated into their case, and therefore well camouflaged when located near mealybugs. We succeeded in raising over two dozen adults, some from pupae, others from young larvae. All were identified as *Ceraeochrysa cincta* (voucher material deposited in the Cornell University insect collection, lot no. 1164).

Closeup observation of *C. cincta* larvae that we took with colonies of *Plotococcus* to a laboratory setting (Archbold Biological Station, Lake Placid, Florida) enabled us to determine that the larvae do indeed construct their packets from wax that they pluck from mealybugs. We removed packets from several larvae with forceps, and then observed how they rebuilt their packets when we returned them to their hosts. Most commenced packet construction at once. They approached individual mealybugs, most often filament-bearing females, and grasped one or more of the filaments with their curved mandibles. They then pulled back, grasping a load of wax powder in the process, together with occasional filaments that became detached. Finally they flexed the head sharply over the abdomen, and deposited the load directly on their back. They often arched the back upward at the same time, so as to bring it within reach of the mandibles. Load after waxy load they sequestered in this fashion, shifting from mealybug to mealybug as they plucked away, until their packet was complete. At times they supplemented their gatherings with scoopings of wax and debris from the leaf surface, but mealybug wax seemed to take priority for all larvae.

In feeding, the chrysopids seemed to prefer the younger stages of the mealybug. They consumed mostly "crawlers" and other early instars, and appeared to avoid the larger filament-bearing forms. We did not observe chrysopids adding sucked-out prey remains to their dorsal packets, perhaps because such packets were already fully formed in individuals we noted feeding. Packets that we had removed from individuals used in the reloading tests, when teased apart, did show presence of whole-mealybug remains.

Ceraeochrysa cincta is evidently a "trash-carrier," a member of that large group of chrysopids whose larvae all build dorsal packets from exogenous materials, including vegetable matter, arthropod remains, and general debris (DeWitz, 1885; Killington 1936, 1937; Slocum and Lawrey, 1976; Smith, 1922). Use of homopteran wax for packet construction is not without precedent. *Chrysopa slossonae,* an obligate predator of the wooly alder aphid, *Prociphilus tesselatus,* plucks wax from its prey and builds a dense shield from this material, which protects it against ants (Eisner *et al.,* 1978). *C. cincta* may be similarly protected by its packet, possibly against other predators as well. The camouflage itself, by reducing conspicuousness to visually oriented predators, including perhaps birds, which might be expected to ignore mealybugs, could provide a first line of defense.

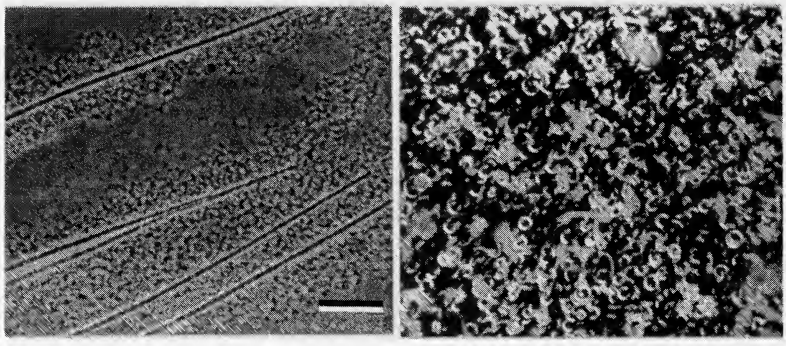

Fig. 2. Left; wax filaments of *Plotococcus eugeniae.* Note loose coating of wax powder on the central shafts (Phase microscopy). Right; isolated particles of wax powder (Dark Field microscopy). (Bar on left, valid for both = 50 μm).

We observed two additional chrysopid predators in the *Plotococcus* colonies, both less numerous than *C. cincta,* as well as one abundant syrphid fly larva. One of the chrysopids, which we succeeded in raising, proved to be *Chrysopodes collaris.* The syrphid, which we also raised, was identified as *Ocyptamus parvicornis.*

Preliminary chemical work by H. M. Fales and R. T. Mason at the National Institutes of Health, Bethesda, Maryland, showed the *P. eugeniae* wax to consist of a mixture of triglycerides of even-numbered (C_{10} to C_{18}) fatty acids.

Postscript and Acknowledgments

We had initially hoped to undertake an in-depth study of *Plotococcus* and its associates, a plan that was thwarted by the tragic death of Robert E. Silberglied. The present paper, written by the senior author, is based on notes taken jointly with Dr. Silberglied. For identification of the chrysopids and syrphid, we are indebted, respectively, to Philip Adams (California State University, Fullerton) and F. Christian Thompson (U.S. National Museum of Natural History). We thank the staff of the Archbold Biological Station, Lake Placid, Florida, for hospitality during our stay. Maria Eisner prepared the illustrations.

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REPRODUCTION AND DISPERSAL IN THE ANT *CATAGLYPHIS CURSOR* (HYMENOPTERA, FORMICIDAE)

By A. Lenoir[1], L. Querard[2], N. Pondicq[2] and F. Berton[2]

Introduction

Cataglyphis cursor (Fonscolombe 1846) is a Mediterranean formicine species, living in dry and arid habitats which have sparce vegetation (Cagniant 1976a). It is also found in areas covered with relatively abundant vegetation, for example in Provence near Apt in abandonned lavender fields (Lenoir *et al.* in prep.) or in meadows of the Catalan coast near Barcelona (Retana, in prep.). Societies are considered to be monogynous and monodomous (Cagniant 1976b, Retana 1986). Elsewhere Cagniant (1973) and Suzzoni and Cagniant (1975) observed, in the laboratory, that orphan workers of this species are able to reproduce by thelytokous parthenogenesis, which enables the colony to gain a recently inseminated queen. As neither queenless colonies, nor isolated females, have ever been observed in the field, we wished to investigate modes of colony foundation in this species.

Material and Methods

All observations were made during July and August from 1983 to 1986 in 3 sites in France: near Apt (Vaucluse—500 m high), near Le Muy (Var—150, 200 m), and on the edge of the Etang de Leucate (St-Hippolyte, Pyr-Orientales, sea level). In some of the sites the entrances of the nests were flagged with a numbered label. When necessary workers and sexuals were captured. They were marked with a dot of paint "céramique à froid" and released 5 or 10 minutes later. This technique was tested in the laboratory, where marked ants immediately reentered their nest without hostility from their nestmates. Marked individuals did not have a higher mortality rate

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(at least over a few weeks). All observations were carried out during the day from 8 to 16 h (Solar Time), which covered all the period of activity of these strictly diurnal ants (Lenoir *et al.*, in prep.).

Results

1. *Number of queens per colony*

Excavation of a nest is easy because of its predictable structure. Under the superficial chambers is a vertical well, which covers chambers where a great number of workers are packed with brood and the queen (Cagniant 1976b). Sometimes the well begins after a more or less inclined tunnel. In each case the queen was found (except when digging was impossible—for example when the nest was under a large stone). The queen was located at various depths, generally 40 to 80 cm deep in April. She moves up in May when the soil is moist, she goes deeper during drier periods. The exact position depends on the nature of the substrate (Cagniant 1976a). In sand, for example on the edge of the Etang de Leucate, nests are above the water level, which is at 60 cm. In limestone they are deeper. More than 150 nests were dug up; each contained only one queen. During a short period following swarming, however, colonies may contain several inseminated females and are temporarily polygynous (see below). In May 1986 one colony was found at St-Hippolyte (Pyr-Or.) with 3 queens. This colony was reared in the laboratory, and we observed the rejection of supernumerary queens on the 5th of July. The two rejected queens were dissected and it appeared that they were not inseminated, so they cannot be considered as true queens.

2. *Colony size*

Fig. 1 represents the number of workers in late April/beginning of May before the first brood appearance. It is known that no brood is present during wintering (Cagniant 1976b, Retana 1986). Estimation of colony size is relatively easy. The nest can be excavated during the resting hours when all the ants are in the nest. With the help of a battery-operated vacuum equipment all the workers and brood can be systematically removed and counted.

The mean number of workers is 675.5 (SD 440, n = 24, range 34–1590). Cagniant (1976b) found the mean number to be 600 (range 5–1300) and Retana (1986) states that worker number varies from 150 to 1500. *C. bicolor* colonies have, on average, 2600

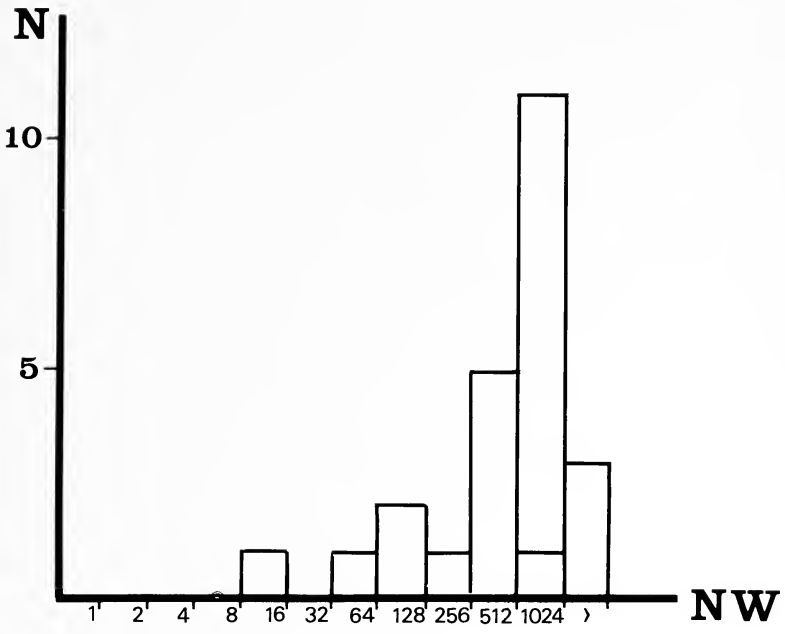

Fig. 1. Frequency of number of workers per colony, including data from Cagniant 1980 (34 workers), and from Cagniant 1983 (1106 workers) N: Number of colonies NW: Number of Workers.

workers; *C. albicans* has 700 (Schmid-Hempel 1987). Figure 1 shows that small colonies are not frequent. Isolated females were not found at any time of the year. Cagniant (1980) found only one small colony with 34 workers, but never isolated queens. In ant species which form new colonies with a solitary female (haplometrosis) it is common to find an isolated queen, or a queen surrounded by a few workers (Wilson 1971). This fact suggests that haplometrosis is unusual or absent in *C. cursor.*

3. *Behavior of sexuals and mating*

The mating period occurs from mid-June until the end of July, depending on the year and the climate. In the Pyrénées-Orientales flight season is finished at the end of June; in the Luberon (Vaucluse) at 500 m it ends one month later. These data are in agreement with the observations of Bernard (1968) and Cagniant (1976b). In Barcelona sexuals appear at the end of May and leave the nest in June (Retana 1986). The exit of sexuals occurs between 9 h and 14 h

(ST), which are the warmest hours of the day. Frequently males and females from one nest do not come out simultaneously (also in *C. sabulosa* (Shalmon 1981) and *C. bicolor* (Schmid-Hempel 1987)).

Behavior of males before mating

Fonscolombe (1846) observed males running around nest entrances. Such behavior can be observed frequently in early summer in the Mediterranean region. When they reach the exit of the nest, the males stop for a few seconds and then fly off. Males are apparently able to fly distances greater than several tens of meters, but we were unable to estimate their exact range. Apparently they do not often come back to their native nest; males captured and marked at the exit of one nest were never seen returning same place ($n = 16$). When a male arrives within 10–15 cm from a nest entrance, he may stay there motionless for several minutes; he may be attacked by workers. When marked males are recaptured later, recapture occurs near the nest entrance where they were originally captured (12% were seen again; $n = 25$).

This observation contradicts the suggestions of Cagniant (1976b), who supposed that mating occurs between the members of the same colony. Apparently this must be exceptional: outbreeding appears to be the rule. In the laboratory we did not observe spontaneous matings between siblings whereas it is easy to produce matings by introducing alien males (observed previously by Cagniant, pers. comm.).

Behavior of females before mating

Alate females often come timidly to the exit of the nest before they finally leave. When alate females prepare to leave the nest, workers and males frequently dance around the entrance. Workers are very aggressive towards males and may kill them: this could indicate that they are from a different colony. Females walk around the nest, within a radius of 1 m. Apparently they cannot fly. Are the wings too short, as supposed by Cagniant (1976b)? Wings seem to be normal but it must be measured in comparison with other species. Santschi (1929) observed one apterous species: *C. theryi.* If males are present, mating occurs immediately. If several males are present around a female, some slight aggressive behaviour may be noticed between the males. In the absence of males, females climb onto a stone or a twig for a few minutes and then descend. They then begin a "sexual calling" behavior, with the gaster bent under

the thorax several times during 2 or 3 min. If no male arrives, they reenter their nest, but frequently males do appear and mate. This female-climbing behavior may be interpreted in two ways. First, a sexual attractant pheromone might be emitted as suggested by the position of the abdomen. Sexual pheromones are known in some ant species (see Discussion). The fact that females do not fly renders use of sexual pheromones an advantage for this species. A second explanation is that the female is more easily seen by the males. It is known that *Cataglyphis* ants have a well developed visual system and workers orientate by vision during their foraging trips (Wehner *et al.* 1983). Males may also use vision to locate females. Acoustic communication by wing vibration is improbable because it cannot be used for distanct communication, and has not yet been observed in the sexual behavior of ants.

Mating

In *C. cursor* mating occurs on the ground (Cagniant 1976b) near the females nest during the hottest hours of the day (9 to 14 h). It lasts from some seconds to one minute. Two positions are possible: the male behind and above the female facing in the same direction, or the male facing in the opposite direction touching the female only by the extremity of the gaster. One male can copulate successively with several females after no more than a one minute intermission. Females may mate successively with one male or with different males. On various occasions in which males and females were present, mating did not occur for unknown reasons.

Male behavior after mating

Following copulation, males stay around the nest. During the night they crawl under stones or on twigs, with their heads directed toward the soil. They die rapidly: life span is probably not longer than 2 or 3 days. They are aggressed by *C. cursor* workers, or killed by predators, essentially spiders. Bernard noted the existence of nocturnal aggregation of *C. cursor* males (in Grassé 1942).

Female behavior after mating

After mating, newly inseminated alate females reenter the nest but sometimes run frenetically around the nest for several minutes. They are helped to reenter the nest by workers. Perhaps the females have difficulty in orienting themselves because it is their first foray into the open. When inseminated, females stay in the nest. These females will soon lose their wings in the nest. During the following days

apterous females may come out and mate again. They are generally inseminated but dissections have shown that there are exceptions. It is well known in ants that virgin queens lose their wings after some delay if they are not inseminated. During this period we find *polygynous* nests in the field. Such nests are rare and polygyny lasts only a few days. Supernumerary queens are rejected by workers if budding does not occur rapidly. Ostracized queens leave the nest and die. We dissected 2 of these rejected queens: they were not inseminated. Dead queens are also expelled from the nest.

Mating in the laboratory

We obtained matings between sexuals of different colonies in the laboratory. The length of mating was variable, from 40 sec. to more than 16 minutes (mean = 333s; n = 9). This may have been related to the low temperature of the laboratory (25° C). These observations are comparable to others in *Formica* where the mean time is 3.1 min (range 0.5–7.5 min) (Rosengren *et al.* 1986). The presence of a full spermatheca indicated a successful copulation. In all the observed cases the females reentered their artificial nest. During this period the societies are *polygynous* with the old queen and newly inseminated queens. In the laboratory some colonies kept several queens for a long time (until wintering). Later they again became monogynous. The mechanism for the elimination of supernumerary queens is unknown: aggression between queens or aggression of queens by workers? Is the surviving queen the old queen? In our colonies the surviving queen was not the old one (as indicated by individual marking), but additional observations are needed.

4. *Foundation of new colonies*

Budding was observed twice in the field in 1985, after the period of mating. Workers transported larvae, cocoons and other workers to a new nest. We may suppose that explorers had previously localized unoccupied holes which could be used as a new nest site. Transporting workers made many journeys between the two nests. Moving was directed towards 3 nest sites in the 1st case (Fig. 2) and 4 nest sites in the second case. The mean distance to the new nests was 6.5 m (range 3.2–11.3 m).

Traffic lasted for two days. In Fig. 2 shows that nest 2 was abandoned, and then occupied later by a colony which moved totally from nest 1. Nest 5 was abandoned after 3 weeks and the colony divided in two sister colonies, at least one of which had a new queen.

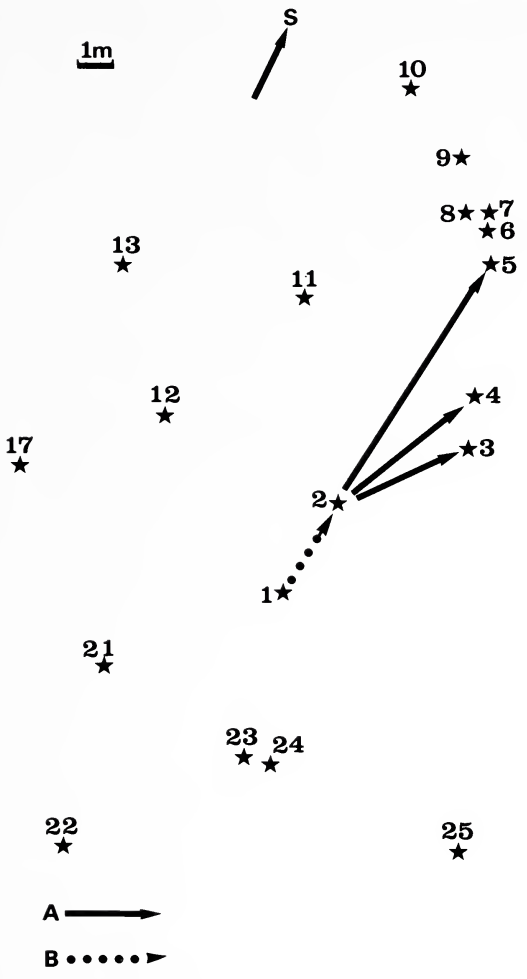

Fig. 2. Map of a population of *C. cursor* colonies showing a budding process. Asterisks indicate positions of the nests. A: fission of colony 2 into 3 daughter colonies 3, 4, and 5. B: second step = nest-moving of colony 1 to the abandoned nest site 2.

In the second observed budding the colony emigratd completely and divided into 4 nests, 2 of which were later abandoned. The two remaining sister nests were dug later, and they comprised 141 and 195 workers each with a new inseminated queen (recognized by a dot of paint). The two colonies were of small size, perhaps because

the mother colony was located at 0.8 m from a big colony with more than 1000 workers. Traffic between the mother and daughter nests was measured for periods of 5 mn during the maximum activity period of the budding day. 6 to 9 workers were transported during 5 mn, which could indicate a population in daughter nests of at least 250–300 workers. Probably some transported workers returned to their mother nest. Division of labor for moving has not been studied: it is not known if the transporters are specialized ants. After budding the new colonies were not very active. It is not known if the old queen survives. In the 4 cases where it was possible to examine this with marked queens the surviving queen was a newly inseminated queen, but we cannot make any decisive conclusion with so few observations.

Colony foundation with isolated queens

A few experiments were conducted with newly inseminated queens either isolated (n = 5) or with 4 or 5 workers (n = 4). Isolated females die in a few weeks and rarely lay eggs (also observed by Cagniant, pers. comm.) Females associated with workers can live for several months, and sometimes longer after wintering. Some larvae were observed but they never developed into callow workers (also Cagniant pers. comm.). These data need to be confirmed with larger samples but it seems that isolated foundation does not exist in *C. cursor*. If possible, it is surely an accessory mode of reproduction of colonies..

A new argument against isolated foundation can be found in the weight of queens and workers. It is generally considered that species with haplometrotic foundation have larger queens relative to the size of their workers (Wheeler 1910, Sudd 1967, Wilson 1971). Most monogynous species have large queens that are highly differentiated from the workers (Baroni Urbani 1968). Table 1 shows that foundresses of *Lasius niger* are 44 times heavier than their nanitic workers. In *Liometopum occidentale* and *L. apiculatum,* two Mexican Dolichoderinae species founding in isolation, the proportions are respectively 33 and 45. In contrast, in mature colonies of *L. niger* the queen/worker ratio is less than 10: workers of mature colonies are 4 times heavier than nanitic workers of young colonies. In *Solenopsis invicta* the first nanitic workers weigh 0.33 mg, the second generation workers 0.6 mg and the workers of mature colonies 0.5 to 1.92 mg (Porter and Tshinkel 1986). By comparison, in small

colonies of *C. cursor* the female is only 1.8 to 3 times the weight of workers. We never found colonies with nanitic workers. We weighed the workers in a small colony composed of 31 workers: they were on average heavier than the overall mean. Perhaps the largest workers, more resistant, are more likely to survive in small colonies issued from budding. This needs to be confirmed with additional small colonies.

The situation is not so simple as in *Iridomyrmex humilis,* a species forming a unique giant polydomous nest in the south of France, where young societies do not exist. The ratio Q/W is 8.28 (Passera and Keller, in prep.). We conclude that a ratio of 30–40 is proof of an independent foundation but a ratio of 7–10 is inconclusive.

5. *Internest Relations*

We observed workers leaving a nest and then entering into a neighboring nest. The workers of these nests were marked with one color for each nest, so that traffic at the entrance could be measured. The data presented here were collected on the plateau of Claparède near Apt (Vaucluse) during July 1983 between 2 nests one meter apart (nest 1 and nest 0). Direct journeys between the two nests were recorded. In most of the passages the workers were not loaded, although they sometimes transported cocoons, a worker or prey. The transporting workers of colony 1 reinforce their society as their traffic is important in direction of colony 0 (Table 2).

The data in Table 2 are indicative because only 50% of the observed ants were marked. This means that the real flux of exchanges was probably double. Table 2 shows that colony 1 is more active at the entrance of colony 0. The activity also varies greatly according to days.

These two colonies were excavated at the end of August: in colony 1 we found 750 workers and 1500 in colony 0. In this case it seems that traffic is inversely proportional with the size of the colony. From the 1st to the 5th of August a second set of observations permitted us to quantify the proportion of ants of one nest found at the entrance of another nest. Each alien ant observed at one entrance was marked with a second spot of paint indicating the number of this entrance. In this experimental design each worker is counted only once. 2 new nests appeared during this period: nest 10 at 40 cm from nest 0 and nest 11 at 1.6 m from nest 1.

Table 1: Fresh weight (mg) of queens and workers in some ant species. Mean (mini-maxi) ± SD, n = number of measures, nanitic workers are weight by 10. [1]after Boomsma and Isaaks 1985; [2]after Cagniant 1980; [3]after Cagniant 1983; [4]after Passera and Keller in prep. (comm. pers.).

	Lasius niger	*Cataglyphis cursor*	*Liometopum*		*Iridomyrmex* humilis
			L. occidentale	*L. apiculatum*	
YOUNG COLONY					
queen	27.4 (25.3–32) n = 4	Alate queens 22.0±0.53 n = 41[2]	39.7±0.57 (33.6–40.7) n = 16	54.3 n = 1	
workers	0.625±0.11 (0.4–0.75) n = 10	10.4±0.41 (5.9–19.1) n = 31	1.2±0.5 n = 5	1.2 n = 1	
Q/w	43.8	1.84	33	45	
MATURE COLONY					
queen	23.6±4.8 n = 20[1]	19.1±3.52 (12.3–24.6) n = 4			3.39±0.13 n = 11[4]
workers	2.45±0.8 (2.07–2.8) n = 10	7.22±0.35 (2.2–15.4) n = 1000[2,3]			0.41±0.005 n = 900[4]
Q/w	9.6	2.75			8.28

Table 2. Number of alien workers leaving or entering nests 0 or 1 (duration of observations 1 h by periods of 5 mn during the day).

Date	Ants from nest 1 at entrance of nest 0	Ants from nest 0 at entrance of nest 1
22/7/83	136	36
23	33	3
25	17	65
26	34	44
27	55	38
28	21	12
29	84	12
mean	54.3	30
nb workers of colony 1: 750	colony 0: 1500	

The two new nests were much less active and nest 11 was closed before the end of the five days observation. Nest 10 closed a few days later and was in fact a secondary nest for colony 0 (when we dug we found superficial galleries connecting 0 and 10). Nevertheless, it was surprising to observe above-ground cocoon transport between the two nests. Nests 10 and 11 were abandoned after their closing. Some exchanges were also observed between more distant nests (4.4 m apart). In another case cocoon transport was observed between two colonies 60 cm apart (each colony had its own queen). Some transport of prey was also observed here, which could be interpreted as intercolonial robbing. This phenomenon seems to be frequent in some ponerine species, e.g. *Ectatomma tuberculatum* (Lachaud pers. comm.).

These observations can be explained by the mode of foundation of new colonies: it is probable that colonies 1 and 0 are sister colonies, given that they keep strong links. The workers probably have a similar colony odor and do not attack each other, which may permit robbing of cocoons or prey. It is more difficult to interpret the late budding trials for nests 10 and 11. When workers occupy a new nest for several days, they transport cocoons. If there is no queen available, they abandon the provisional nest (84 workers were marked at the entrance to nest 11; when it was excavated we found only 4 workers). This reflects a tendency toward budding to form new societies after the mating season. Other budding trials were observed: one with 4 workers and 5 cocoons, another with 30 workers and a few cocoons, another completely abandoned.

Table 3. % of workers of one nest observed at the entrance of another nest.

		Destination nest				Number of
		0	1	10	11	workers
Source nest	0	75.4%	10.6%	14%	0%	236
	1	5	93.2	1.8	0	163
	10	22.6	11.8	65.6	0	93
	11	7.1	38.1	3.6	51.2	84
						576

Additional field experiments confirmed the existence of relatedness between interacting societies. In July 1984, 3 colonies were orphaned and all the workers marked with a dot of paint. They were abandoned the next day either at their old nest, or at a distance of two hundred meters. In the former case we observed numerous transports of workers and brood in direction of neighboring nests, whereas in the latter case no transport occurred (Lenoir and Cagniant 1986). Transports are probably possible if the abandoned workers are closely related to the resident ants. When the colonies are near, they are probably related by budding. We tested this hypothesis at St-Hippolyte (Pyr. Or.) during 1986. When a colony is excavated to remove the queen, although workers are not marked, it is easy to observe transports in direction of neighboring colonies. This phenomenon is possible because immature workers found by foragers in the outside arena are retrieved into the nest. (Nowbahari and Lenoir, MS). Bonavita and Clément (1986) observed the same behavior with *Camponotus vagus* nurses where foragers retrieve all ants (callows, nurses) into the nest which are not normally there.

To experiment on the closure of societies, workers were transferred to the entrance of another society. A worker was captured when leaving its nest, marked and placed near the entrance (less than 5 cm) of an alien nest in a small box. When the ant was calm the box was opened and the behavior of the ant noted for 5 min. Five recipient nests were chosen, the intruders coming from various nests more or less distant (max. 50 m). The results are presented in Table 4.

84% of control workers enter their own nest within the 5 min observation, while only 22.5% of displaced workers entered the foreign nest. It is not known if these ants were adopted or were later rejected. 4 of them were observed during the following days: they

Table 4. Transfer experiments, % of workers entering the nest, n = number of ants tested, $x^2 = 92.868$ ($P < .001$), x^2 for experimental group = 6.595 (NS).

		Nest Number				
	controls	1	2	3	4	5
% workers entering the nest	84	7.5	25	27.5	27.5	25
n	50	40	40	40	40	40

behaved normally in their new colony where they seemed to be completely adopted. Some nests are very closed: only 7.5% of ants entered nest 1. Control ants, after marking, seemed to recognize their entrance and they were ignored by resident ants: in 50 tests they encountered only 9 resident ants (18%). On the contrary alien ants were more excited and they more frequently encountered the resident ants (35.5%). Encounters were followed by aggressive reaction in 2 cases for controls and in 34 out of 71 (47.9%) cases for aliens, which were sometimes dragged as prey (Table 5).

These experiments show that most colonies are relatively open: they tolerate and adopt foragers of neighboring societies. We did not find a correlation between the % of adoption and distance between the nests, except for very close nests (1 m or less) which accept 90 or 100% of aliens. For greater distances (but still less than 50 m) the % of adoption varies from 0 to 90% regardless of the distance. These results indicate that colonies in the same habitat behave more or less as kin. It is a supplementary argument in favor of the budding process for dissemination unless the results indicate nothing about the actual relationship between colonies.

6. *Role of parthenogenesis in colony foundation*

Cagniant (1973) observed in the laboratory that *C. cursor* workers can reproduce by thelytokous parthenogenesis. This phenomenon was later studied in detail by Suzzoni and Cagniant (1975) and Cagniant (1980, 1982, 1983, 1984).

When orphaned in the laboratory after wintering, non-inseminated workers lay diploid eggs which produce workers and females. The sexuals leave the nest, females are inseminated by flying males and reenter the nest. In this way the colony can get a new queen. This sequence was easily verified in our laboratory. The existence of parthenogenesis in the field is, however very doubtful. Lenoir and

Table 5. Behavior of transferred ants and reaction toward resident ants.

	Control	Alien
Resident reaction		
Attacked	1	1
Escape	0	15
Dragged as prey	1	16
Submission	0	2
Number of encounters	9	71
Aggressive encounters	2/9 (22%)	34/71 (47.9%)
% of tested ants	18%	35.5%
Number of ants tested	50	200

Cagniant (1986) hypothesized that groups of workers which leave the nest at the end of the summer (as indicated in paragraph 5) could produce sexuals during the next springtime by parthenogenesis. If this occurred we should from time to time find groups of orphan workers, but that was never the case. Moreover it was observed that during budding, groups of workers transport a young queen, who is preventing parthenogenesis. Thus, if parthenogenesis occurs under natural conditions, it seems to be an accessory mechanism (for example in the case of queen death). These ants live frequently in sandy sites where nest collapse may occur. Thelytoky may also occur when the queen is senescent and becomes sterile. To verify this, we orphaned several colonies in late April or during the first days of May before the queens had laid eggs. 22 colonies were dug up and the queen removed together with a hundred workers which were reared in the laboratory. The rest of the colony was left on the site. Seven of these orphaned colonies were found in July exactly at the same place with an inseminated functional queen laying small eggs, which are characteristic of queen eggs (Cagniant 1982). Six of these colonies were easily distinguished from other normal neighboring colonies: they had a small number of workers (102.5, $n = 4$ vs 577.5, $n = 4$) and very few cocoons (cocoons are numerous in normal colonies). In these orphaned colonies, the ratio of cocoons: workers was less than 10%, versus 43% in normal colonies. Two colonies did not yet have cocoons. The seventh colony had a large number of cocoons and is probably another colony which had moved. The small size of orphaned colonies is the consequence of the perturbation induced by artificial orphaning.

In the laboratory, recognition tests were performed with the sister groups of workers: old workers reared in the laboratory after orphaning and the new ones captured in the field in July. It is known that *C. cursor* societies recognize their sisters and readopt them more easily then strangers (80% vs 50%—Berton and Lenoir 1986). Recognition tests were performed for colonies number 1 to 4: 75 to 85% of adoptions were observed which is in agreement with the fact that the workers were siblings. In colony number 7 only 40% of ants were adopted, suggesting that it was another colony. A doubt persists about the origin of the queen: was she produced by parthenogenesis or was she adopted after swarming from normal colonies? The second hypothesis seems to be improbable as it has been shown that closure is fairly similar in orphan and normal societies (Berton and Lenoir 1986), so adoption of a new queen must be difficult. This needs to be verified in the field by observations during the swarming period.

Discussion

We have confirmed that *Cataglyphis cursor* is a *monogynous* and *monodomous* species as indicated by Cagniant (1976b) and contrary to Bernard who thought that females were rare (1968) or absent (1983). It seems that all the species of the genus are monogynous but some can be polydomous. *C. iberica* (De Haro and Cerda 1984), *C. bicolor* (Wehner *et al.* 1983), *C. albicans* (Cerda 1986, Schmid-Hempel 1987) and the five species from Israel (Shalmon 1982) have polycalic societies with a principal nest containing the queen and secondary queenless nests. In these societies workers are observed passing from one nest to another transporting workers and brood. *C. hispanica* could be monodomous as we collected two queenright societies near Toleda (Spain), but this needs to be confirmed.

Dispersal of the species

This does not seem to be carried out by solitary females as is frequently the case in monogynous ants. Numerous arguments have been presented here that lead us to reject this possibility for *C. cursor* in favor of a budding process. The nuptial flight is replaced by a nuptial race and the inseminated females reenter their natal nest. During a few days polygynous societies can be found. Later, a group of workers leaves the mother nest with brood, other workers and a young queen. De Haro (1981) observed one queen transport

between two nests of *C. cursor*: this could have been during a budding period. After budding the sister colonies keep contact and numerous exchanges are possible. Sometimes the smaller colony continues to reinforce itself. As a consequence of this form of dispersal, colonies in the same habitat are probably kin. This explains the fact that some displaced workers can be adopted into an alien colony, and that nurses and callows found on the surface are transported by foragers into the nest (cf par. 5). This result has also to be related to the adoption experiments conducted in the laboratory by Nowbahari and Lenoir (1984): 50% of the workers introduced into an alien colony are adopted if they originate from the same habitat. This is surprising for monogynous species which are generally considered to have closed societies (Hölldobler and Wilson 1977).

Readoption of newly inseminated females is not exceptional in polygynous species, for example in mound-building *Formica, Iridomyrmex humilis, Monomorium pharaonis, Myrmica ruginodis microgyna, Lasius sakagamii* (see Hölldobler and Wilson 1977, Rosengren and Pamilo 1983, Yamauchi *et al.* 1981). Budding is usual in polygynous social insects like termites as discovered by Grassé and Noirot (1951) in *Anophotermes* and *Trinervitermes.* These authors called the phenomenon *Sociotomy:* a fragmentation of the society in different parts where the castes are represented and which can reproduce a complete society (Grassé 1984). New data are available on *Nasutitermes* (Thorne 1982, 1984; Roisin and Pasteels 1986a, b). Budding is exceptional in wasps where it is known only for *Polybinii* (Evans and West-Eberhard 1970, Spradberry 1973). Budding seems also to exist in social spiders (*Agelena consociata,* Darchen 1978; *Achaeranea wau,* Lubin and Robinson 1982). In ants it is found in polygynous and polydomous species like *Lasius sakagamii* (Yamauchi *et al.* 1981), the *Formica rufa* group (*F. aquilonia* and *F. polyctena* (Mabelis 1979, Rosengren and Pamilo 1983) and in *Leptothorax curvispinosus* (Stuart 1985). It occurs also in *Ponerinae* lacking a reproductive caste like some *Rhytidoponera* species, or *Ophtalmopone berthoudi,* where workers are inseminated (Crozier *et al.* 1984, Peeters and Crewe 1984, Pamilo *et al.* 1985). Traniello (1982) pointed out that budding could exist in *Amblyopone pallipes* but precise observations are missing. Budding is the rule in *Dorylinae* army ants: the colony reproduces by binary fission, one group containing the old queen and the other the successful daughter queen (Schneirla and Brown 1950, Raignier and van Boven 1955,

Rettenmeyer 1963, Franks 1985). This mechanism is similar to the swarming of bees. Budding was noted in *Oecophylla* by Ledoux (1950) who thought that groups of workers could be isolated from the colony and reproduce a new queen by thelytokous parthenogenesis, but it was not confirmed by Hölldobler and Wilson (1983). Ledoux (1971, 1973, 1976) also observed budding in *Aphaenogaster senilis* where the majority of workers leave the nest with the abandoned brood of the old queen. This mechanism, if confirmed, is different from the one observed in *C. cursor* where budding occurs by splitting the society in different groups, each having its own queen. *Iridomyrmex purpureus* has a remarkable diversity in its mode of colony foundation. New colonies can originate from a single foundress (haplometrosis), or foundress associations, or by colony budding, or by adoption of newly-mated queens (Hölldobler and Carlin 1986). Claustral colony foundation and colony fission were also observed in *Chelaner* sp. a probably polygynous ant from Australia (Briese 1983). Colony fission seems to appear in this species under stress conditions such as drought. Colombel (1972) observed in *Odontomachus troglodytes* (= *O. haematodes*) a grafting process where a new isolated queen can attract workers from surrounding colonies. This could explain similar observations on *O. assiniensis* (Ledoux 1952). It seems, after this review, that *Cataglyphis cursor* is the first observed occurrence of a real budding process in monogynous, monodomous non-nomadic ants. Very little is known about the foundation of other *Cataglyphis* species. Cerda (1986) demonstrated that the polycalic *C. iberica* can produce new nests by fission, but the mode of foundation of new societies is unknown. Fridman and Avital (1983) observed foundresses of *C. bicolor nigra* bringing dead ants back to their nesting hole. This unique observation, which needs to be confirmed, could indicate an independent foundation, and that *Cataglyphis* is an heterogeneous genus. However, Schmid-Hempel never observed this phenomenon in *C. bicolor* during a two years study in Tunisia (Comm. pers).

Mating Behaviour

Hölldobler and Bartz (1985) distinguished two types of strategies in mating behaviour. The first is called the "male aggregation syndrome." It is characteristic of species that form very large colonies. Males gather at specific mating sites where females fly to mate. Males produce a sexual attractant pheromone as in *Camponotus*

(Hölldobler and Maschwitz 1965). Multiple insemination is common among these species. The second strategy, called "female calling syndrome," has been found in several phylogenetically primitive species, and a number of socially parasitic or dulotic ants where the females emit a sexual pheromone attractant. The females usually mate once. Mature colonies of these species tend to be relatively small and produce few new reproductives per year. The mating behaviour of *C. cursor* is probably related to the female calling-strategy , although it is not yet known if the female emits sexual pheromone. The "degeneration" of nuptial flight is known in other species: in *Formica uralensis* where females reenter their nest after insemination which occurs frequently with brothers (Rosengren and Pamilo 1983) and in parasitic species where mating occurs in or near the host nest (Wilson 1971). In *Cataglyphis* the absence of nuptial flight is the rule but at least in one species (*C. sabulosa*) females fly some distance (Shalmon 1981).

Parthenogenesis

As indicated thelytokous parthenogenesis seems to be an accessory mechanism in the reproduction of the societies of *C. cursor*. We do not have much information about parthenogenesis in other *Cataglyphis* species: Cerda (1986) failed to find it in *C. iberica,* but recent experiments indicate that it exists in *C. bicolor* (Dartigues *et al.* in prep). In bees *Apis mellifera capensis* orphan workers are also able to reproduce by thelytoky but they become very aggressive and mortality is important (Anderson 1963, Moritz 1986). In ants the only certain case is *Pristomyrmex pungens,* a myrmicine lacking a queen (Mizutani 1980, Ono 1983, Itow *et al.* 1984). Other reports in the literature need to be confirmed. Ledoux (1950) supposed that parthenogenesis could play a central role in the life cycle of the weaver ant *Oecophylla longinoda* where alternation of generation methods may appear: foundation by inseminated queens, and fission by groups of workers which rear new queens by thelytoky. Unfortunately this result was not observed by Way (1954) or by Hölldobler and Wilson (1983). A similar cycle has been proposed for *Harpagoxenus americanus* (Wesson 1939), and four species of *Crematogaster* (Soulié 1960). For the first species Buschinger and Winter (1978) demonstrated that the production of diploid eggs was due to ergatoid inseminated females. *Lasius niger* (various authors and Bier 1952), *Lasius flavus* (Leutert 1963), *Atta cephalotes* (in

Wilson 1971), *Formica polyctena* (Otto 1960) are reported as thelytokous species but the data are not very convincing. Often they are not confirmed (as in *Atta,* Bazire-Benazet 1970). In *Aphaenogaster senilis* thelytoky seems to exceptionally appear after a thermic shock to workers (Ledoux 1984). Thelytoky has also been noted in virgin females of two species of *Aphaenogaster* (Haskins and Enzmann 1945), *Solenopsis invicta* (Tshinkel and Howard 1978), and perhaps in the termite *Reticulitermes* (Howard *et al.* 1981).

In summary *Cataglyphis cursor* is a remarkable *Formicine* species: females do not fly and instead mate near their natal nest which they re-enter. Societies reproduce by budding with the departure of workers with a young queen. Dispersal distance is limited to the walking range of workers (less than ten meters). Neighboring societies are more or less closely related and this permits a particular strategy for exploiting the resources of their habitat (Lenoir *et al.* in prep.). This species may reproduce by thelytoky but it seems to be an accessory possibility in the case of the queen death.

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VARIATION AND DEVELOPMENTAL CHANGE IN ACTIVITY OF GREGARIOUS CATERPILLARS, *HEMILEUCA LUCINA* (SATURNIIDAE)

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Introduction

Variation in behavior of individuals within an aggregation may result in a nominal division of labor or roles (Wilson, 1971). Individuals may play a particular role throughout the course of development or change roles often. Such variation seems to occur in tent caterpillars of the genus *Malacosoma* (Lasiocampidae) (*M. californicum pluviale,* Wellington, 1957; *M. disstria,* Laux, 1962 (as *M. neustria*), Greenblatt and Witter, 1976; *M. americanum,* Edgerly and Fitzgerald, 1982). Evidence for permanent polyethism (in terms of active or inactive individuals) was reported for *M. c. pluviale* by Wellington (1957) but was not found by Myers (1978), and Wellington's statistical analysis has been criticized (Papaj and Rausher, 1983). In other tent caterpillar species, individuals were not consistently active or inactive but shifted from one to the other state over a few days (Laux 1962; Greenblatt and Witter, 1976; Edgerly and Fitzgerald, 1982). Nonetheless, those larvae that were currently active played a critical role in determining the foraging pattern of the aggregation. For instance, small subgroups of *M. americanum* larvae left the tent before the main body of caterpillars, fed, and returned, depositing a fresh recruitment trail that the other larvae then followed to the feeding site (Fitzgerald, 1980).

To date, only *Malacosoma* species have been investigated for behavioral variation among larvae in aggregations even though many gregarious species exhibit distinct foraging patterns where individuals of various activity levels might be important. Furthermore, none of the *Malacosoma* studies assessed activity instar by

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instar, which might be expected to change as mobility increases with larval size and as availability of food and presence of predators changes through the larval season. Larvae of the buckmoth, *Hemileuca lucina* Hy. Edw. (Saturniidae), provide an excellent example for comparison with tent-making species. *H. lucina* larvae lay silk trails, probably with a chemical marker, as do *H. oliviae* (Capinera, 1980) and move with tandem trail-following. *H. lucina* larvae often defoliate portions of the hostplant, *Spiraea latifolia* (Ait.) Borkh. (Rosaceae) and the aggregations are then forced to move to new feeding sites. Even newly-hatched larvae move substantial distances relative to their size to find food (Bowers and Stamp, unpubl. data). Larvae also may move distances of 3 m or more for thermoregulation, when they are attacked by predators and parasitoids, and when they molt (Bowers and Stamp, unpubl. data).

Transient polyethism in some tent caterpillars (e.g. *M. americanum*) may be associated with central-place foraging, web maintenance and group cohesion (Greenblatt and Witter, 1976; Edgerly and Fitzgerald, 1982). In contrast, *H. lucina* larvae would be predicted to exhibit patterns of individual behavior different from *Malacosoma* species because *H. lucina* larvae are nomadic foragers, do not construct webs and exhibit a declining tendency to aggregate over development that occurs sooner than in *Malacosoma* species.

Our objective was to examine individual variation in activity, using distance traveled as an index, in larvae of *H. lucina*. Specifically, we determined: 1) whether larvae were consistently slow, fast or intermediate travelers relative to the group when tested several times within an instar, 2) whether patterns of larval activity (as measured by relative distance traveled) were consistent across instars, and 3) whether larval activity was correlated with larval weight.

Methods

Four egg masses of *H. lucina* were collected from a population in Dover, Massachusetts. The groups were reared separately on *S. latifolia* in petri dishes. During the first through third instars, larvae were kept in a growth chamber at 25°C day: 20°C night, with a photoperiod of 16 h day: 8 h night. For the remaining instars, larvae were reared in the laboratory at 25°C in large plastic containers (46 $\times$ 30 $\times$ 7 cm) to prevent overcrowding.

Each larva was individually marked using a three-dot, color-coding system with seven colors of acrylic paint (Liquitex™) and weighed 4 days after each molt. Reliable identification of individuals was maintained by isolating individuals just before molt, remarking them after molt and then returning them to their groups, within 12 hr of separation from the group. Thus, larvae could be identified individually throughout their development and during testing, while remaining with their sibling groups. In contrast, other studies have isolated individuals for substantial periods (Greenblatt and Witter, 1976; Edgerly and Fitzgerald, 1982), which may alter larval behavior.

During the first through fifth instars, larvae from each group were tested for distance traveled as an index of activity. We did not test the last (sixth) instar because those larvae are not gregarious. Larvae were tested at 4 days after molting and were starved for 24 h prior to testing. The test arena was a petri dish (diameter 14 cm) lined with a sheet of paper on which were drawn a series of concentric circles, 2.5 mm apart. A paper rope was suspended vertically by a string so that the bottom touched the center of the dish. The ropes were made from paper towels soaked in 50% ethanol and twisted into 300-mm lengths. When dry, the ropes were marked in pencil at 2.5 mm intervals. These ropes simulated the natural form of a branch along which larvae forage. A clean rope was used for each test. A sprig of *S. latifolia* was placed at the top of the string and a heat lamp was placed 1 m above that to induce the larvae to travel up the rope.

At the beginning of the test, the larvae were arranged on the paper sheet in a ring around the base of the rope. Larvae faced towards the rope and were 5 cm from it. They then were allowed to move around the dish or up the rope for 8 min for the first through third instars and for 4 min for the fourth and fifth instars. The reduction in test time was necessary due to an increase in overall larval activity in the later instars. The rank order of all larvae on the rope and the distance each had traveled from the starting point were recorded at the midpoint and end of each trial.

Each group of larvae was tested in 5 trials during each instar. Because individual larvae could be identified throughout the tests, we were able to obtain data on behavior of individuals at several levels: 1) variation within a trial (i.e. did larvae change ranks during

the course of a trial?); 2) variation from one trial to another within an instar (i.e. were larval ranks consistent from one trial to another?); and 3) variation from one instar to the next.

One-tailed Spearman rank correlation was used to assess the degree of changing ranks within trials by larvae (i.e. due to turning around or possibly passing one another) with 1 indicating perfect agreement between ranks (i.e. no change) and 0 indicating no agreement.

To examine whether individual larvae were consistently ranked the same with regard to distance traveled, over the five trials within an instar, we used Kendall's coefficient of concordance (W) (Conover, 1080; Edgerly and Fitzgerald, 1982). If individuals were consistently ranked the same among trials, $W = 1.0$, whereas if rank varied randomly from trial to trial, $W = 0$.

To determine whether distance traveled by individual larvae was consistent from one instar to the next, larvae were ranked on the basis of total distance traveled in 5 trials per instar and Spearman's rank correlation (r_s) was used.

Frequency distributions of distances traveled by individuals within an aggregation tend to exhibit a graded series (or hierarchy), in which relatively few individuals travel far and many individuals travel relatively short distances over a short test period (e.g. Fitzgerald, 1980; Edgerly and Fitzgerald, 1982). Following the terminology and definitions of Weiner and Solbrig (1984), we believe that the analytical methods used by plant ecologists to evaluate a graded series of sizes of individuals within a population are particularly appropriate for behavioral data such as distance traveled when: 1) the aggregation yields large variation in individual distances, 2) there are relatively few large distances and many small ones, and 3) the few large distances contribute greatly to the observed pattern. Weiner and Solbrig (1984) indicate that standard measurements of skewness are inappropriate because they are designed to be insensitive to the degree of variability and only reflect the second aspect of the three listed above. Specifically in our study, it is inequality among larvae in distance traveled, not asymmetry in the distribution of distances ((2) above), that is of biological interest here.

Therefore, the variation in distance traveled was represented graphically using Lorenz curves and evaluated using the Gini statistic (Weiner and Solbrig, 1984). Gini coefficients take into

account all three characteristics listed above. Individuals were ranked according to total distance traveled (over 5 trials) and the cumulative percent of distance traveled plotted against the cumulative percent of the individuals per group. If all larvae traveled the same distance, a plot of this would yield a diagonal line from the origin to upper right (e.g. a Lorenz curve with a Gini coefficient = 0). The degree of deviation from the diagonal is a measure of inequality and is evaluated by the Gini coefficient, where 0 indicates all individuals are equal in distance traveled and a maximum of 1 represents complete inequality (i.e. all individuals but one having a value of 0; Weiner and Solbrig 1984).

Thus, when inequalities in distance traveled were present, the Lorenz curves and Gini coefficients provided a means to assess the degree to which the inequalities change from instar to instar and relative proportion of individuals responsible for these inequalities. For example, a high Gini value would indicate that a few individuals traveled either a small distance or quite far relative to the others and those two possibilities can be distinguished by the shape of the curve.

Results

Individuals usually did not change ranks after half way through a trial (Table 1), although a few individuals turned around or passed others. For half the tests (9 of 19), ranks of individuals, as determined by distance traveled, were stable from trial to trial (Kendall's coefficient of concordance, Table 2). Total distance traveled in each instar was not correlated consistently with larval weight (Table 3) and therefore we concluded that distance traveled was unrelated to larval size.

Total distance traveled by each larva was compared between instars to determine whether those inequalities in distance traveled within an instar persisted into the next one. In most instances, total distance traveled in one instar was not correlated with distance traveled in the previous instar (Table 4). When a significant correlation occurred, it was between the third and fourth instars and between the fourth and fifth instars.

The pattern of considerable variation in distance traveled among larvae is illustrated graphically by the Lorenz curves, which show the inequalities in total distance traveled in 5 trials by individuals in

Table 1. Comparison of ranks of individuals in groups after half the test period and at the end of the test, with Spearman rank correlation (r_s). Significance level (P) for one tailed test with $\alpha = 0.05$ is shown. In this case, 1 indicates no change in ranks by individuals between the half way point and the end of the test period, and 0 represents no agreement between those ranks. In the cases below, a significant correlation indicates agreement between ranks of individuals half way through the test and their ranks at the end. Dashes represent no movement by any individuals in that trial. First instar larvae of Group D did not move so no correlation coefficient could be calculated.

Group	Instar	n	r_s	P
A	1	50	0.641	<0.001*
	2	45	0.821	<0.001*
	3	43	0.559	<0.001*
	4	36	0.739	<0.001*
	5	28	0.577	<0.001*
B	1	50	0.771	<0.001*
	2	41	0.888	<0.001*
	3	40	0.842	<0.001*
	4	37	0.574	<0.001*
	5	35	0.760	<0.001*
C	1	48	0.876	<0.001*
	2	41	0.851	<0.001*
	3	38	0.686	<0.001*
	4	39	0.933	<0.001*
	5	25	0.476	<0.006*
D	1	50	–	–
	2	34	0.767	<0.001*
	3	35	0.833	<0.001*
	4	33	0.750	<0.001*
	5	26	0.488	<0.006*

*Indicates statistical significance.

groups (Fig. 1). In the first and second instars, each group had many individuals that either did not move or only traveled short distances and a few individuals that moved relatively long distances (Fig. 1A, B, C). In contrast, in the third through fifth instars, inequalities still occurred but with a few individuals traveling quite short distances and a few traveling far.

But one group (D) exhibited a different pattern than the others. In 5 trials, none of the first instar larvae moved and thus there was no Gini coefficient, and in contrast to the other groups, only a few second instar larvae remained stationary (Table 5; Fig. 1D).

Table 2. Comparison of distance traveled among 5 trials, with n = number of larvae, W = Kendall's coefficient of concordance, and significance (P) < 0.05 indicated by *. The null hypothesis for the Kendall test was W = 0 when distances varied randomly from trial to trial. Thus, a significantly high value indicates that distances traveled by individuals were consistent from trial to trial.

Group	Instar	n	W	P
A	1	50	0.307	>0.10
	2	45	0.330	>0.05
	3	43	0.458	<0.001*
	4	36	0.245	>0.50
	5	28	0.327	>0.10
B	1	50	0.197	>0.50
	2	41	0.289	>0.20
	3	40	0.479	<0.001*
	4	37	0.370	<0.05*
	5	35	0.715	<0.001*
C	1	48	0.402	<0.01*
	2	41	0.334	>0.05
	3	38	0.338	>0.05
	4	39	0.326	>0.05
	5	25	0.599	<0.001*
D	1	50	-	-
	2	34	0.190	>0.50
	3	35	0.609	<0.001*
	4	33	0.464	<0.01*
	5	26	0.428	<0.05*

Because it was common for larvae to remain massed for several hours at a time, we could not justify ignoring that group (D) in our statistical analysis on the grounds that it was abnormal. But consequently, we could not apply the appropriate statistical test, a nonparametric two-way ANOVA which requires values in all cells, to the Gini coefficients, and a parametric test was inappropriate because it is unclear what assumptions can be made about the underlying distribution of Gini coefficients (Weiner and Solbrig, 1984). Therefore, we analyzed only instars II-V. The Gini coefficients were significantly different among instars II-V (Friedman's test, followed by multiple comparisons (Conover, 1980); Friedman $\chi^2 = 8.400$, df = 3, P = 0.04; Table 5, Fig. 1). Thus, inequalities in distances traveled decreased from instar to instar.

Table 3. Relationship of larval weight and total distance traveled by individuals in groups. Spearman rank coefficients (r_s) and probability (P) at $\alpha = 0.05$ are indicated.

Group	Instar	n	r_s	P
A	1	48	-0.11	0.48
	2	43	0.16	0.32
	3	33	0.27	0.13
	4	33	0.23	0.20
	5	25	0.67	0.0002*
B	1	44	0.24	0.12
	2	40	0.03	0.85
	3	38	0.51	0.001*
	4	32	-0.24	0.14
	5	34	0.25	0.15
C	1	48	-0.16	0.28
	2	40	0.45	0.003*
	3	36	0.33	0.049*
	4	33	0.46	0.006*
	5	27	0.58	0.001*
D	1	-	-	-
	2	29	0.42	0.02*
	3	24	0.44	0.03*
	4	25	0.38	0.06
	5	25	-0.06	0.80

*Indicates statistical significance

Discussion

In general, studies on *Malacosoma* species (Laux, 1962; Greenblatt and Witter, 1976; Edgerly and Fitzgerald, 1982) and *Hemileuca lucina* reveal only transient leaders and followers, at most. For instance, Edgerly and Fitzgerald (1982) found a significant behavioral difference among *M. americanum* larvae in only 3 of 8 colonies, and they found no correlation in activity levels across trials. In contrast to that study, we examined larval behavior more directly by following marked individuals within trials, among trials and across instars, and found that in some cases individual *H. lucina* were consistently traveling relatively long distances across trials and instars. But no pattern emerged that would allow us to predict which individuals might lead or in which instar that might occur. For example, Group C had two instars in which rankings among trials were stable (i.e. some individuals were consistently traveling faster than others), showed a significant positive correlation

Table 4. Relationship between instars for total distance traveled by marked individuals in groups. Spearman rank coefficients (r_s) and probability (P) at $\alpha = 0.05$ are indicated.

Group	Instar	n	r_s	P
A	1–2	42	0.227	0.15
	2–3	34	0.218	0.22
	3–4	27	0.308	0.12
	4–5	20	0.097	0.69
B	1–2	36	0.156	0.37
	2–3	36	–0.176	0.31
	3–4	32	0.668	0.001*
	4–5	32	0.403	0.02*
C	1–2	40	0.177	0.28
	2–3	34	0.313	0.07
	3–4	33	0.447	0.01*
	4–5	27	0.418	0.03*
D	1–2	–	–	–
	2–3	25	0.369	0.07
	3–4	23	0.446	0.03*
	4–5	21	0.303	0.19

*Indicates statistical significance

between larval weight and distance traveled for Instars II-V, and exhibited a significant correlation between distance traveled between instars for two such combinations. In contrast, Group A had only one instar in which rankings were stable among trials and one instar in which distance traveled was correlated with weight.

In *H. lucina,* transient polyethism occurred at several levels: 1) Over the course of a trial, larval ranks did not change; thus, leaders during a single foraging bout (represented here by a single trial) remained at the forefront. 2) In some cases, ranks of individual larvae were constant from one trial to the next within an instar. The instar in which this was most prevalent was the third (for 3 or 4 groups). However, in other cases, there was no consistency in larval ranking from trial to trial. Thus, in some groups the same individuals led a series of foraging bouts, whereas in others, the leaders varied from bout to bout. In some instances, a significant positive correlation occurred between larval weight and distance traveled, but in other cases, there was no correlation. Thus, within a foraging group, the largest larvae were sometimes the leaders, sometimes randomly distributed within the traveling group, but were never consistently the slowest (i.e. none of the negative correlation coeffi-

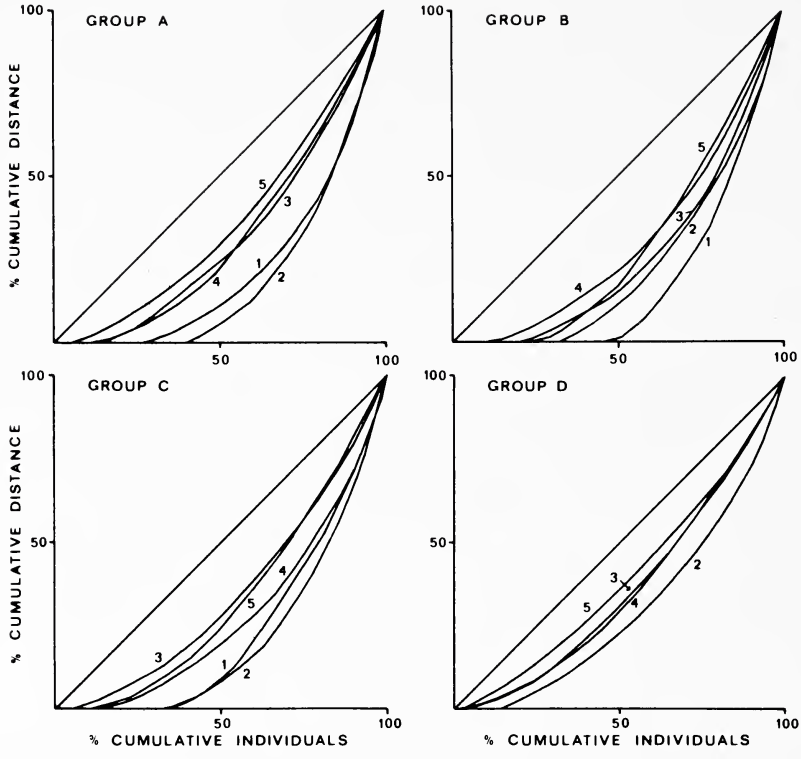

Figure 1. Pattern of inequality in distance traveled by individual larvae in sibling groups. Numbers adjacent to curves indicate the instar tested. Groups A, B, C and D are shown. First instar larvae of Group D were tested, but they remained aggregated and thus are not shown.

cients in Table 3 were significant). 3) In a quarter of the tests, ranks of individual larvae from one instar to the next remained consistent. This was primarily between the third and fourth instars (for 3 of 4 comparisons).

The Lorenz curves and Gini coefficients showed that the patterns of distance traveled by individuals changed over instars. In many cases, especially in the early instars, a few individuals moved great distances whereas others hardly moved. By the later instars, variation was still large but the inequalities (or skewness) among individuals were much less.

Table 5. Patterns of larval variability in total distance traveled over 5 trials by larvae in groups. Gini coefficients (unbiased estimator, G') are shown, with 0 representing complete equality and 1 indicating total inequality among larvae. First instar larvae of group D were tested but remained aggregated.

	Instar				
Group	1	2	3	4	5
A	0.569	0.612	0.380	0.365	0.282
B	0.640	0.543	0.486	0.401	0.418
C	0.532	0.583	0.310	0.450	0.342
D	-	0.405	0.279	0.272	0.212

The changes in larval activity of *H. lucina* revealed by the Lorenz curves and Gini coefficients parallel other developmental changes we have observed in *H. lucina*. These larvae exhibit distinct changes in behaviors between the early and late instars. While they have strong aggregation tendencies through the third instar and remain in groups in the fourth and fifth instars unless disturbed, the tendency to aggregate declines steadily and sixth (last) instar larvae are solitary (Cornell, et al., 1987). *H. lucina* larvae also have a repertoire of defensive and escape behaviors that changes from one instar to the next. The most dramatic changes occurs between the third and fourth instars, from primarily defensive behaviors to largely escape behaviors (Cornell, et al., 1987). The marked inequalities in distance traveled among early instar larvae compared to the more normal distribution of distances traveled of later instars may reflect those changes in behavior, in particular the declining tendency to aggregate. Thus, a pattern of a few leaders and many slower individuals is less likely when larvae are older and less compelled to stay with the group.

Another factor contributing to the pattern of some larvae traveling long distances with others hardly moving may be digestive periods. *H. lucina* larvae alternate feeding with periods of inactivity, as is true for many caterpillars (Edwards, 1964; Ma, 1972; Fitzgerald, 1980; Capinera, 1980; Fitzgerald and Costa, 1986; Reynolds, et al., 1986). Hungry and, therefore, temporarily active larvae tend to stir up the group, by tactile stimulation of group members. As a result, quiescent individuals eventually follow the other, more active group members, as long as the tendency to aggregate is strong (which it is through the third molt, Cornell, et al., 1987). That tendency to aggregate, which could induce less hungry larvae to follow hungrier

and more active individuals, may reflect advantages of staying with the group (e.g. for defense and thermoregulation). In this scenario, when the level of hunger is skewed (i.e. some individuals are hungry but most are still digesting food) we would expect a temporary pattern of leaders and followers; when the level of hunger is distributed normally among individuals in a foraging group we would expect no clear pattern of leaders and followers. Some caterpillar species alter searching behavior when the larvae are starved (Jones, 1977; Cain et al., 1985). But the idea that consistency in leadership reflects a skewed distribution in hunger-levels remains untested here because we did not attempt to assess state of hunger. However, in our study all groups were deprived of food for 24 h before testing. Thus, individuals should have been approaching equal hunger levels, but even with 24-h starvation, the amount of food in the gut of third and fourth instar *H. lucina* varies considerably (Bowers and Stamp, unpubl. data).

In these experiments, we used Lorenz curves and Gini coefficients to evaluate behavioral data, in this case skewed distributions of distance traveled. Previously, these techniques have been applied to questions of market-share and distribution of wealth in economics and biomass or size distributions in plant populations (Weiner and Solbrig, 1984, and references therein). The market-share concept does not apply to distances traveled by aggregated caterpillars *per se* because there does not seem to be a premium on obtaining a larger share, or in this case, being more active or traveling faster than other group members. But it is a similar situation in that the distributions of interest here tend to be skewed. That is, during the course of the experiments, the most active larvae leave the aggregation first and travel farthest, whereas other larvae remain quiescent longer and travel shorter distances. Therefore, these techniques are appropriate for our study and allow us to address the biological question of interest (i.e. what is the pattern of inequality or variation among individuals), which other measurements of skewness do not (Weiner and Solbrig, 1984). Lorenz curves and Gini statistics are applicable to other kinds of behavioral data, in particular situations where resources are limiting, and as a result, measurements of individuals yield a skewed distribution (e.g. number of matings, number of offspring).

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QUEEN REPLACEMENT IN DEQUEENED COLONIES OF THE ARGENTINE ANT *IRIDOMYRMEX HUMILIS* (MAYR)

By Luc Passera,[1] Laurent Keller[2] and Jean-Pierre Suzzoni[1]

Introduction

Replacement of killed or damaged queen by a new inseminated queen produced in the same nest is regularly accomplished in honey bees (Butler, 1967; Wilson, 1971; Michener, 1974). In the lower termites, e.g., *Calotermes,* it has been known for a long time that the removal of the sexual pair leads to the differentiation of neotenic reproductives from larval, pseudergate or nymphal forms (Grassé and Noirot, 1946; Nagin, 1972). In the higher termites, e.g., *Nasutitermes,* dequeened societies may produce either neotenic reproductives or differentiate young alates who have fully developed wings (Harms, 1927; Noirot, 1956, 1969; Thorne, 1982; Roisin and Pasteels, 1986).

In contrast, the replacement of queens by new inseminated queens produced in the same nest is very rare in ants. When colonies are orphaned, workers often start to lay eggs (see review in Passera, 1984) but these eggs are not fertilized and therefore develop into males. Furthermore, after a colony has been dequeened, it often starts to rear queen larvae, then produces virgin queens (Passera, 1984). But these virgin queens are not inseminated and thus may not replace the absent mated queens. Insemination generally occurs only during the nuptial flight. The probability that winged queens will return to their natal society after the nuptial flight is very low.

The aim of this study was to determine whether queen replacement occurs in dequeened colonies of *Iridomyrmex humilis.*

Material and Methods

Large societies of the Argentine ant were collected in December 1985 in Port-Leucate, near Perpignan, in Southern France. These

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societies considered as stock colonies were kept in large plastic boxes and reared in conditions similar to those described in Passera *et al.* (1988).

Forty-seven experimental queenless units were constituted by splitting four queenright stock colonies from 10/12/85 to 23/5//86. Each experimental unit consisted of about 650 workers and brood ranging from eggs to worker pupae. The brood was carefully monitored with the aim of avoiding the introduction of differentiated sexual larvae which are easily distinguished from worker larvae on the basis of size and/or color. Queen larvae never develop in queenright colonies (personal observation) so they were not present in any of the stock colonies. Moreover their matt color and their large size contrast sharply with those of the worker larvae. Male larvae are periodically produced in such stock colonies (Passera *et al.*, 1987) in the presence of the queens, so we selected periods when they were absent. The experimental units were then monitored daily for the presence of sexual forms.

Results

Males: Of the 47 experimental units, 44 (93.6%) produced male larvae. This is explained by the fact that male brood is always present in stock colonies but its development is dependent on the trophic status of the society. This trophic status depends on the worker/larva ratio and/or queen number per colony (Passera *et al.*, 1988). Males pupated between the 7th and 95th day after the beginning of the experiment ($N = 758$; mean in days $\pm$ SD $= 38 \pm 15$). So the period of emergence of males is rather broad.

Queens: Thirty-seven of the 47 experimental units (78.7%) produced queen larvae. In queenright societies queen larvae were never produced whatever the brood composition or trophic status.

Queen production was not dependent on the season. In December the brood used in experimental units was a little overwintered but the brood used later in spring was supplied by stock colonies kept at a high temperature (28°C) in the laboratory for several months. In both cases the experimental units produced queen larvae. This differs from other ant species in which sexuals forms generally develop only from overwintered brood (Passera, 1984).

Queen larvae differentiated 24 to 53 days after the queens were removed. The first queen larvae were produced only after 24 days

because caste determination occurs very early at the beginning of the larval stage (Passera and Keller, unpublished data). Consequently, pupation of female sexuals occurred no earlier than day 32 and continued as far as day 84 (N = 94; mean ± SD = 56 ± 8). Winged virgin queens emerged later (N = 28; mean ± SD = 64 ± 12).

Mating and colony growth: At the time of the emergence of virgin queens there were always males of varied age because of the broad period of their emergence. On the other hand, the number of males was always large because the sex ratio favors these later: a total of 758 male pupae and only 94 queen pupae were produced over all the experimental units.

Of the 38 winged queens monitored, 36 (95%) succeeded in copulating with males in the nest. This is explained because in this species there is no mating flight (Newell and Barber, 1913; Markin, 1970; Benois, 1973) and mating usually occurs in the nest.

In our experimental units, copulation occurred very quickly after queen emergence: 5.1 ± 1.9 days (N = 36) after emergence queens were dealated and egg laying by queens began immediately. The number of remaining workers was greatly decreased, but was still large enough to rear the new brood. The first callow workers emerged about 50 days after queen mating and about 130 days after the societies were dequeened.

Discussion

The production of virgin queens in queenless societies has been demonstrated in a number of species including *Hypoclinea quadripunctatus* (Torossian, 1967), *Plagiolepis pygmaea* (Passera, 1969, 1984), *Leptothorax nylanderi* (Plateaux, 1971), *Leptothorax recedens* (Dejean, 1974), *Odontomachus haematodes* (Colombel, 1978), *Camponotus aethiops* (Dartigues, 1978; Suzzoni *et al.,* 1986), *Myrmica rubra* (Brian, 1979, 1983), *Solenopsis invicta* (Vargo and Fletcher, 1986). In all these cases, the new virgin queens were never inseminated inside the nest resulting in the failure of the replacement of the mated queen. The replacement of mated queens has been reported in only three species.

The first case is the red imported fire ant *Solenopsis invicta* (Tschinkel and Howard, 1978). When monogynous colonies in the field are orphaned by removing the queens, censuses made several

weeks later, often show the presence of a new inseminated egg-laying queen. But the process of the regulation is different than in *I. humilis:* the replacement queens does not originate from a new rearing of sexual larvae. Rather they were probably surviving foundresses remaining in the societies after the pleometrotic colony founding, which leads the authors to hypothesize that these societies were functionally monogynous.

The second case of regulation exists in *Cataglyphis cursor.* The mechanism is again completely different than in *I. humilis.* In the laboratory, workers in queenless societies lay arrhenotokous eggs which develop into males and thelitokous eggs which develop into queens (Cagniant, 1976). After mating, which occurs near the nest at ground level (Cagniant, 1976), queens return to their society. By this mechanism, societies display the ability to replace the mated queen when she is experimentally removed in field colonies (Lenoir *et al.,* 1986).

The third case of queen replacement is found in *Monomorium pharaonis* which displays a similar mechanism as in the Argentine ant; namely when societies are dequeened, males and winged queens are produced and mate within the nest (Peacock and Baxter, 1949; Petersen-Braun, 1975).

Hence, *M. pharaonis* is the only species which displays a similar mode of queen replacement as the one described in *I. humilis.* Such a mechanism involves three factors:

—Mating must occur within the nest or in the immediate vicinity. This condition involves a polygynous colony structure as occurs in both *M. pharaonis* and *I. humilis.* Several pairs of closely related species are known, one being monogynous and the other polygynous, e.g., *Myrmica ruginodis, macrogyna* and *microgyna* (Brian and Brian, 1955), *Pseudomyrmex ferruginea* and *P. venefica* (Janzen, 1973), *Lasius niger* and *L. sakagamii* (Yamauchi *et al.,* 1981). In these three pairs, the first species is monogynous and queens mate outside the nest during a nuptial flight, whereas the second species is polygynous and queens often mate within the nest. In monogynous species, mating within the nest is probably selected against because the deleterious effect of inbreeding (Bruckner, 1980; Brian, 1983). On the contrary, in polygynous species in which sexuals are produced by several queens, e.g., *I. humilis* (Keller, unpublished data), mating within the nest is possible without a high degree of inbreeding.

—In queenless colonies, female brood may develop into queens at any time of the year.

—Male brood always exists in societies and generally develops into males when the societies are dequeened.

These three conditions being infrequently connected within a species renders queen replacement a rather rare phenomenon in ants.

Summary

When experimental societies of the polygynous ant *Iridomyrmex humilis* were dequeened, they produced both male and queen larvae. This production of sexuals may occur at any time, because the differentiation of sexuals is not connected with overwintering of the brood.

The emergence of queens occurred about 70 days after queen removal, whereas males emerged generally earlier. Since mating flights are lacking in this species, the newly-produced virgin queens and males copulated within the nest less than 8 days after emergence of queens. Then newly inseminated queens began to lay eggs rapidly after mating and the first callow workers emerged 50 days later.

This form of social regulation is rather uncommon in ants. Factors allowing this regulation are discussed.

Acknowledgments

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LOBOSCELIDIINAE, NEW SPECIES AND A NEW GENUS FROM MALAYSIA (CHRYSIDIDAE, HYMENOPTERA)

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Loboscelidiinae is one of the most aberrant and poorly understood groups of Chrysididae. Even the family placement of *Loboscelidia* Westwood has varied considerably over the years. Throughout this entire period, as recounted by Day (1978), none of the authors involved recognized the difference between the sexes. Maa and Yoshimoto (1961) treated them as separate genera, *Loboscelidia* (males) and *Scelidoloba* Maa and Yoshimoto (females).

These wasps are strongly sexually dimorphic, making association of the sexes difficult. Males have a long slender flagellum and tend to be less robust looking than females. The female flagellum is short, flattened and broad. In addition, the sexes do not appear to share the same modifications of the face, mesopleuron, legs and scutellum within a species. However, the wing venation and development of the notauli is apparently the same in conspecific males and females. To further complicate matters fewer than 10% of the specimens in collections are female.

Loboscelidia is characterized by having the antennae insert mid face; head prolonged posteriorly into a necklike projection; pronotum not freely hinged to scutum; tegulae very large, covering both wing bases and held in place by a ridge on the mesopleuron; mesopleuron smooth without sculpturing; propodeum without horizontal dorsal surface and with shelflike lateral projections; forewing lacking a stigma and costal vein, and the abdomen with 4 (females) or 5 (males) external gastral segments.

A complete revision of this group would be premature at this point. However, there are a large number of new taxa in this subfamily, which need to be published in anticipation of a monograph on the family being prepared by myself and R. M. Bohart.

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China (BEIJING) American Entomological Institute, Gainesville, Florida, U.S.A. (GAINESVILLE, H. Townes), Australian National Insect Collection, C.S.I.R.O., Canberra City, Australia (CANBERRA, J. C. Cardale), Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A. (HONOLULU, G. Nishida), British Museum (Natural History), London (LONDON, M. C. Day), Canadian National Collection, Ottawa, Ontario (OTTAWA, L. Masner), Department of Primary Industries Insect Collection, Indooroopily, Queensland, Australia (INDOOROOPILY, K. J. Houston), and Bohart Museum of Entomology, University of California, Davis, USA (DAVIS, R. O. Schuster).

Loboscelidia **asiana** Kimsey, new species
(Figs. 3, 9)

Holotype male. Body length 3 mm. Frontal projection triangular in front view, appearing truncate in profile (fig. 3); frons smooth with sharp fold extending from frontal projection along ocular margins to vertex; cervical projection slightly convex in profile; scape with narrow transparent flange extending two-thirds scapal length; F-I length 2.4× breadth; F-II shorter than I, length 2.2× breadth; pronotum longer than broad along transverse and longitudinal midlines; scutum with complete notauli; propodeal projections angular, less than 1 MOD tall; forewing with faint maculation, R1 0.6×, cu-a 0.3× and Rs 1.4× as long as stigmal vein; femora and tibiae with numerous ventral macrochaetae; mid and hindlegs (fig. 9); midfemoral flange extending less than one half as long as femur; midtibial flange narrow, two-thirds tibial length; hindfemoral flange slender, as long as femur; hindtibial posterior margin bicarinate, flange 0.75× as long as tibia. Body reddish brown, wings maculate.

Female unknown.

Holotype male.—VIET NAM: Dalat, 1500 m, 29 April–4 May 1960, L. W. Quate (HONOLULU).

Discussion. This species is closest structurally to *defecta* Kieffer, and less so to *atra* Krombein, based on the V-shaped frontal projection below the antennal sockets, Rs less than half as long as stigmal vein, R1 and cu-a present and distinct, and F-II more than twice as long as broad. It can be distinguished from these species by the lengths of cu-a and R1 and shape of the frons.

Loboscelidia **australis** Kimsey, new species
(Fig. 1)

Holotype male. Body length 2.5 mm. Frontal projection narrow, elongate and apically truncate in front view, forming an acute tooth in profile (fig. 1), and with smaller projection beneath antennal socket; frons smooth, with obtuse fold extending along ocular margin from antennal socket; cervical projection strongly convex in profile; scape with small, short, transparent edge near base; F-I length 1.6× breadth; F-II length 1.3× breadth; pronotum as long as broad along transverse and longitudinal midlines; scutum without notauli, parapsides indicated by shallow lines; propodeal projections angular, less than 1 MOD tall; femora and tibiae with few, fine macrochaetae; midtibial flange very narrow extending less than half tibial length; hindfemoral flange large, two-thirds femoral length; hindtibial posterior margin with 1 carina, flange two thirds tibial length; forewing R1 0.5×, cu-a 0.6× and Rs 1.3× as long as stigmal vein. Body reddish brown, somewhat darker on mesopleuron, metathorax and propodeum; wings maculate.

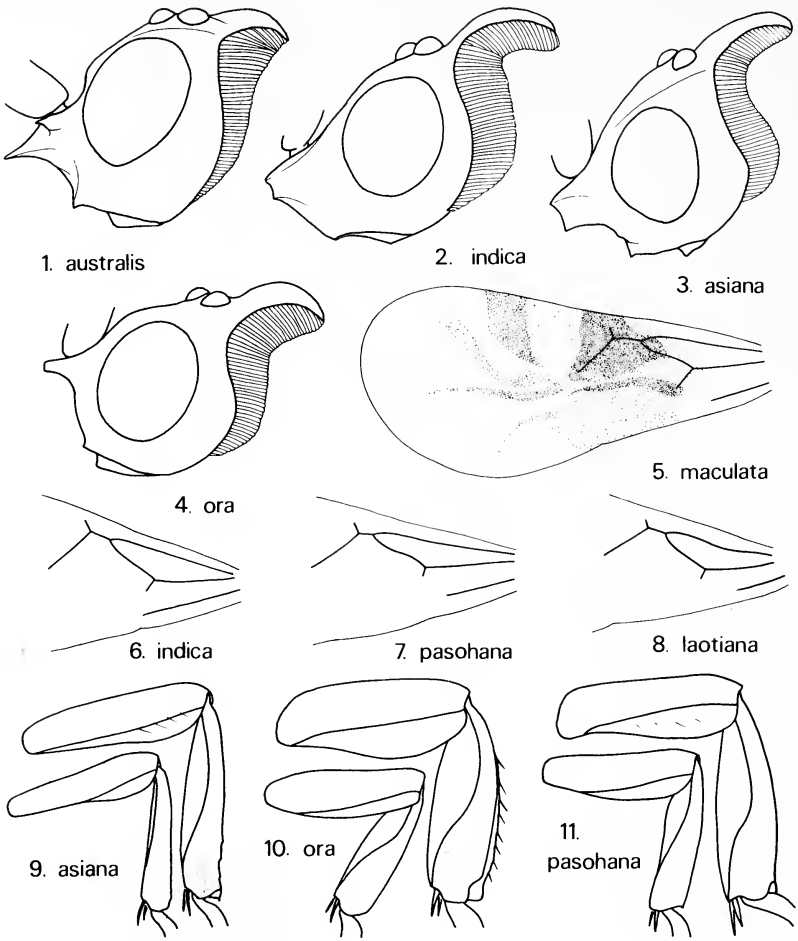
Female unknown.

Holotype male.—AUSTRALIA: N.S.W., Spencer, 11-14 January (GAINESVILLE).

Discussion. The majority of Australian *Loboscelidia,* including *australis,* lack notauli on the scutum. The elongate and noselike subantennal projection of *australis* will immediately distinguish it from these. Additional diagnostic features include: cu-a slightly more than half as long and R1 half as long as stigmal vein, and hindtibial flange only extending about two-thirds of tibial length.

Loboscelidia **indica** Kimsey, new species
(Figs. 2, 6)

Holotype male. Body length 4 mm. Frontal projection broadly bilobate, lower carina forming a narrow rectangle, broadly truncate in profile (fig. 2); frons smooth with sharp fold extending from frontal projection, along ocular margin to hindocellus; cervical projection strongly convex in profile; scape with transparent flange along entire length; F-I and II length 2.2× breadth; pronotum as long as broad along transverse and longitudinal midlines; scutum



Figs. 1–11. *Loboscelidia* species. Figs. 1–4. Lateral view of head. Fig. 5. Forewing. Figs. 6–8. Forewing venation. Figs. 9–11. Lateral view of hindleg (above) and midleg (below).

with parapsides and notauli nearly complete; propodeal angles broadly rounded, about 1.5 MOD tall; femora and tibiae with numerous macrochaetae; miditibial flange large, extending over two-thirds of tibia; hindfemoral flange large, extending along two-thirds of femur; hindtibial posterior margin bicarinate, flange extending for entire tibial length; forewing (fig. 6), R1 0.6×, cu-a

0.8× and Rs 2.3× as long as stigmal vein. Body dark reddish brown, forewing maculate.

Female unknown.

Holotype male.—INDIA: Nilgiri Hills, May 1961, P. S. Nathan (OTTAWA).

Discussion. Closely related to both *sarawakensis* and *philippinensis* Fouts, because of the similar wing venation and leg flanges, *indica* can be distinguished from these species by Rs more than twice as long as the stigmal vein, hindtibial flange extending the entire tibial length, and the subantennal projection broadly truncate and smooth below, without carinae or rugae.

Loboscelidia **loatiana** Kimsey, new species
(Fig. 8).

Holotype male. Body length 2.0 mm. Frontal projection broadly triangular in front view, broadly truncate in profile; frons smooth with broadly obtuse fold extending from frontal projection along ocular margin dorsally; scape with narrow flange extending entire length; F-I and II lengths 1.8× breadths; pronotum broader than long along transverse and longitudinal midlines; scutum with parapsides and complete notauli; propodeal projection angular, more than 1 MOD high; femora and tibiae with sparse macrochaetae; midtibial flange extending two-thirds of tibial length; hindfemoral flange as wide as femur and extending entire length; hindtibial posterior margin bicarinate, flange extending entire length; forewing (fig. 9), R1 0.6×, cu-a 0.4× and Rs 3× as long as stigmal vein. Body reddish brown, forewing faintly maculate.

Female unknown.

Holotype male.—LAOS: Vientiane Prov., Ban Van Eue, 15 May 1967, native collector (HONOLULU). Paratypes: 9 males, same data as type, except dates September 1965 to September 1967 (HONOLULU, DAVIS); 2 males: VIET NAM: Fyan, 11 July–9 August 1961, N. R. Spencer (HONOLULU, DAVIS).

Discussion. The frontal projection and general wing venation of *laotiana* are closest to that of *pasohana.* However, *laotiana* can be distinguished from *pasohana* by the shorter Rs vein, smaller average body size (2 mm as opposed to 3 mm in *pasohana*), and paler brown color.

Loboscelidia **maculata** Kimsey, new species
(Fig. 5)

Holotype male. Body length 3.5 mm. Frontal projection trilobate in front view with medial lobe elongate and apically truncate, sharply truncate in profile; frons smooth; vertex with short elevated welt on outer side of hindocellus; gena angular behind eye; cervical projection broadly convex in profile; scape with flange extending entire length; F-I-II lengths 1.8× breadths; pronotum broader than long along transverse and longitudinal midlines; scutum without notauli, parapsides indicated by broad grooves; propodeal projection angulate, less than 1 MOD tall; femora with few macrochaetae; tibiae with numerous ones; midtibial flange extending two-thirds of length; hindfemoral flange extending most of femoral length; hindtibial posterior margin bicarinate, flange extending two-thirds of tibial length; forewing (fig. 5), R1 0.6×, cu-a and Rs 2.2× as long as stigmal vein. Body dark brown, forewing with dark brown maculae.

Female unknown.

Holotype male.—AUSTRALIA: Qld., Mulgrave R. Rd., 7 km sw Bellenden Ker, 2 April 1984, A. Calder and T. Weir (CANBERRA). Paratypes: 2 males, Mossman Gorge, 17–23 February 1984, L. Masner (OTTAWA); 1 male, Kuranda, 17–24 February 1984, L. Masner (OTTAWA); 1 male, Shiptons Flat, 16–18 May 1981, A. Calder and J. Feehan (CANBERRA).

Discussion. The absence of notauli and wing venation indicate a close relationship with *ora,* and less so *australis. L. maculata* can be further distinguished from these species by the subantennal projection acutely V-shaped, appearing blunt and truncate in profile, the vertex with a welt or fold on the outer side of the hindocellus, and the wings darkly maculate.

Loboscelidia **nigricephala** Kimsey, new species

Holotype male. Body length 3 mm. Frontal projection broadly V-shaped in front view, truncate in profile; frons with fine dense scratches or rugae, with short, obtuse lateral fold extending dorsad from frontal projection; cervical projection broadly curved in profile; scape with flange dark, forming large basal lobe; gena broadened behind eye; F-I and II lengths 1.8× breadths; pronotum broader than long along transverse and longitudinal midlines; scutum with parapsides and incomplete notauli; propodeal angles large and evenly rounded, about 1.8 MOD high; femora and tibiae with

sparse macrochaetae; midtibial flange extending along two-thirds of tibia; hindfemoral flange large, extending along entire femoral length; hindtibial posterior margin weakly bicarinate, one faint, the other expanded and flangelike, ventral flange large, extending entire length; forewing R1 0.3×, cu-a as long as and Rs 2× as long as stigmal length. Body reddish brown, except flagellum, head, leg joints, tarsi and abdomen dark brown, head blackish dorsally; forewing maculate.

Female unknown.

Holotype male.—AUSTRALIA: Qld., Hugh Nelson Ranch, 21 km s Atherton, 9 January–10 February 1984, Storey and Brown (INDOOROOPILY). Paratypes: 6 males, same data as type (INDOOROOPILY, DAVIS).

Discussion. This is the only Australian species described which has notauli. Other characteristics, particularly the large hindleg flanges, short Rs and long cu-a veins, show a distinct similarity to *ora*. However, the presence of notauli and contrastingly dark head will distinguish *nigricephala*. In addition, *nigricephala* has a pronounced medial carina below the frontal projection.

Loboscelidia **ora** Kimsey, new species
(Figs. 4, 10)

Holotype male. Body length 2.5 mm. Frontal projection forming an extremely flattened triangle in front view, narrowly truncate in profile (fig. 4); frons smooth with faint fold extending dorsad from frontal projection along ocular margin; cervical projection broadly curved in profile; scape without clear flange, with brown carina; F-I and II lengths 1.8× breadths; pronotum as long as broad along transverse and longitudinal midlines; scutum with parapsides indicated by a crease, without notauli; propodeal projection angulate, 1.5 MOD tall; femora and tibiae with sparse macrochaetae; mid and hindlegs (fig. 10); mid and hindtibial and hindfemoral flanges extending almost entire length of respective tibia or femur; hindtibial posterior margin bicarinate, inner carina expanded and transparent, flangelike; forewing R1 0.3×, cu-a as long as and Rs 2× as long as stigmal vein. Body reddish brown, forewing maculate.

Female unknown.

Holotype male.—AUSTRALIA: Qld., Bingil Bay, Cedar Creek, 14 May 1980, I. D. Naumann, J. C. Cardale (CANBERRA). Paratypes: 2 males, same data as type; 1 male, Mission Beach, Laceys Creek,

17.54S 146.06E, 13–14 May 1980, same collectors (CANBERRA, DAVIS); 1 male, Petford, 29 April 1976, R. I. Storey (CANBERRA). Non-type material: 9 females were seen from Bribie Is., Millstream Falls National Park, Slacks Creek, Toowomba and Shiptons Flat. These are not designated as paratypes due to the uncertainty in associating the sexes.

Discussion. Diagnostic features of *ora* include: the absence of notauli, face smooth below frontal projection, frontal projection broadly V-shaped and nearly linear in front view, and head and thorax concolorous. The wing venation most closely resembles that of *maculata* and *nigracephala.*

This is one of the few species with associated females. In this particular instance the females have the same wing venation, scutal sculpturing, hindleg flanges, and frontal projection as the males.

Loboscelidia **novoguineana** Kimsey, new species

Holotype male. Body length 2.5 mm. Frontal projection nearly linear in front view, triangular in profile; frons with fine dense rugae medially; cervical projection broadly curved in profile; scape with flange indicated as small, subbasal, dark lobe; gena not broaded behind eye; F-I and II lengths 2.3× breadths; pronotum broader than long along transverse and longitudinal midlines; scutum with parapsides and incomplete notauli; propodeal projection large and evenly rounded, about 1.4 MOD high; femora and tibiae with sparse macrochaetae; midtibial flange narrow, extending about 0.5 tibial length; hindfemoral flange extending along half femoral length; hindtibia weakly bicarinate along posterior margin, flange 0.75× tibial length; forewing Rs 2×, R1 0.5× and cu-a subequal to stigmal vein length. Body dark brown, forewing weakly maculate, with dark band across Rs and R1.

Female unknown.

Holotype male.—NE NEW GUINEA: East Highlands, Aiyura, 1800–1900 m, 6 January 1965, J. and M. Sedlacek (HONOLULU). Paratypes: 2 males (HONOLULU); Karimui, 1080 m, 9 July 1963, M. Sedlacek, NEW BRITAIN: Gazelle Pen., Mt. Sinewit, 900 m, 5–10 November 1962, Sedlacek (HONOLULU).

Discussion. This species most closely resembles *nigricephala* in wing venation, and the incomplete notauli. The slender hindleg flanges, concolorous head and thorax, and linear frontal projection,

which lacks carinae or rugae below the antennal sockets, distinguish *novoguineana* from *nigricephala* and other species.

Loboscelidia **pasohana** Kimsey, new species
(Figs. 7, 11)

Holotype male. Body length 3 mm. Frontal projection with elongate rectangular medial lobe and smaller lateral lobe beneath each antennal socket in frontal view, bilobate in profile; frons smooth, with lateral fold along ocular margin; cervical projection strongly convex; scape with transparent flange along entire length; F-I length 1.6× breadth; F-II length 1.7× breadth; gena widened behind eye; pronotum as broad as long along transverse and longitudinal midlines; scutum with parapsides and complete notauli; scutellum with dense striae and ridges laterally; propodeal projection broadly rounded, about 1 MOD high; femora with sparse macrochaetae; mid and hindlegs (fig. 11); midtibial flange extending about two-thirds tibial length; hindfemoral flange extending almost entire length of femur; hindtibial posterior margin bicarinate, flange extending entire length; forewing (fig. 7), R1 0.7×, cu-a 0.5× and Rs 4.5× as long as stigmal vein. Body dark brown, forewing lightly maculate.

Female unknown.

Holotype male.—MALAYSIA: Pasoh Forest Reserve, Negri Sembilan, 17 April 1980, P. Becker and M. Wong ("E. and M. Becker") (GAINESVILLE). Paratypes: 9 males, same data as type, except dates between April 1978 and April 1980.

Discussion. This species most closely resembles *laotiana,* from which it can be distinguished by the longer Rs vein (3.5–4.0× as long as stigmal vein), larger body size, and darker color. Additional diagnostic features include the presence of a troughlike sulcus below the tegular clip on the mesopleuron, strongly projecting and subtruncate frontal projection, and short F-I.

Loboscelidia **sarawakensis** Kimsey, new species

Holotype male. Body length 2.5 mm. Frontal projection acutely V-shaped, truncate in profile; frons smooth, with faint fold extending dorsad from frontal projection along ocular margin; cervical projection curved in profile; scape with clear flange extending along entire length; F-I-II lengths 2× breadths; pronotum slightly broader than

long along transverse and longitudinal midlines; scutum with complete notauli, without parapsides; propodeal projection angulate, 1.3 MOD tall; femora and tibiae with sparse macrochaetae; mid and hindtibial and hindfemoral flanges large and extending almost entire length of respective tibia or femur; hindtibal posterior margin weakly bicarinate; forewing R1 0.8×, cu-a 0.4× and Rs 2.5× stigmal vein length. Body dark reddish brown, forewing maculate.

Female unknown.

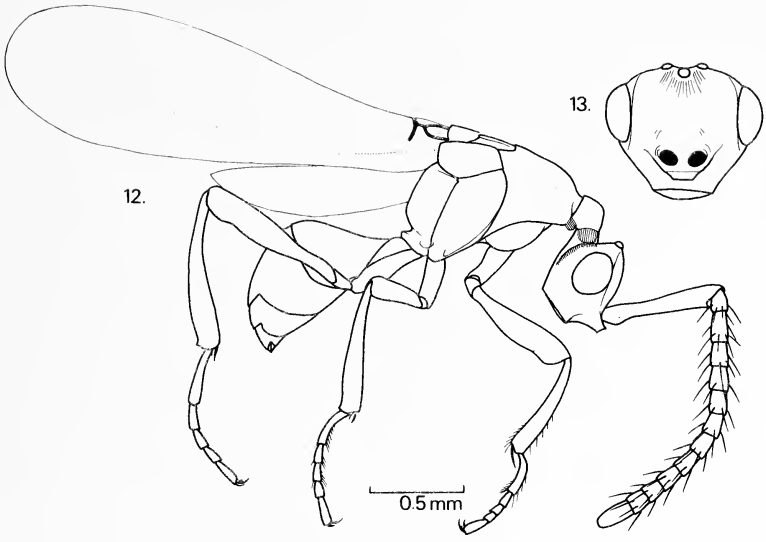
Holotype male.—SARAWAK: 4th div., Gn. Mulu, 17 September to 23 October 1977, D. Hollis (LONDON). Paratypes (LONDON, DAVIS): 18 males, same data as type; 2 males, same data as type except 1978 and no collector; 1 male, G. Mulu Pk., Long Pala, 1–6 July 1978, V. F. Eastop; G. Mulu, Mellinau Gorge, Keranges Forest, July 1978, M. Vallack; 10 males, BRUNEI: Labi, mixed dipterocarp forest, 200 m, August–September 1979, I. Gauld; 1 male, Bikit Sulang nr. Lamunin, N. E. Stork; 3 males, N. BORNEO: Mt. Kirabalu, 1 April 1964, S. Kueh. In addition, 1 male was seen from Indonesia: Sulawesi, Ulara, Dumoga-Bone.

Discussion. Most closely resembling *indica* in wing venation, *sarawakensis* can be distinguished from that species by the larger hindfemoral flange and face with a triangular subantennal projection. Additional diagnostic features are the longitudinally scratched scutellum, face below the frontal projection smooth and ecarinate, and R1 and cu-a subequal in length.

Loboscelidia **sinensis** Kimsey, new species

Holotype male. Body length 3 mm. Frontal projection acutely truncate, appearing truncate in profile; frons finely and densely rugose medially, with sharp fold extending from frontal projection along ocular margin; cervical margin broadly rounded; scape without flange; F-I-II lengths 1.8× breadth; pronotum broader than long along transverse and longitudinal midlines, sharp edged laterally; scutum with complete notauli and parapsides; scutellum coarsely scratched and punctate; propodeal projection subtriangular, about 1.6 MOD tall; femora and tibiae with sparse macrochaetae; midtibial flange narrow, about 0.5× tibial length; hindfemoral and tibial flanges about 0.7× as long as respective femur or tibia; hindtibia weakly bicarinate posteriorly; forewing R1 0.3×, cu-a 0.4× and Rs 1.8× stigmal vein length. Body dark reddish brown, wings maculate.

Female unknown.



Figs. 12–13. *Rhadinoscelidia malaysiae.* Fig. 12. Lateral view of body. Fig. 13. Front view of face.

Holotype male.—China: Hainan Is., Tien Fong Mts., 21 May 1983, Z. Bouçek (Beijing). Paratypes: 3 males, same data as type (London, Davis).

Discussion. *L. sinensis* has the very short R1 and cu-a veins characteristic of *bakeri* Fouts, *asiana* and *defecta.* However, the coarsely sculptured scutellum, broad and sharp edged pronotum, and acute V-shaped frontal projection separate *sinensis* from these species.

Rhadinoscelidia Kimsey, new genus

Diagnosis. Vertex strongly elevated above cervical extension of head; cervical extension constricted behind ocelli and eyes, and posteriorly expanded and shieldlike dorsally, with narrow ovoid row of ribbonlike setae along anterolateral edge of shield; head with narrow postocular row of ribbonlike setae; scape long, flattened and slender, as long as pedicel + F-I-IV; pronotum slender, narrower than head, laterally rounded and somewhat constricted medially, with anterolateral lobe subtended by small tuft of ribbonlike setae; scutum with notauli and posterolaterally lobate; propodeum strongly indented above petiolar insertion, with apical skirt-like rim;

coxae slender and elongate; tibiae slender and slightly curved, without transparent flanges; forewing venation highly reduced, restricted to basal 1/13th of wing, consisting of Rs, R1, Sc+R, M and M+Cu, and a stained line and fold indicating 1A; tarsal claws with small medial tooth; body integument smooth and impunctate.

Female unknown.

Etymology: *Rhadino*—slender, *scelidia*—legged, f., Gr.

Type: *Rhadinoscelidia malaysiae* Kimsey, new species.

Discussion. These are small slender wasps, closely related to *Loboscelidia.* They are characterized by having many reduced characteristics, including the slender cervical projection, narrow wings with reduced venation, small combs of ribbon-like setae on the head and pronotum, and small flanges on the legs. In addition, the bonnet-shaped cervical projection and angulate vertex distinguish this genus from *Loboscelidia.*

Rhadinoscelidia malaysiae Kimsey, new species
(Figs. 12, 13)

Holotype male. Body length 2 mm. Frontal projection with truncate medial and lateral lobes in front view (fig. 13), bilobate in profile (fig. 12); frons with dense fine scratches radiating from midocellus; vertex with transverse carina extending from hindocellus to, and part way down ocular margin; scape 1.2× head length, without transparent flange; F-I 1.6× as long as broad; F-II length 1.5× breadth; pronotum longer than broad along transverse and longitudinal midlines, broadly rounded laterally; scutum with parapsides and notauli; propodeal projections angulate and 1 MOD high; femora with small apical flange; tibiae without flanges; hindtibial posterior margin without distinct carinae; forewing R1 2× and Rs 3× as long as stigmal vein (fig. 12). Body reddish brown, with scattered long erect pale setae, forewing with apical third brown-stained.

Holotype male.—MALAYSIA: Pasoh Forest Res., Negri Sembilan, 13 October 1979, P. Becker and M. Wong ("E. and M. Becker") (GAINESVILLE).

Discussion. Diagnostic features of this species are difficult to distinguish from generic characteristics. However, the narrow wings, abbreviated wing venation and slender body will immediately distinguish this species from other loboscelidiines.

Summary

A number of new taxa are described in the chrysidid subfamily Loboscelidiinae, including 8 new species of *Loboscelidia* Westwood, *asiana, australis, indica, laotiana, maculata, nigricephala, novoguineana, ora, pasohana, sarawakensis* and *sinensis,* and the new genus and species *Rhadinoscelidia malaysiae.*

Acknowledgment

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MATING BEHAVIOR OF THE SOCIALLY-PARASITIC ANT *POLYERGUS BREVICEPS:* THE ROLE OF THE MANDIBULAR GLANDS

By Howard Topoff[1] and Les Greenberg[2]

Introduction

The ant genus *Polyergus* consists of four species, all of which are obligatory social parasites of the related formicine genus *Formica.* There are two principal behavioral contexts in which host workers form a social attachment to the slave makers. The first is inside the *Polyergus* nest, where the parasitic workers, queen, and brood must be fed and otherwise cared for by *Formica* individuals. These slave ants are obtained during group raids, in which a swarm of *Polyergus* workers invades a nest of *Formica,* disperses the adult workers and queen, and carries off the pupal brood (Topoff et al., 1984, 1985). A portion of this raided brood is reared in the slave-maker nest, and workers which eclose perform their typical functions (i.e., foraging, feeding, nest defense) as permanent members of the parasite colony.

The second context of social-bond formation occurs during colony founding by *Polyergus* queens. Because queens are not capable of rearing even their first brood, a newly-mated female penetrates a colony of *Formica,* kills the resident queen, and becomes accepted by the *Formica* workers (Topoff et al., in press).

The mating and post-mating behavior of *Polyergus* queens includes several adaptations for locating colonies of *Formica.* After the mating flight of *P. lucidus,* for example, dealate queens often return to a *Polyergus* colony and follow subsequent slave-raid swarms to target colonies (Kwait & Topoff, 1984; Marlin, 1971; Talbot, 1968).

In this manuscript, we report the results of a study on mating behavior of the western slave-making ant *P. breviceps.* Queens of

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this species have an even more efficient mechanism for reaching *Formica* colonies. Instead of a mating flight, winged *P. breviceps* queens copulate during the slave raids. The queens stop running momentarily, attract males with a pheromone produced in the mandibular glands, mate and shed their wings, and then promptly continue with the raiding workers to the target nest.

Preliminary Field Studies

This study was conducted at the Southwestern Research Station, located 5 km west of Portal, Arizona. At an altitude of 1646 m, the ground in this habitat is covered with bunch grass and contains extensive leaf litter from alligator juniper, Arizona oak, and Chihuahua pine. A total of six colonies were monitored during the period when sexual individuals were present (July 15–August 10, 1987). During each day, three of the colonies were observed continuously from 1400 to 1800 hr (MST).

Males and queens of *P. breviceps* appeared outside the nest 1–2 hr before raiding, along with the milling workers, and ran around the nest perimeter. The males flew off intermittently during milling, until the onset of raiding. But we only observed two instances of flight by *Polyergus* queens, as compared with over 100 queens (from the six colonies) that mated in slave-raid swarms with no prior flight. This contrasts markedly with the related species *P. lucidus,* in which queens fly off 5–30 min after the males' departure (Marlin, 1971; Talbot, 1968). The number of alate queens running in the raid swarms ranged from 8–29 ($n = 9$ observations, $\bar{x} = 18$). Although we could detect no obvious behavioral display, some queens vibrated their wings while running. At varying distances from the home nest, the queens ceased running. This inactivity was immediately followed by the appearance of highly-aroused males. The males ran erratically in circles, either around the queen or slightly off to the side. They often mounted each other. When a male finally copulated with the queen, she immediately pulled off her wings and continued running in the slave-raid swarm towards the target *Formica* nest.

Preliminary field tests showed that squashing a *Polyergus* queen near a raiding column attracted males. To determine the source of the chemical attractant, queens were collected from slave-raid swarms and frozen. Using microdissection scissors, we sectioned

each queen into head, thorax and abdomen. These three body parts were put into separate vials and taken to *Polyergus* nests. We then used the blunt end of a small plastic paintbrush to squash the body part on a small rock near a raiding swarm. For three tests (each with a different colony), males responded to the squashed heads by running in circles and mounting each other. No males appeared when we crushed the thorax or abdomen.

Laboratory Studies

Methods

To determine the source of the queen's sex pheromone, glands dissected from the heads of *P. breviceps* queens were presented to males confined in a laboratory enclosure. Because of its large size, the primary candidate for the sex attractant was the mandibular gland and its reservoir. Dissections were done in a wax-lined petri dish, filled with mineral oil (to retard evaporation of the volatile pheromone). First, the cuticle around the queen's mandible was cut (or removed). By holding the queen's head firmly with forceps and then gently pulling on the mandible, we were able to remove the mandibular gland. Only those preparations containing the intact glandular reservoir were used for bioassays. As a control, we used the remains of the head after the mandibular glands were removed.

The behavioral tests were conducted with seven *Polyergus* males, confined together in a plastic box (16.5 cm × 12.5 cm × 6.5 cm high). The lid of the box had a large opening (10 cm × 8 cm), covered by a mesh screen. Additional ventilation was provided by holes (2.5 cm diam) cut into opposite ends of the box. Rubber tubing (5.0 cm long and capped with nylon mesh) was placed tightly into these holes. All tests were conducted under artificial light, both to maintain the experimental chamber at 29°C, and to inhibit the males' typical approach response to the day-time sky. At the start of a test, one mandible with the attached gland and reservoir (or remaining head) were held in forceps near the rubber tube's outer opening. A constant current of air through the box was provided by a fan placed 2 m from the chamber. After recording the number of active males during a 10-s interval, each preparation was crushed with the forceps. We then recorded the number of males active during a second 10-s interval, after which the preparation was removed. In all cases, we recorded a response as positive if the males

exhibited at least one of the following behaviors: flying; running in circles; or mounting other males. Both glands from each queen were tested (except when the reservoir or mandible broke during dissection), followed by a similar test with the remaining head. The interval between all tests was 5 min. Glands and heads from 10 different queens (5 alate, 5 dealate) were used. Finally, we also tested two dissected maxillary and postpharyngeal glands, as well as squashed heads from two workers and two males. Unfortunately, by the time this laboratory study was established, it was the end of the reproductive season. As a result, the same 7 *Polyergus* males had to be used for all tests.

Results

Table 1 shows the results for the 10 queens and 7 males. The proportion of males active before squashing the mandibular gland reservoir was 0.02 (summed over all trials; $n = 126$). Afterwards the proportion was 0.84. For tests with squashed queen heads after removal of the mandibular glands, the proportion of males active was 0.27 ($n = 56$ cases). The latter activity may be due to occasional leakage of mandibular substance into the head during the dissection. The behavior of the males during positive tests was very similar to their responses to crushed queen heads in the field. Although sustained flight was impossible in the small plastic enclosures, the squashed mandibular glands immediately caused the males to run excitedly in circles inside the box, and they occasionally even mounted each other. The mandibular glands of dealate queens (which were collected near raiding columns or from *Polyergus* nests) were as effective in exciting males as those of alate queens. Finally, no activity by the experimental males was elicited either by dissected maxillary and postpharyngeal glands, or by squashed heads from two workers and two males.

Discussion

The mating behavior of *P. breviceps* queens is ecologically similar to the "female calling syndrome" that is commonly found in primitive and socially-parasitic ants (Hölldobler & Bartz, 1985). A principal characteristic of this process is that new queens do not disperse widely; instead, they remain close to their nest of origin and secrete male-attractant pheromones. Also typical of this behavior is the production each year of relatively few reproductives, and nuptial

Table 1. Response of *Polyergus* males to sex pheromone of queens. Values shown are the number of males (n = 7) active before and after squashing either the mandibular gland or the remaining head.

		No. males responding to mandibular glands		No. males responding to head without mandibular glands	
Queen #	Gland #	Before	After	Before	After
1 (D)	1	0	7	---	---
	2	---	---	---	---
2 (A)	1	1	6	0	4
	2	0	5		
3 (D)	1	0	6	0	1
	2	0	6		
4 (D)	1	0	7	0	1
	2	0	7		
5 (D)	1	0	6	1	1
	2	1	4		
6 (D)	1	0	5	0	1
	2	0	6		
7 (A)	1	0	7	0	1
	2	0	6		
8 (A)	1	0	2	0	5
	2	0	7		
9 (A)	1	0	7	---	---
	2	---	---		
10 (A)	1	0	5	0	1
	2	1	7		
Totals		3	106	1	15

(A): alate; (D): dealate
---: test not conducted

flights that are not well synchronized between the sexes (Buschinger, 1975).

To date, the most detailed studies of sexual calling behavior in parasitic ants have been conducted on the myrmicine tribe Leptothoracini. Thus in both *Harpagoxenus canadensis* and *H. sublaevis,* queens attract males by poison-gland secretions released from the extruded stinger (Buschinger & Alloway, 1979). In species of ants in which mandibular glands are the source of sex attractants, it is typically males that release the pheromone. In myrmicine harvester ants of the genus *Pogonomyrmex,* for example, males are attracted

in large numbers by mandibular-gland secretions that other males discharge upon arrival at the mating arena. Queens are subsequently "lured" to these arenas by the collectively-secreted male pheromone (Hölldobler, 1976, 1984). In the formicine ant *Camponotus herculeanus,* mass flights of winged queens from the nest are also stimulated by secretions from the males' mandibular glands (Hölldobler & Maschwitz, 1965). Although queen honey bees secrete a sex pheromone (trans-9-keto-2-decenoic acid) from their mandibular glands (Butler, 1971), *Polyergus breviceps* is the first species of ant in which the queen's sex-attractant pheromone has been traced to the mandibular glands.

In an extensive review of flight activities, Kannowski (1963) reported a distinct tendency for ground mating in formicine ants. In *Formica rufa* and *F. subnuda,* for example, ground mating occurs after a nuptial flight. But in *Formica subintegra* and *F. montana,* winged females typically remain near their nest, with approaching males forming a "ground swarm" that terminates in mating. Alate queens of *Polyergus breviceps* have apparently adapted this behavioral pattern to a parasitic mode of life, especially their inability for independent colony foundation (Topoff et al., in press). By running and mating in slave-raid swarms, mated queens of *P. breviceps* arrive at colonies of *Formica* whose workers and queen are scattered across the substrate. Such disorganization in the target colony could facilitate the usurpation of *Formica* colonies by *Polyergus* queens.

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A NEW SPECIES AND NEST TYPE OF *MISCHOCYTTARUS* FROM COSTA RICA (HYMENOPTERA: VESPIDAE; POLISTINAE), WITH DESCRIPTIONS OF NESTS OF THREE RELATED SPECIES

By James M. Carpenter[1] and John W. Wenzel[2]

While engaged in a study of the nest architecture of paper wasps, one of us (JWW) discovered a remarkable nest of *Mischocyttarus* in the collection of the U.S. National Museum. The four associated adults proved to be an undescribed species. The genus *Mischocyttarus* is the most speciose among social wasps, with 189 species recognized in the recent revision by Richards (1978). Snelling (1983) synonymized one of these species, but described one new one and raised one subspecies, and Raw (1985) described two more for a total of 192 presently recognized species. Nest architecture in the genus differs mainly in detail (Richards, 1978), but the new species builds a nest very different from its congeners. It is described below to bring it to the attention of behaviorists working in Costa Rica.

Mischocyttarus pelor Carpenter, NEW SPECIES

Diagnosis: A member of the subgenus *Monogynoecus* Richards, with a short pronotal carina, weak pronotal fovea, and weakly asymmetrical third segment of the midtarsus. In Richards (1978) it keys to *fraudulentus* Richards, with which it shares a blunt enlarged hindclaw. It differs in the shape of the first metasomal segment (*cf.* Figs. 1 and 2), in having the propodeum with the longitudinal carina more effaced dorsally (*cf.* Figs. 2 and 3), and all metasomal terga are brown and banded with yellow.

Type material: Holotype ♀ and three paratype ♀♀, Turrialba, Costa Rica, 31 May 1951 (O. L. Cartwright). The holotype, two paratypes and nest are deposited in the U.S. National Museum; one paratype is in the Museum of Comparative Zoology.

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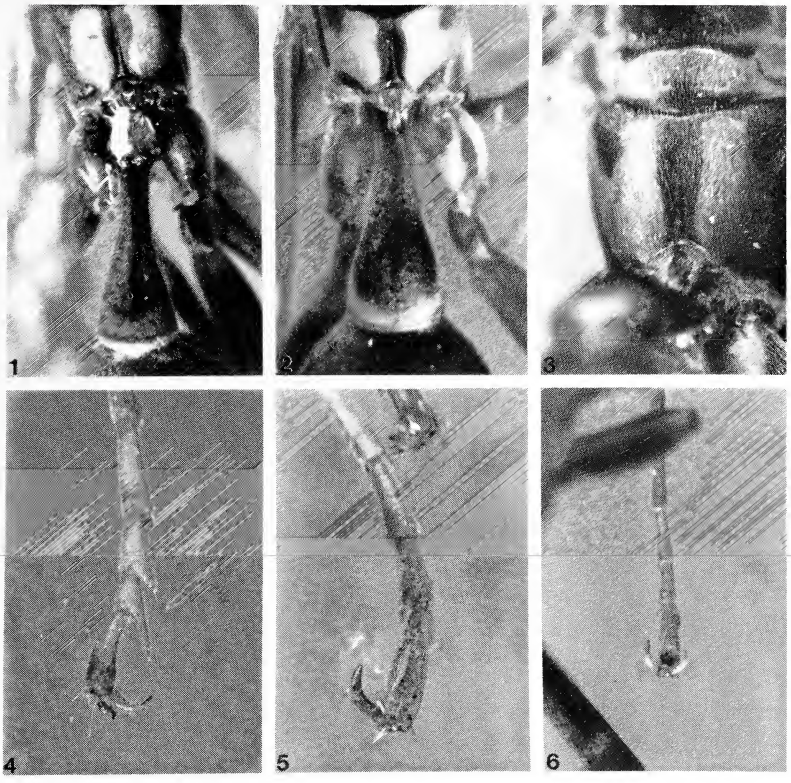
Description of holotype: Forewing length 8.6 mm. *Structure*—Clypeus weakly bidentate below, emargination narrower than an antennal socket; pronotal carina ending at about level of secondary spiracular entrance; pronotal fovea shallow, obtuse prominence present below this; propodeum with longitudinal carina and posterior cavity essentially obliterated dorsally (Fig. 3); third segment of midtarsus almost symmetrical; inner lobe of third segment of hindtarsus short (Fig. 6); enlarged claw of hindtarsus thick and blunt (Fig. 6); metasomal tergum I more than twice as long as wide, flask-shaped (Fig. 1). Integument finely granulate throughout, dull. Vestiture consisting of scattered yellow hairs shorter than an ocellar diameter. *Color*—(Discolored by alcohol). Brown. Red are mandibular teeth, ventral margin of clypeus and tips of claws. Yellow are antennae beneath, clypeus, marks above and below interantennal area, inner margins of eyes extending above and behind ocelli, most of genae narrowing to stripes above, mandibles, pronotal carina, anterior and posterior margins of pronotum, longitudinal stripes below humeri, two longitudinal stripes on scutum, tegulae, anterior margin and posterior transverse stripes on scutellum, metanotum except posterior margin, two broad longitudinal stripes on propodeum, a large spot above dorsal groove, broad anterior and posterior stripes on mesepisternum, connected below, metapleura broadly above, metasomal sternum I posteriorly, posterior bands on terga I–VI and sterna II–V, forecoxae, anterior half of midcoxae, three stripes on hindcoxae, foretrochanters and distal margins of mid and hindtrochanters, forefemora and tibiae mostly, mid and hindfemora anteriorly, mid and hindtibiae except for stripes, tarsi and claws except for mid and hind first tarsal segments proximally. Wings hyaline with veins yellowish, verging into brown basally.

Male: Unknown.

Etymology: The name, a noun in apposition, is taken from the Greek word pelor, meaning monster or prodigy, and refers to the nest.

Remarks: There is little variation among the paratypes. Taking forewing length as an indicator of size, the paratypes are all 8.4 mm. The yellow is more extensive on the pronotum in two of the paratypes, and on the mesepisterna, metapleura and propodeum of one of these specimens.

During a recent visit to the British Museum, JMC compared the type series with the types of *M. fraudulentus* and *alienus,* the two



Figs. 1–2. Metasomal petiole. 1, *M. pelor,* 11×. 2, *M. fraudlulentus,* 12×. Fig. 3. *M. pelor,* propodeum, 17×. Figs. 4–6. Hindtarsus. 4, *M. alienus,* 15×. 5, *M. fraudlulentus,* 17×. 6, *M. pelor,* 11×.

species at the couplet to which *pelor* keys. Both species were originally described from Colombian specimens. Now, in addition to the type material mentioned in Richards (1978), there are two specimens and one nest of *alienus* and four specimens and two nests of *fraudulentus* in the British Museum, all determined by Richards. The *alienus* are from Bolivia ("La Paz, Caranavi 1000 m., 15-V-1979, M. Cooper") and Costa Rica ("Cartago, Prov. Tapanti, 2 July 1963 4000 ft., C. D. Michener" determined as "sp. nr. *alienus*"; the hindtarsi are missing). The *fraudulentus* are all from the type locality, Barbacoas in Div. Nariño in Colombia, collected on 5-IV-1974, 20-VII-1974 and 6-I-1975 by M. Cooper. Besides this material, three

additional *alienus* specimens from Costa Rica in the collection of the Snow Entomological Museum were seen; these have identical collection data to the one in the British Museum and are labelled as "from nest #CR 04" and "Det. Starr, 1981." Finally, another specimen of *fraudulentus* from the collection of the Museum of Natural History of the University of Georgia was examined. This was collected in Costa Rica ("Sirena, Corcovado Nat. Pk., Puntarenas 22-III-1981, C. K. Starr, nest series no. 204"), determined as "? *fraudulentus*" by Richards, and was accompanied by a nest.

M. alienus is distinguished from *pelor* by its larger size (forewing length 9.5–10.6 mm), less asymmetrical third segment of the mid and hindtarsi (Fig. 4), and nest (see below), but is similar in having the propodeal longitudinal carina dorsally effaced. The enlarged hindclaw is usually narrower in *alienus* (Fig. 4), but this feature varies somewhat. *M. fraudulentus* is more similar to *pelor:* the third segment of the mid and hindtarsi is similarly asymmetrical and the enlarged hindclaw is blunt (Figs. 5 and 6), the size overlaps (forewing length 8.0–9.1 mm), and the nest (see below) is similar. But the shape of metasomal segment I and propodeal sculpture are different. Segment I is relatively narrower basally and more abruptly expanded posteriorly in *pelor* (*cf.* Figs. 1 and 2), and the propodeal carina is more reduced dorsally (*cf.* Figs. 2 and 3). The color is also distinctive. *M. fraudulentus* is lighter on the mesosoma, with more yellow on the sides of the thorax and propodeum, and the legs brown. The metasoma is black, at most tinged with yellow apically, on the three posterior segments in *fraudulentus.* It is brown and banded with yellow in *pelor.*

These three species together with *M. moralesi* Zikán may form a monophyletic group, sharing the apomorphy of an emarginate clypeus. Other species in *Monogynoecus* have the clypeus pointed or rounded (Richards, 1978). The emargination is broader in *moralesi,* which may be derived, and the other morphological features shared by *pelor, fraudulentus* and *alienus* appear primitive in the subgenus, e.g. pronotal fovea present. But the nests of *pelor* and *fraudulentus* probably show derived similarity (see below), so these species may be sister-groups. They are generally quite similar, and further collecting may yet show that the differences represent geographical variation in one species. At present, they are best regarded as distinct species.

Nest diagnosis: Since the nest of *pelor* is a museum specimen not accompanied by notes, its original substrate and orientation are unknown. It may have been on the underside of a leaf, as suggested by an impressed central furrow along the line of pedicels. In the following description we assume that the substrate was horizontal and that the nest hung beneath it. This nest differs from those of all other known *Mischocyttarus* by its presumed mode of expansion (Fig. 7). A line of short pedicels supports cells which grow laterally parallel to the substrate. Successive rows of cells apparently point to alternate sides of the central line of pedicels. A central plate, probably homologous to the back side of an ordinary *Mischocyttarus* nest, serves as the common base of back-to-back rows. Near either end of the rows, cells may grow at angles intermediate between the alternate rows and some cells are initiated on the walls of others, giving the nest the false appearance of a hemisphere of radially expanding cells (Fig. 8).

Nest description: Egg-shaped with long axis parallel to substrate, slightly flattened vertically, 34 mm long, 24 mm wide, 11 mm deep from substrate to lowest margin of downward pointing cells. Carton mottled brown with some pale stripes, brittle, composed of coarse, inflexible wood fiber and chips, reinforced with glossy secretion in region of pedicels and adjoining sheet. Three pedicels less than 2 mm long, aligned on central axis, initially supporting separated cells; fourth colinear pedicel secondarily added between wall of growing cell and substrate (Fig. 8c). Sheet (27 mm by 24 mm, but fragmented in specimen) fibrous and irregular, covering substrate, impressed along central line of pedicels with shallow furrow suggestive of the rib of a leaf; probably built outward from pedicels, peripherally fusing to side walls of those cells that contact substrate. Eight closed pupal cocoons (one broken), strongly domed about 2 mm beyond end of cells 10 mm long and covered over with wood fiber applied to silk, nine open cocoons. Eighty-four irregular cells, initial three laterally pointing to same side of the line of pedicels (primary side), younger cells radiating outward in all directions, more irregular on primary than secondary side, most parallel to substrate, may have walls straight or curved through 45 degrees, up to 6 mm deeper than their adjacent neighbors, may support younger cells of different orientation on their walls when divergent from or deeper than neighbors, one row of five short (less than 2 mm) cells pointing

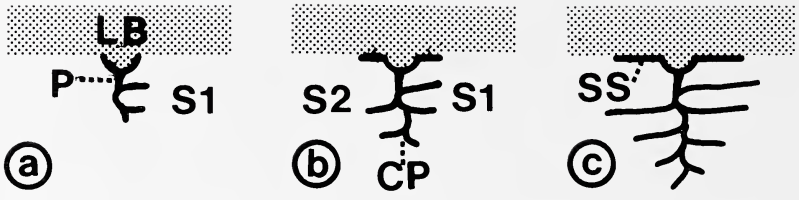


Fig. 7. Hypothetical cross-section through an expanding nest, edge view, perpendicular to row of pedicels. 7a: LB = leaf blade, P = pedicel, S1 = primary side of comb. 7b: S2 = secondary side of comb, CP = central plate axis, with central row of downward cells. 7c: SS = substrate sheet.

directly away from the substrate. Shining bright light through nest reveals between younger rows (but perhaps not between older cells) a central plate perpendicular to substrate, roughly coplanar with line of pedicels, dividing the nest into halves and supporting on its lower edge the row of five downward pointing cells.

Remarks: Unusual architecture involving unconvential comb design and multiple pedicels upon a leaf rib is known for other *Mischocyttarus,* such as *insolitus* Zikán or *latissimus* Richards (Herre *et al.,* 1986, JWW unpubl. data). The nest of *pelor* is most similar to that of the closely related *fraudulentus,* which builds on a leaf midrib. One *fraudulentus* specimen (BMNH #279) on an arum leaf has four short (2 mm) pedicels supporting 13 cells (one missing) which are parallel to the leaf blade and fused to form a continuous horizontal row (Fig. 9). A fifth pedicel (broken) supports six cells in a regular hexagonal array, separated from the row. All cells point to the same side of the rib, many bearing acute longitudinal ridges. The nest has three intact long cells; one of 10 mm is capped by the 1 mm dome of a cocoon. Unlike *M. pelor,* the carton is thoroughly reinforced with clear secretion forming irregular transparent windows as large as 1 mm^2, and there is no sign of a substrate sheet of paper. The specimen in the Museum of Natural History of the University of Georgia is similar. Separated by 13, 12 and 9 mm are four pedicels 2 mm long on the rib of a leaf and supporting 22 shallow (2–3 mm) cells (one broken), arranged very like the British Museum specimen in one or two rows and all pointing to the same side of the rib. The remnant of a fifth pedicel 9 mm from the last marks either an incipient pedicel or a broken and missing section of the nest. Like

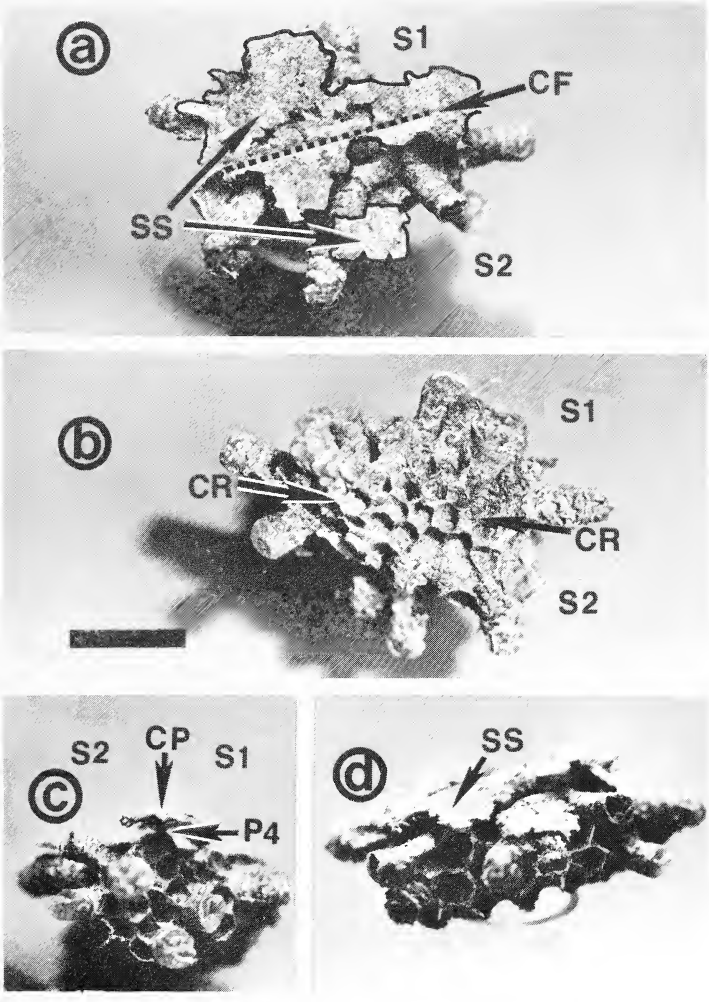


Fig. 8. Nest of *M. pelor*. 8a: Oblique top view. SS = substrate sheet (outlined), CF = central furrow, S1 = primary side, S2 = secondary side. 8b: Oblique bottom view. CR = central row of five downward cells; scale bar equals 10 mm. 8c: Edge view. Cp = central plate axis viewed on edge, P4 = fourth pedicel. 8d: Retouched to highlight cell walls. SS = substrate sheet.

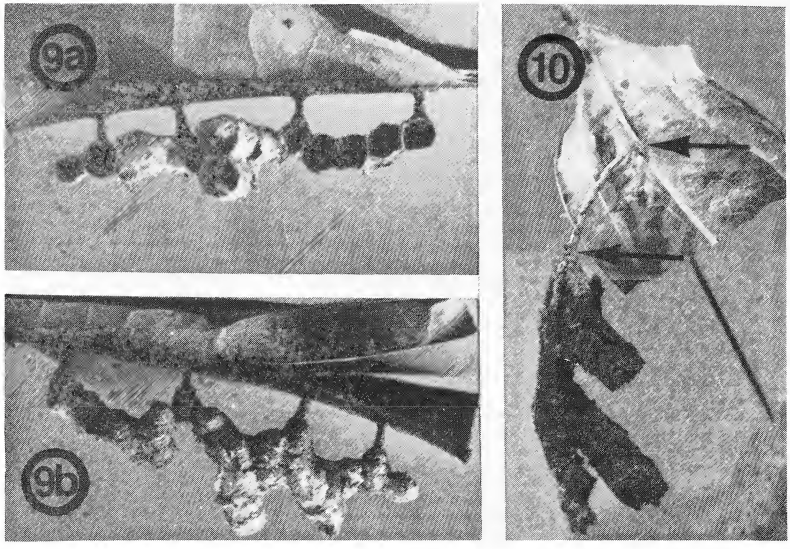


Fig. 9. Nest of *M. fraudulentus* (BMNH #279). 9a: Front view. 9b: Rear view.

Fig. 10. Nest of *M. alienus* (BMNH #216), lateral view. Arrows mark ends of pedicel, previously perpendicular but now unnaturally subparallel to leaf due to preservation.

the British Museum specimen, the carton is glossy with clear secretion, but there are neither windows nor longitudinal ridges on the cell walls. A photograph (by C. K. Starr) of this nest *in situ* shows that the nest contained only or mostly eggs. If larger *fraudulentus* nests also have cells pointing opposite to the first row, they would be very similar to *pelor* nests.

The closely related *M. alienus* (BMNH #216) and *moralesi* Weyrauch (in the Museum of Comparative Zoology) hang a single vertical row of cells from a long pedicel, which is pale in color, contains little pulp and apparently incorporates air bubbles. The *alienus* specimen is a nest of eight cells, including a pupa 13 mm long, suspended from a 12 mm pedicel (Fig. 9). The *moralesi* specimen is similar but smaller; an 8 mm pedicel supports 6 cells of which 3 are pupae, one 12 mm long. Although this design is very different from those described above, these two species share with *fraudulentus* the longitudinal ridges on the cell walls and the glossy carton with windows. All four species described here apparently initiate pedicels

on leaf veins, point cells roughly laterally (as opposed to vertically), build some cells much deeper than neighboring cells, and paste carton onto the silk caps of cocoons strongly domed beyond the end of the cells.

Discussion

Recognition of this new species, defined morphologically, should not be interpreted as support for the widespread and probably erroneous opinion that every species of paper wasp has a distinctive nest form of its own. However, the obvious differences between the nests described here demonstrate that closely related species may vary greatly in architecture. *M. alienus* and *moralesi* build a long, pale pedicel and continue mostly along the vertical axis. *M. fraudulentus* builds simultaneously several short pedicels and separate groups of cells that fuse mostly horizontally. *M. pelor* probably begins like *fraudulentus* but shows the peculiar back-to-back arrangement of cells in subsequent construction.

It is rare to find pupae in polistine nests as small as those described for *M. alienus, moralesi* and *fraudulentus.* With several nests now examined, it seems that founding females of these species ordinarily provision few larvae simultaneously, and provision unevenly, producing few pupae per comb. This would result in unusually small colony size after worker emergence. To accommodate for this low productivity, perhaps females simultaneously maintain several nests separately, as is known for *Polistes* (Jeanne, 1979) and *Ropalidia* (Itô, 1986), or build and abandon several nests sequentially, as suggested for one *Ropalidia* species (Wenzel, 1987). Present information is inadequate to determine if either of these possibilities occurs. Unlike these three species, the size of the *M. pelor* nest (and presumably the colony) is not unusual for *Mischocyttarus.*

The architecture of the *M. pelor* nest is perhaps caused by continuous building in a confined place or by inversion of a small comb and subsequent disorientation of ordinary cues used by the builders. However, several facts support the opinion that this nest is not such a monstrosity. Most nests built in too small a cavity are soon abandoned or modified to fit the space available. If the nest was built on the rib of a leaf, it probably would not have been confined in such a way as to explain the architecture. In many genera, including *Mischocyttarus,* most nests which have been rotated or inverted during construction are not remodeled completely, but rather older

regions remain as they were built and new sections are soon built normally within the new orientation (JWW, unpubl. data). This nest has pupae pointing in all directions in the uppermost cells, suggesting that they were built back-to-back early in the nest's history, just as are the younger cells below them.

Back-to-back cells originating at the margin of a central plate have long been falsely reported for the Old World genus *Polybioides* (van der Vecht, 1966). This design is currently known in the South American *Stelopolybia lobipleura* Richards (Richards, 1978), which builds such combs in cavities. Whether the nest described here is typical for its species and how it expands await confirmation by observers in the field.

Acknowledgments

A. S. Menke loaned the type series to JWW. M. C. Day assisted JMC while at the British Museum, and C. L. Smith sent the material from the University of Georgia. C. K. Starr was of great assistance with his notes on Costa Rican Polistinae. Thanks to C. D. Michener, J. Pakaluk and S. G. Reyes for improving the manuscript. Support for JMC was provided by NSF grant BSR-8508055, and for JWW by NSF grant BNS 82-00651 (C. D. Michener, principal investigator).

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A CHECKLIST OF THE ANTS OF MONTANA

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The history of myrmecology in Montana probably began in 1913 with Wheeler's description of *Formica subpolita* from Helena and 1914 when he described a new species, *Manica hunteri* from Gallatin County. A considerable hiatus ensued until 1932 when Cole recorded *Pogonomyrmex occidentalis* from Custer County.

In 1973 Borchert and Anderson published a thorough ecological analysis of the ants of the Bearpaw Mountains, one of the small ranges, which is mostly in Hill County. Thirty-three species were reported.

In 1984 Youngs and Campbell published the results of a study of ants preying upon the western spruce budworm near the western border. They reported 4 species of *Camponotus* and 7 species of *Formica* from 3 localities in Missoula County and one in Sanders County, but they failed to indicate which species was taken in which locality. These records are indicated by YC.

Six other authors have contributed a few records each. From Wing we got four records as spots on maps. D. R. Smith contributed three species for the whole state. Five records are represented by gifts of specimens from Creighton.

Finally we are greatly indebted to Roy R. Snelling for sending us 63 additional records based on specimens in the Los Angeles County Natural History Museum.

During the summers of 1956, 1961, 1963, 1964 and 1965, while we were still at the University of North Dakota (Grand Forks), we made seven field trips into Montana to observe and collect ants in 32 of the 56 counties. These expeditions yielded a total of 151 records in 64 species. (A record is a species in a locality.)

From all these records we extracted a list of 76 species of ants for the state of Montana.

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The Biomes of Montana

Our usual guide to biomes is Odum's map, but this time it has failed us, for it puts the whole of Montana in the Grassland Biome. Only the eastern third is in that biome and is continuous with the Grassland Biome in North Dakota. The middle third might be considered ecotone between the Grassland Biome and the Coniferous Forest Biome of the western third, for the prairie is broken by many small mountain ranges, which are outliers of the Rocky Mountains and the Coniferous Forest Biome. In the western mountains the timberline is at about 9500 ft in the south to 6000 ft in the north. Above that is the Alpine Biome.

With only limited ecological data we have made no attempt to list the ants which characterize each biome.

Type Localities in Montana

We have found only two type localities in Montana:—

Manica hunteri. Wheeler, W. M. 1914: 121. "Described from a dozen specimens taken by Dr. S. J. Hunter from a couple of nests on the slopes of two mountains on the Madison River, nearly opposite the mouth of Beaver Creek, Montana, at an altitude of about 7,500 feet."

Formica curiosa. Creighton 1935: 8. "TYPE LOCALITY.—Lake McGregor, Montana. This is a small lake about 35 miles west of Kalispell."

Plan for the List

Subfamilies and genera are arranged as in the Smithsonian catalog (Smith 1979). The species in each genus are arranged alphabetically except in *Formica* where they are first divided into species-groups; here we do not follow Smith, because we have transferred the *microgyna* species-group into the *rufa* species-group.

The localities in which a species has been collected are grouped by counties (see Figure 1) which are arranged alphabetically. The localities represented by our collecting are preceded by an asterisk. Those in the Borchert-Anderson study are followed by (BA); those of Youngs-Campbell by (YC); those from Snelling by (LA). (See introduction.) Others are followed by the name of the author and year of publication of the book or article. Finally the elevation above sea level is given wherever known.

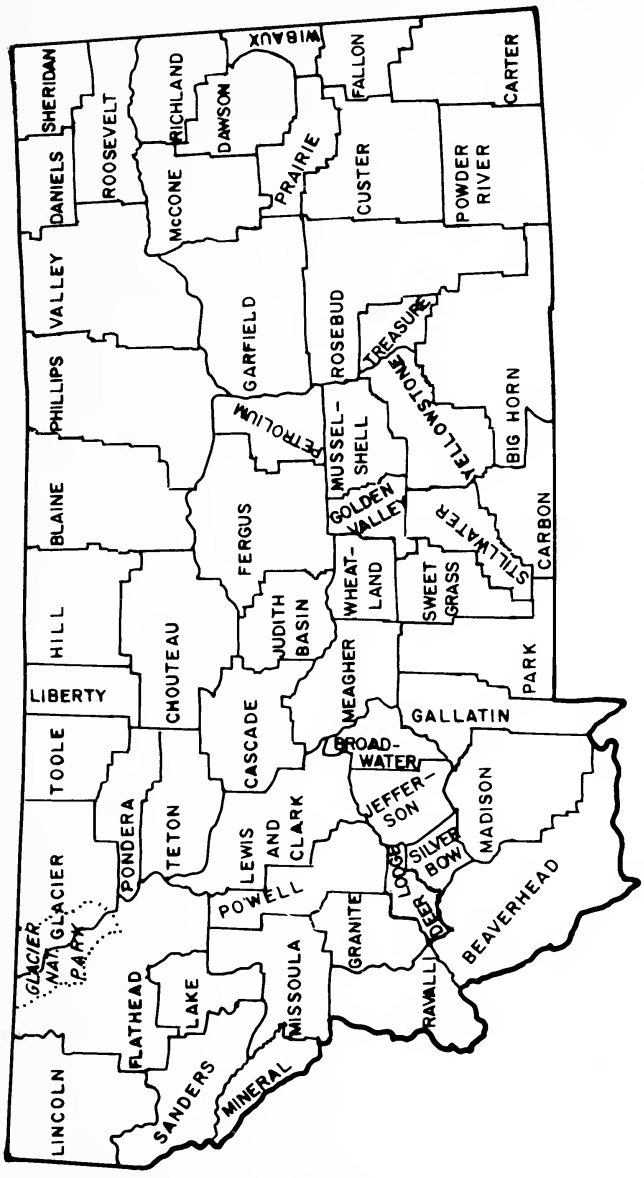

Figure 1. Counties of Montana.

Abbreviations and Symbols

CO. = county; Cr. = Creek; ft = feet; For. = Forest; Hwy. = Highway; mi = miles; Mon. = Monument; Mt. = Mountain; Mts. = Mountain; Nat. = National; nr = near; NL = No locality cited; Pk. = Park; R. = River; St. = State.

Compass directions are represented by symbols N, E, S, W and various combinations thereof. It is understood that they are followed by the word "of", e. g. "5 mi S Ekalaka" would be read aloud as "five miles south of Ekalaka." For localities not near any town we use the legal description. For those not familiar with the legal description we recommend an American treatise on surveying or our 1963 book (p. 76–77). Take, for example, a locality in Richland County: 24-19N-57E; the complete legal description would read "section 24, Township 19 North, Range 57 East" which would be abbreviated to "sec. 24, T. 19 N., R. 57 E."; to save space we resort to extreme abbreviation 24-19N-57E.

The Ants of Montana

Myrmica americana Weber. CARTER CO. *5 mi S Ekalaka. GLACIER NAT. PK. NL (LA). LEWIS AND CLARK CO. Helena (Weber 1948). MUSSELLSHELL CO. *Roundup; *20 mi S Roundup in Bull Mts. PARK CO. *Cooke City. RICHLAND CO. *24-19N-57E.

Myrmica brevinodis Emery (= *incompleta*). CASCADE CO. *13 mi S Neihart on US Hwy. 89 in Little Belt Mts. FLATHEAD CO. 7 mi N Kalispell (LA); 4 mi W Whitefish (LA); McGregor Lake (LA). GLACIER CO. *8 mi SE St. Mary on US Hwy. 89. HILL CO. Bearpaw Mts. (Weber 1950); 28-29N-16E 4000 ft, 23-28N-16E 4700 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA). LEWIS AND CLARK CO. Helena (Weber 1950). LINCOLN CO. *US Hwy. 2 nr Idaho boundary; Happy's Inn (LA). PARK CO. *Cooke City 7500 ft.

Myrmica brevispinosa Wheeler. CASCADE CO. Belt (Weber 1950).

Myrmica emeryana Forel. CASCADE CO. *5 N Neihart in Little Belt Mts. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FREGUS CO. *Maiden 5000 ft in Judith Mts.; *Rock Cr. 5800 ft in Big Snowy Mts. GLACIER NAT. PK. Fish Cr. Ranger Sta. (LA). HILL CO. 28-29N-16E 4000 ft, 23-28N-16E 4700 ft, 32-27N-16E 4700 ft, 19-28N-16E 5000 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA). LAKE CO. Flathead (LA).

Myrmica fracticornis Emery. FERGUS CO. *Maiden 5000 ft in Judith Mts.; *Rock Cr. 5800 ft in Big Snowy Mts. FLATHEAD CO. McGregor Lake (LA). GLACIER CO. Browning (Weber 1948). PARK CO. *Cooke City 7500 ft.

Myrmica lobifrons Pergande. CASCADE CO. *Monarch in Little Belt Mts. DAWSON CO. *4 mi SW Intake. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Maiden 5000 ft in Judith Mts. GLACIER CO. *13 mi SE St. Mary on US Hwy. 89. HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft, 32-27N-16E 4700 ft, 19-28N-16E 5000 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA).

Myrmica monticola Wheeler. GALLATIN CO. *Quake Lake 7000 ft.

Myrmica tahoensis Wheeler. NL (Smith 1979).

Manica hunteri (Wheeler). CASCADE CO. Belt (LA). FERGUS CO. *Maiden 5000 ft in Judith Mts.; *Rock Cr. 5800 ft in Big Snowy Mts. GALLATIN CO. *Quake Lake 7000 ft; Madison R. nr Beaver Cr. 7500 ft (Wheeler 1914) (Type locality). GLACIER CO. St. Mary (LA). HILL CO. 23-28N-16E 4700 ft, 32-27N-16E 4700 ft, 19-28N-16E 5000 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA). MEAGHER CO. *18 mi E Townsend 5000 ft. PARK CO. *Cooke City 7500 ft.

Pogonomyrmex occidentalis (Cresson). CARBON CO. *3 mi N Warren. CARTER CO. *10 mi SW Ekalaka 3500 ft; *Medicine Rocks St. Pk. 3500 ft. CUSTER CO. NL (Cole 1932). DAWSON CO. *Makoshika St. Pk. 8 mi S Glendive; *Glendive; *4 mi S Intake. FERGUS CO. *US Hwy. 191 at Missouri R. MUSSELSHELL CO. *Roundup. RICHLAND CO. *24-19N-57E; *32-21N-58E; *11-20N-59E; *4 mi SSW Sidney. ROSEBUD CO. *Rosebud. TREASURE CO. *Bighorn. YELLOWSTONE CO. *Pompeys Pillar St. Pk. (summit).

Pogonomyrmex owyheei Cole. NL (Smith 1979).

Aphaenogaster occidentalis (Emery) (= *subterranea*). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft and 19-28N-16E 5000 ft in Bearpaw Mts. (BA). LINCOLN CO. Troy (LA). PHILLIPS CO. *Landusky and *Zortman in Little Rocky Mts.

Veromessor lobognathus (Andrews). *CARTER CO. 10 mi SW Ekalaka 3500 ft (Wheeler and Wheeler 1967).

Crematogaster cerasi (Fitch). CARTER CO. *Medicine Rock St. Pk. 8 mi S Glendive 3500 ft. DAWSON CO. *Makoshika St. Pk. 8 mi S Glendive. YELLOWSTONE CO. *Pompeys Pillar St. Pk. (summit).

Monomorium minimum (Buckley). DAWSON CO. *4 mi SW Intake.

Solenopsis molesta (Say). BIG HORN CO. *Pryor Mt. (W side). CUSTER CO. *Miles City. DAWSON CO. *4 mi SW Intake; *Makoshika St. Pk. 8 mi S Glendive. HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA).

Leptothorax muscorum (Nylander). FERGUS CO. *Maiden 5000 ft in Judith Mts.; *Rock Cr. 5800 ft in Big Snowy Mts. GLACIER CO. *2 mi, *8 mi and *13 mi SE St. Mary on US Hwy. 89. GLACIER NAT. PK. Avalanche Cr. (LA); Fish Cr. Ranger Sta. (LA); Logan Pass (LA). HILL CO. 32-27N-16E 4700 ft in Bearpaw Mts. (BA).

Lepthothorax nevadensis Wheeler. PHILLIPS CO. *Landusky in Little Rocky Mts.

Leptothorax provancheri Emery. FLATHEAD CO. McGregor Lake (LA).

Leptothorax rugatulus (Emery). HILL CO. 28-29N-16E 4000 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA). LINCOLN CO. Troy (LA). PHILLIPS CO. *Landusky in Little Rocky Mts.

Subfamily Dolichoderinae

Forelius pruinosus (Roger). CARTER CO. *10 mi SW Ekalaka 3500 ft. RICHLAND CO. *24-19N-57E.

Conomyrma insana (Buckley). CARTER CO. *Medicine Rocks St. Pk. 3500 ft.

Tapinoma sessile (Say). BIG HORN CO. *Pryor Mt. (N slope). CARTER CO. *5 mi S. Ekalaka. CASCADE CO. *Monarch in Little Belt Mts. FERGUS CO. *Rock Cr. 5800 ft in Big Snowy Mts. GLACIER CO. *13 mi SE St. Mary on US Hwy. 89; Browning (LA). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft and 19-28N-16E 5000 ft in Bearpaw Mts. (BA). PARK CO. *Cooke City 7500 ft. PHILLIPS CO. *Zortman in Little Rocky Mts.

Subfamily Formicinae

Camponotus herculeanus (Linnaeus). CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FLATHEAD CO. 7 mi S Somers (LA). GLACIER CO. *8 mi and *13 mi SE St. Mary on US Hwy. 89. HILL CO. 32-27N-16E 4700 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA). MISSOULA CO. (YC). PARK CO. *Cooke City 7500 ft. SANDERS CO. (YC).

Camponotus laevigatus (F. Smith). LINCOLN CO. *US Hwy. 2 nr Idaho boundary. MISSOULA CO. and SANDERS CO. (YC).

Camponotus modoc Wheeler. MISSOULA CO. and SANDERS CO. (YC).

Camponotus vicinus Mayr. CARTER CO. *5 mi S Ekalaka. BROADWATER CO. *5 mi E Townsend. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Rock Cr. 5800 ft in Big Snowy Mts. FLATHEAD CO. McGregor Lake (LA). HILL CO. 28-29N-16E 4000 ft and 19-28N-16E 5000 ft in Bearpaw Mts. (BA). LEWIS AND CLARK CO. Helena (LA). LINCOLN CO. *13 mi W Libby; Troy (LA). MISSOULA CO. and SANDERS CO. (YC).

Lasius alienus (Foerster). CASCADE CO. *Monarch in Little Belt Mts. FLATHEAD CO. McGregor Lake (LA). GLACIER NAT. PK. Fish Cr. Ranger Sta. (LA). HILL CO. 16-30N-16E 3300 ft and 28-29N-16E 4000 ft in Bearpaw Mts. (BA). PARK CO. *Cooke City 7500 ft. PHILLIPS CO. *Landusky and *Zortman in Little Rocky Mts.

Lasius crypticus Wilson. DAWSON CO. *Makoshika St. Pk. 8 mi S Glendive.

Lasius fallax Wilson. GALLATIN CO. *Quake Lake 7000 ft.

Lasius flavus (Fabricius) (= *brevicornis microps*). CASCADE CO. *Monarch in Little Belt Mts. HILL CO. 28-29N-16E 4000 ft, 23-28N-16E 4700 ft and 17-28N-15E 3900 ft in Bearpaw Mts. (BA). MEAGHER CO. *18 mi E Townsend 5000 ft. PHILLIPS CO. *Zortman in Little Rocky Mts.

Lasius neoniger Emery. BROADWATER CO. *5 mi E Townsend. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft, 28-29N-16E 4700 ft, 19-28N-16E 5000 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA).

Lasius sitiens Wilson. BLAINE CO. *15 mi SW Cleveland in Bearpaw Mts.

Lasius sitkaensis Pergande (= *pallitarsis*). CASCADE CO. Belt (LA). CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Maiden 5000 ft in Judith Mts.; *Rock Cr. 5800 ft in Big Snowy Mts. FLATHEAD CO. 4 mi S Somers (LA); 4 mi W Whitefish (LA). GLACIER CO. *13 mi SE St. Mary on US Hwy. 89. GLACIER NAT PK. Logan Pass (LA). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft, 19-28N-16E 5000 ft, 23-28N-16E 4700 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA). LINCOLN CO. Troy (LA).

Lasius subumbratus Viereck. CASCADE CO. Belt (LA). GLACIER NAT. PK. Fish Cr. Ranger Sta. (LA). HILL CO. 19-28N-16E 5000 ft, 23-28N-16E 4700 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA).

Lasius umbratus (Nylander). GLACIER CO. Browning (LA). HILL CO. 16-30N-16E 3000 ft in Bearpaw Mts. (BA).

Acanthomyops coloradensis (Wheeler). NL (Wing 1968). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft and 19-28N-16E 5000 ft in Bearpaw Mts. (BA).

Acanthomyops interjectus (Mayr). RICHLAND CO. *24-19N-27E.

Acanthomyops latipes (Walsh). HILL CO. 16-30N-16E 3300 ft and 28-29N-16E 4000 ft in Bearpaw Mts. (BA). LAKE CO. Flathead Lake (LA).

Acanthomyops murphyi (Forel). CARTER CO. *5 mi S Ekalaka. CASCADE CO. Belt (LA).

Acanthomyops occidentalis (Wheeler). NL (Wing 1968).

SPECIES-GROUP *NEOGAGATES* OF *FORMICA*

Formica bradleyi Wheeler. CARTER CO. *Medicine Rocks St. Pk. 3500 ft. MISSOULA CO. Missoula (Halverson et al. 1976).

Formica lasioides Emery. BLAINE CO. *15 mi SW Cleveland in Bearpaw Mts. CARTER CO. *5 mi S Ekalaka. CASCADE CO. *5 mi N Neihart in Little Belt Mts.; Belt (LA). FLATHEAD CO. McGregor Lake (LA). GALLATIN CO. *Quake Lake 7000 ft (slave of *F. puberula*). HILL CO. 16-30N-16E 3800 ft, 25-29N-16E 4000 ft and 23-27N-16E 4700 ft in Bearpaw Mts. (BA). MISSOULA CO. and SANDERS CO. (YC).

Formica limata Wheeler. PHILLIPS CO. *Landusky in Little Rocky Mts.

Formica neogagates Emery. BIG HORN CO. *Pryor Mt. (-6S-26E).

SPECIES-GROUP *FUSCA* OF *FORMICA*

Formica altipetens Wheeler. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Crystal Lake 6200 ft in Big Snowy Mts. HILL CO. 28-29N-16E 4000 ft in Bearpaw Mts. (BA).

Formica argentea Wheeler. BLAINE CO. *15 mi SW Cleveland in Bearpaw Mts. DAWSON CO. *4 mi SW Intake. MISSOULA CO. (YC). RICHLAND CO. *24-19N-57E. SANDERS CO. (YC).

Formica fusca Linnaeus. CASCADE CO. *5 mi N Neihart in Little Belt Mts. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Maiden 5000 ft in Judith Mts.; *Rock Cr. 5800 ft in Big Snowy Mts. (slave of *F. puberula*). FLATHEAD CO. 7 mi N Kalispell

(LA). GLACIER NAT. PK. *Hanging Gardens; Fish Cr. Ranger Sta. (LA); Logan Pass (LA). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft, 19-28N-16E 5000 ft, 20-28N-16E 5700 ft, 23-28N-16E 4700 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA). LAKE CO. Flathead Lake (LA). LINCOLN CO. *13 mi W Libby; Troy (LA). MISSOULA CO. and SANDERS CO. (YC).

Formica hewitti Wheeler. FLATHEAD CO. McGregor Lake (LA). GLACIER NAT. PK. Fish Cr. Ranger Sta. HILL CO. 28-29N-16E 4000 ft in Bearpaw Mts. (BA). MISSOULA CO. and SANDERS CO. (YC).

Formica montana Emery. BEAVERHEAD CO. 6 mi N Dell (LA). HILL CO. 19-28N-16E 5000 ft in Bearpaw Mts. (BA)

Formica neoclara Emery. BLAINE CO. *Zurich. CASCADE CO. Belt (LA).

Formica neorufibarbis Emery. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Maiden in Judith Mts. FLATHEAD CO. 4 mi NE Bigfork (LA). GALLATIN CO. 8 mi W Yellowstone (LA). GLACIER CO. *2 mi and *8 mi SE St. Mary on US Hwy. 89. GLACIER NAT. PK. Fish Cr. Ranger Sta. (LA); Many Glaciers (LA); Avalanch Cr. (LA); Logan Pass (LA). HILL CO. 19-28N-16E 5000 ft, 20-28N-16E 5700 ft, 23-28N-16E 4700 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA). MISSOULA CO. (YC). PARK CO. *Cooke City 7500 ft. SANDERS CO. (YC).

Formica subpolita Mayr. HILL CO. 19-28N-16E 5000 ft in Bearpaw Mts. (BA) LEWIS AND CLARK CO. Helena (Wheeler 1913: 561).

Formica subsericea Say. CARBON CO. *11 mi NE Wyoming boundary on US Hwy. 212 (temporary slave of *F. fossaceps*). CARTER CO. *5 mi S Ekalaka (slave of *Polyergus breviceps*). CASCADE CO. *Monarch and *5 mi N Neihart in Little Belt Mts. FLATHEAD CO. 7 mi N Kalispell (LA). MISSOULA CO. (YC). PARK CO. *Cooke City 7500 ft; 5 mi NW Gardiner (LA). SANDERS CO. (YC).

SPECIES-GROUP *EXSECTA* OF *FORMICA*

Formica opaciventris Emery. YELLOWSTONE NAT. PK. *NE Entrance 7200 ft.

SPECIES-GROUP RUFA (INCLUDING FORMER *MICROGYNA*) OF *FORMICA*

Formica ciliata Mayr. FERGUS CO. *S wall of Missouri R. valley on US Hwy. 191. JEFFERSON CO. Elkhorn Mt. (LA).

Formica comata Wheeler. NL (Smith 1979).

Formica criniventris Wheeler. HILL CO. 19-28N-16E 5000 ft in Bearpaw Mts. RICHLAND CO. *24-19N-57E.

Formica dakotensis Emery. BIG HORN CO. *Pryor Mt. (-6S-26E). CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). HILL CO. 16-30N-16E 3300 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA). GLACIER CO. Browning (LA). LEWIS AND CLARK CO. Helena (LA).

Formica fossaceps Buren. CARBON CO. *11 mi NE Wyoming boundary on US Hwy. 212 (-9S-19E).

Formica haemorrhoidalis Emery. BIG HORN CO. *-7S-26E. BLAINE CO. *15 mi SW Cleveland in Bearpaw Mts. HILL CO. 20-28N-16E 5700 ft in Bearpaw Mts. (BA).

Formica integroides Emery. GALLATIN CO. Gallatin (LA).

Formica laeviceps Creighton. TREASURE CO. *Bighorn.

Formica microgyna Wheeler. HILL CO. 28-29N-16E 4000 ft in Bearpaw Mts (BA).

Formica obscuripes Forel. BLAINE CO. *15 mi SW Cleveland in Bearpaw Mts. CARBON CO. *15 mi S Bridger. CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). GLACIER NAT. PK. Fish Cr. Ranger Sta. (Coll. by Creighton). HILL CO. 16-30N-16E 3300 ft, 19-28N-16E 5000 ft and 20-28N-16E 5700 ft in Bearpaw Mts. (BA). LAKE CO. Flathead Lake (Coll. by Creighton). MISSOULA CO. and SANDERS CO. (YC). VALLEY CO. Fraze (LA).

Formica obscuriventris Mayr. LAKE CO. Flathead Lake (Creighton 1940). PARK CO. *Cooke City 7500 ft. RAVALLI CO. 30 mi S Missoula (Coll. by Creighton).

Formica oreas Wheeler. BIG HORN CO. *Pryor Mt. (N slope). CASCADE CO. *5 mi N Neihart in Little Belt Mts. FERGUS CO. *Rock Cr. 5000 ft in Big Smoky Mts. FLATHEAD CO. *Hungry Horse 3000 ft. GLACIER CO. Browning (LA). GLACIER NAT. PK. *3 mi S Logan Pass 5500 ft. MEAGHER CO. *18 mi E Townsend 5000 ft.

Formica querquetulana Kennedy & Dennis. PARK CO. *Cooke City 7500 ft.

Formica spatulata Buren. FLATHEAD CO. McGregor Lake (LA). HILL CO. 20-28N-16E 5700 ft in Bearpaw Mts. (BA).

Formica whymperi Forel. GLACIER NAT. PK. Fish Cr. Ranger Sta. (Coll. by Creighton). LAKE CO. Flathead Lake (LA).

Species-group *sanguinea* of *Formica*

Formica curiosa Creighton. FLATHEAD CO. McGregor Lake (Creighton 1935. Type locality) (LA). ROOSEVELT CO. Culbertson (LA).

Formica obtusopilosa Emery. BROADWATER CO. *5 mi E Townsend.

Formica puberula Emery. FERGUS CO. *Rock Cr. 5800 ft in Big Snowy Mts. (slave: *F. fusca*). GALLATIN CO. *Quake Lake 7000 ft (slave: *F. lasioides*). HILL CO. 16-30N-16E 3300 ft in Bearpaw Mts.

Formica rubicunda Emery. HILL CO. 28-29N-16E 4000 ft in Bearpaw Mts. (BA).

Formica subnuda Emery. CASCADE CO. Belt (LA). CHOUTEAU CO. 17-28N-15E 3900 ft in Bearpaw Mts. (BA). FERGUS CO. *Maiden 5000 ft in Judith Mts. GLACIER CO. *13 mi SE St. Mary on US Hwy. 89. GLACIER NAT. PK. Avalanche Cr. (LA); Fish Cr. Ranger Sta. (LA). HILL CO. 16-30N-16E 3300 ft, 28-29N-16E 4000 ft, 19-28N-16E 5000 ft, 23-28N-16E 4700 ft and 32-27N-16E 4700 ft in Bearpaw Mts. (BA).

Polyergus breviceps Emery. CARTER CO. *5 mi S Ekalaka (slave: *Formica subsericea*). JEFFERSON CO. Elkhorn Mts. (M. R. Smith 1947). LAKE CO. Flathead Lake (M. R. Smith 1947).

Interesting Montana Ants

THATCHING ANTS. Figure 2. Thatching ant mounds are conspicuous features of the grasslands. This is partly due to the size of the mound itself, but also to the fact that vegetation around the nest is taller than that of the surrounding prairie. Most of the nest is underground, but it is surmounted by a dome-shaped thatch mound. A typical mound is about 25 inches (66 cm) in diameter and 12 inches (30 cm) high. It is constructed of twigs, grass blades, dried herbaceous stems or any other slender bits of material, assembled by the workers from neighboring vegetation. The thatching ants collected in Montana are *Formica haemorrhoidalis, F. obscuripes, F. obscuriventris* and *F. oreas.*

MOUND-BUILDERS. The most common mound-builder is the harvester *Pogonomyrmex occidentalis,* which is distributed throughout

Figure 2. Thatch mound of *Formica obscuripes*. Carbon Co. 15 mi south of Bridger. The card measures 3 by 5 inches.

the grasslands. A typical mound is conoidal or paraboloidal, 24 inches (60 cm) in basal diameter and 5½ inches (14 cm) high. It is composed of excavated soil and covered with a layer of fine gravel collected by the workers from the surface of the surrounding soil. A mound is rendered more conspicuous by a circular bare area which surrounds it. These areas average 5 ft (1.5 m) in diameter. The mounds of *P. owyheei* are similar.

OBLIGATORY SLAVE-MAKERS. Obligatory slave-makers are incapable of performing any of the nest-functions and are therefore wholly dependent upon their slaves. The story of how they raid the nest of some species of *Formica* to get their slaves is fascinating but too long for this essay. The Montana slave-maker was *Polyergus breviceps* and its slave was *Formica subsericea.*

FACULTATIVE SLAVE-MAKERS. These are in the genus *Formica* and they enslave other species of *Formica.* They are, however, capable of performing all necessary nest functions; hence they can, and often do, get along without slaves. The species of this group that

have been taken in Montana are the five species in the *sanguinea* species-group. The reported slaves were *F. fusca* and *F. lasioides.*

HARVESTING ANTS. These ants collect seeds when they are abundant and store them in the nest to be consumed in times of scarcity. Montana harvesting species are *Pogonomyrmex occidentalis, P. owyheei* and *Veromessor lobognathus.* The last named species is—for us—the most interesting Montana ant. During the ten years preceding 1965 we traveled 50,000 miles to observe and collect ants in all the continental states (except Alaska) and provinces (except Saskatchewan) north of Mexico and west of the 100th meridian and did general collecting in all biomes. We were, however, especially alert for *V. lobognathus* ever since we had discovered it in North Dakota in 1955 (Wheeler and Wheeler 1956). "We suspected that if this species occurred in southwestern North Dakota and on the western border of South Dakota, it might also be found in southeastern Montana. Consequently our first stop was at Ekalaka, where we called upon Mr. Marshall Lambert, Director of the Carter County Museum. As a paleontologist Mr. Lambert is thoroughly acquainted with the region. We described the desired habitat. He showed us on our contour map where to go and how to get there. Within 15 minutes after we arrived at the place he had recommended, we found a nest of *V. lobognathus.*" (Wheeler and Wheeler 1967.) As in the Dakotas this nest was on a treeless south-facing slope where much of the surface was bare. The slopes were always near junipers which were on the north-facing slope. This species is a characteristic inhabitant of the Pinyon-Juniper Biome.

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PARADOXICAL POST-COUPLING COURTSHIP IN *HIMANTIGERA NIGRIFEMORATA* (DIPTERA, STRATIOMYIDAE)

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If the function of male courtship behavior is to inform the female of a male's species identity, or to otherwise induce her to allow mating to occur, then continuation of courtship after copulation has begun would seem to be non-functional. Such post-coupling courtship does occur in some species, however (see summary in Eberhard 1985, also Loher and Rence 1978, Speith 1984, Longair et al. 1987, Goldsmith 1987, Mora 1987, Wcislo in prep.). It might be argued that post-coupling courtship is selectively trivial, perhaps a sort of overflow that results from high excitement levels in males. On the other hand, male courtship behavior could be selectively important, serving to induce females to perform key additional reproductive processes such as allowing copulation to proceed until semen transfer is complete, transporting sperm to storage sites, ovipositing, rejecting additional suitors, etc. The possibility that such "cryptic female choice" (Thornhill 1983) occurs after copulation begins has substantial theoretical significance, and a general theory explaining the rapid and divergent evolution of animal genitalia (Eberhard 1985) relies on the supposition that post-coupling courtship is often performed by the male's genitalia. This paper reports observations suggesting that post-coupling female choice is indeed selectively important in the stratiomyid fly *Himantigera nigrifemorata* (Macquart).

Materials and Methods

All flies were observed between 10:00 and 14:00 on sunny or partly cloudy days between June and September 1987 in early second growth near San Antonio de Escazù, San Josè Province, Costa Rica. Small piles of recently cut weedy vegetation were used to attract flies. Fifteen copulating pairs were observed. In some

cases a screen was laid over the pile of vegetation to make it easier to spot pairs before they became hidden in the vegetation. Video recordings of four copulating pairs were analyzed frame by frame (30 frames/sec.); two other pairs were observed with lenses giving 4–8× magnification.

Flies were raised from a pile of cut vegetation which had been left on the ground for 3 days, then placed in a gunny sack with a clear plastic bag attached to its open end. Voucher specimens are deposited in the U.S. National Museum, Washington, DC 20560.

Results

Male flies began to arrive within 5–10 minutes after the vegetation was cut, and often accumulated in large numbers (up to more than 30 per square meter) within 30 minutes. They alternately perched on the vegetation, and flew, often in short darting flights toward other flies, producing brief collisions and clashes, or short pursuits. They did not defend territories, but gradually drifted over the cut vegetation and nearby plants. Occasionally they hit and momentarily seized other males that were either perched or, more rarely, in flight. On four occasions a male bumped briefly against a mating pair resting on the vegetation, but none of the pairs separated as a result. Flies collected in two aggregations about one hour after vegetation was cut were nearly all males (31 of 32 and 41 of 41).

I saw the initial stages of pair formation on two occasions. The male seized the female in the air 1–2 cm over the vegetation and the pair immeditely landed, with the male on the female's dorsum. The male immediately made genital contact as he scrambled briefly with his front legs on the female's head. Then he rested quietly on her dorsum for <5 seconds before beginning a series of courtship movements. Although the durations and sequences of the movements varied somewhat, at least three types of behavior were recognizable.

Tapping

A male tapped by raising his front legs, usually holding them briefly immobile as they projected more or less forward over the female's head, then "winding up" by bringing them sharply back and upward over his head, and then "swinging" them sharply downward over the female's head with a whipping motion (Figs. 1 and 2). The leg usually (perhaps always) stopped just short of hitting the

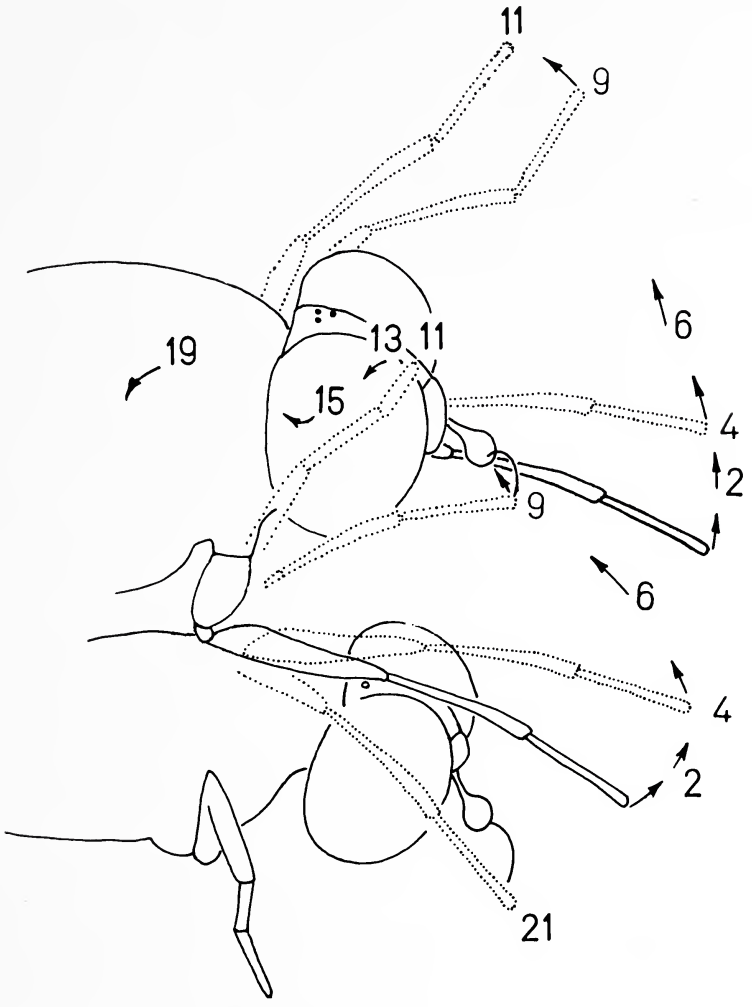

Fig. 1. Initiation of tapping movements of front legs of a copulating male *H. nigrifemorata* seen from the side and slightly above (drawn from tracings from a video recording). Numbers and dotted lines indicate number of frames (30 frames/sec.) after starting leg position (solid lines) and positions of legs at these times. Both legs were raised simultaneously until they were over the male's head (frame 11); then, after a brief pause, the right leg was brought further back (frames 13–19), then tapped briskly downward (frame 21). It was not possible to determine from the videotape whether the tarsus contacted the female's arista.

female's eye (Fig. 1); in at least some cases (probably often, but certainly not always) the leg hit against the arista of the female's antenna.

Tapping occurred in short bouts averaging 5.0, 4.6, 3.8 and 4.3 taps/bout in four different pairs (range 1–17, coeff. of variation averaged 56% in the four pairs). The average times between bouts for four pairs were 2.6, 3.5, 4.2, and 4.6 sec. (range 1.1–14.7, coeff. of variation averaged 56%). Usually the male held both front legs directed more or less anteriorly over the female's head (solid lines in Figs. 1 and 2) during pauses between bouts. Bouts nearly always (88 of 95 cases) began with the male raising both front legs simultaneously (Fig. 1). Then one leg wound up and swung, and, as soon as it came to rest, the other leg wound up and swung. From then on tapping was nearly always strictly with alternate legs (205 of 207 cases; in one case both legs hit simultaneously, and in the other the same leg hit twice in succession). The leg not being swung was held immobile while the other was lifted and swung. Average times between the downstrokes of taps were .41, .43, .44, and .49 sec. (range 0–1.5, coeff. of variation averaged 41%). Usually (40 of 50 cases) the interval between the first two taps was shorter than that between the second and third.

Twitching

Twitching occurred between bouts of tapping when both of the male's front legs had been immobile and apparently in contact with the female's aristae. Twitching probably caused deflections of the aristae. To the naked eye the movements of the legs resembled rubbing, but the videotapes showed very rapid, brief (usually only 1–2 frames), and variable movements. The legs moved dorsally, ventrally, or laterally to either side. Sometimes both front legs were twitched simultaneously, while in others only one was moved. More than a single twitch was performed in 9 of 20 pauses with twitches (maximum was 6). Individual males differed in their tendencies to twitch: three flies twitched at least once during 20 of 56 pauses, while the fourth did not twitch in any of 20 pauses ($p < .05$ with Chi-Squared Test).

Rocking and scrabbling

Scrabbling involved movements of the male's body and all of his legs. The front and middle legs rubbed erratically on the female's head and body, and his body moved short distances both laterally and forward and backward, also in an erratic pattern.

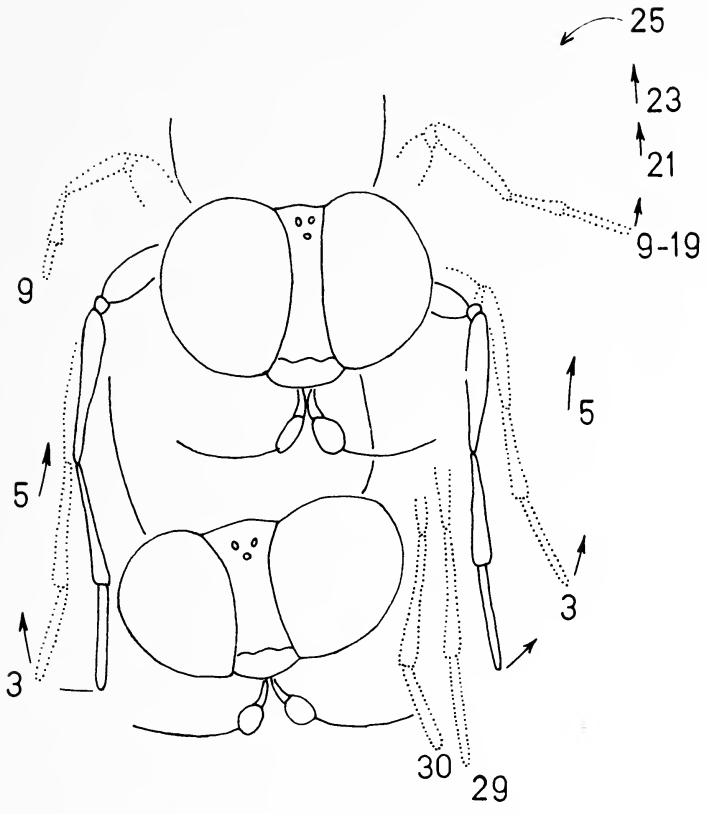

Fig. 2. Initiation of tapping movements by a different male *H. nigrifemorata* seen from above and in front (drawn from tracings from a video recording). Numbers and dotted lines indicate number of frames after starting leg position (solid lines) and positions of legs at these times. After both legs were raised simultaneously to point upward over the male's head (frame 9), the left leg was held immobile (9–19) while the right leg swung back and down (not shown); then the left leg was swung back (21–25) and then down (25), then moved slightly to the side (30). It was not possible to determine from the videotape whether the tarsus contacted the female's arista.

Often the joined tips of the male and female abdomens were raised and lowered repeatedly during or just before or after scrabbling. The female rocked forward when her abdomen was lifted. Apparently these movements were caused by the male rather than the female, since in two pairs observed after their genitalia became uncoupled, the male's scrabbling movements were often accompanied by brisk lifts of his abdomen which probably correspond to the

rocking movements observed in pairs (a screen prevented these females from walking down into the vegetation; genital contact terminated after about two minutes but the male remained on the female and continued to execute courting movements). The dorsal and forward force generated during male lifting movements probably came from his hind legs, which were usually braced on the substrate. Probably the effect of the rocking movements was to drag the female slightly forward by her genitalia.

In each of the ten courtship sequences in which I observed termination, the female walked down into the vegetation. In all but one case, when the male was scraped off by protruding vegetation, the male was still riding on her dorsum when she disappeared. The dislodged male hovered for several seconds about 5 cm over the site where the female had disappeared, then flew away. Females probably oviposited when they walked down into the pile of vegetation, as flies were raised (14 males and 15 females) from a pile into which mated females had disappeared.

Discussion

There are several reasons for classifying the behavior of copulating males as courtship. The patterns were relatively stereotyped, both in form and, to a lesser extent, in sequence; the males' movements undoubtedly caused stimulation of the female; they were performed consistently in male-female interactions and never in other contexts; and they were unlikely to have any other functions for the males. None of the movements described was performed before genitalic coupling was achieved, while all males made at least some of the movements soon after coupling began. It is unlikely that the post-coupling male behaviors were some sort of selectively irrelevant "overflow" courtship, because they never began until after coupling had occurred.

Demonstration that male *H. nigrifemorata* only court females after achieving genitalic coupling supports the idea that post-coupling courtship in this and, by extension, other species with post-coupling courtship can be selectively significant. This demonstration of the importance of cryptic female choice is, in turn, in accord with the argument that male genitalia are often selected to perform "internal courtship" after intromission has begun (Eberhard 1985).

It is not certain which female post-coupling reproductive process(es) male *H. nigrifemorata* were attempting to induce. Rocking behavior may serve to start the female walking, causing her to move away from other males down into the vegetation.

Strictly post-coupling courtship involving body parts other than genitalia also occurs in the bee *Centris pallida* (Alcock and Buchmann 1985), the sphecid wasp *Glenostictia satan* (Longair et al. 1987), another stratiomyid, *Merosargus stamineus* (Fabricius) (pers. obs.), and perhaps the phorid fly *Megaselia* sp. (W. Wcislo in prep.). It may be significant that in all of these species males swarm (or, in the case of the phorid, are at least common) at sites where receptive females occur, and compete to grab females before other males do so. Males in such swarms may have to postpone courtship until they have the female "in hand" and protected from the advances of other males. That females consistently allow immediate coupling in these species argues against the supposed need for females to make males prove their species identity with elaborate courtships before they allow them to copulate.

Summary

Males of *Himantigera nigrifemorata* consistently courted females, but only after they had achieved genitalic coupling. Courtship consisted of a complex series of partially stereotyped behaviors. Such post-intromission courtship is in accord with the idea that "cryptic female choice" is selectively important.

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INTERCOLONIAL AGGRESSION IN THE SUBTERRANEAN TERMITE *HETEROTERMES AUREUS* (ISOPTERA: RHINOTERMITIDAE)*

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Introduction

Foraging parties of the subterranean termite, *Heterotermes aureus,* are present throughout the year in the southwestern United States, but peak foraging activity coincides with the summer "monsoon" season when the weather is warm with ample precipitation (Haverty *et al.,* 1974). Average foraging territory for a colony of *H. aureus* is estimated to be approximately 12.5 square meters and each colony apparently maintains a discrete boundary with other conspecific colonies (Haverty *et al.,* 1975). How these termites achieve colony isolation is unknown, although aggressive interactions have been observed between groups of conspecifics (Nutting, unpublished observations). Intraspecific territoriality and aggressive behavior have been described in other termites (Clément, 1978; Darlington, 1982; Greaves, 1962; Howick and Creffield, 1980; Levings and Adams, 1984; Nel, 1968; Thorne, 1982) and in several other social insects (Hölldobler and Lumdsen, 1980; Levings and Traniello, 1981). The events preceding an encounter between individuals, the recognition and discrimination factors, and the consequences of aggression are not well understood in *H. aureus.* This study was done to examine the aggressive behavior between *H. aureus* colonies from different field locations and describe intercolony interactions of both paired individuals and simulated foraging groups.

Materials and Methods

Termites

Groups of *H. aureus* were collected at various locations surrounding Tucson, Arizona, during the spring and fall of 1986. Fallen

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branches and dead trunks of *Cercidium floridum* (blue palo verde) or *C. microphyllum* (little-leaf palo verde) were used as a source of termites even though *H. aureus* will utilize a variety of desert plants as hosts (Haverty and Nutting, 1975). The branches were brought back to the laboratory at the University of Arizona and the termites extracted from each branch. Each termite group from a single tree was maintained separately in a plastic shoe box lined with moist paper towels.

Arenas

Rectangular arenas were assembled for pairs of termites from two thin plastic strips and two machine nuts. The components were arranged so the plastic strips were adjacent to the machine nuts and the unit placed on paper to give the termites a "grip." This construction made manipulation of arena size easy and deterred termite escape. Glass arenas were used for simulated foraging studies (Fig. 1). The arena dimensions were 17 × 21 × 1 cm and could accommodate approximately 1000 termites.

Soldier and worker interactions: arena size

Each soldier was placed in an arena and observed until its behavior stabilized. A soldier or worker from the same colony was introduced and the pair observed for 3 minutes. The added soldier or worker was removed and a soldier or worker from a different colony was placed in the arena with the same soldier for 3 minutes. Observations for soldier/soldier interactions were at a single arena size (1.5 cm^2) while soldier/worker observations were made at 4 arena sizes (1.5, 3.0, 4.5, and 6.0 cm^2). Two replicates of 10 soldiers, each with 8 pairings of different workers, were completed for a total of 160 observations. During the 3-minute period the number of snaps of the mandibles was recorded, the time to a fatal snap, the number of encounters, and any behavior that was consistent throughout the course of the experiment.

Soldier vs. worker interactions: immobilization of soldiers or workers

Termite aggression was investigated by immobilizing workers or soldiers between the head and the thorax with a small card with a V-shaped notch cut in the edge. The immobilization procedure in no way injured the animal, because normal behavior resumed when the card was lifted. In one experiment only the worker head was exposed to a freely moving soldier. In another, only the worker

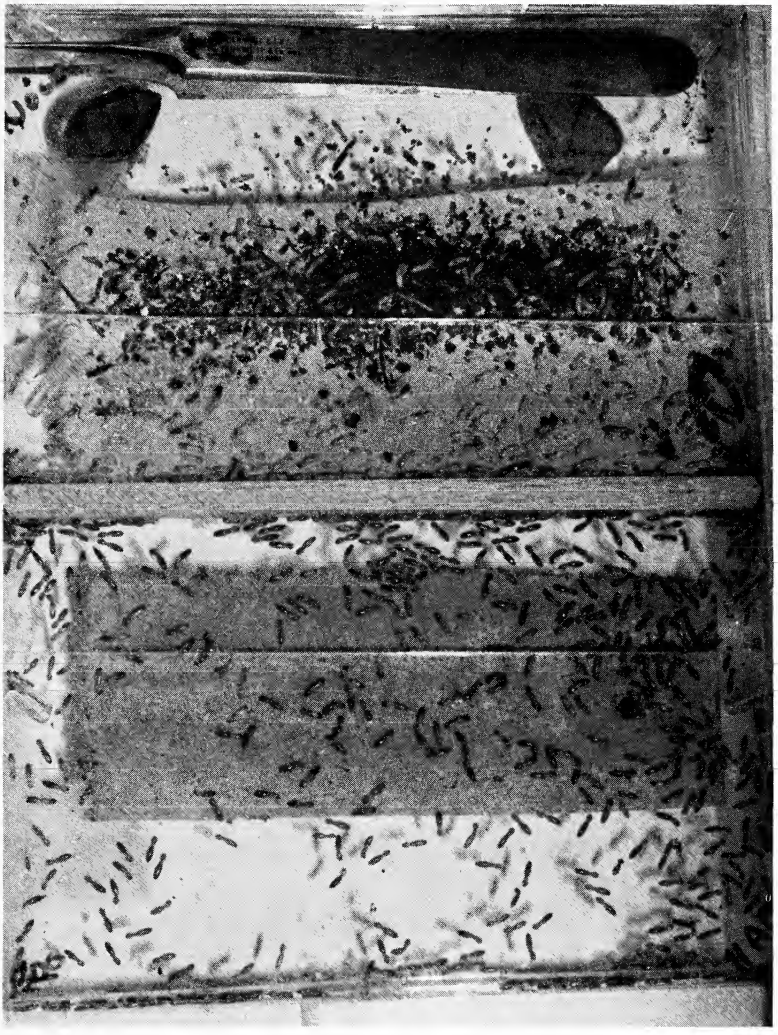

Figure 1. Arena for simulated foraging tests of conspecific, intercolonial aggression of *Heterotermes aureus*.

abdomen was exposed to a freely moving soldier. Similar observations were made of worker behavior when soldiers were immobilized with only the abdomen or only the head exposed. Ten pairings in each of the four categories were made.

Simulated foraging experiments

Termites are generally found in foraging groups when observed in the field. Field conditions were simulated in the laboratory with a glass arena containing a balsawood barrier to separate termites from different colonies (experimental) or from the same colony (control) (Fig. 1). One group of termites was dyed with Sudan Red 7B by the method of Lai *et al.* (1983) before each experiment. Large groups (approximately 500) of mixed soldiers and workers were placed on each side of the arena. The termites required approximately 1 hour to start foraging behavior and nearly 8 hours to penetrate the barrier. Termite behaviors were documented and examined using high magnification video recording equipment.

Results

Soldier vs. soldier interactions

When two soldiers from different colonies were paired in an arena, each would walk until there was contact. These encounters resulted in a brief to extended period of antennation, followed by the retreat of one or both, opening and repeated snapping of the mandibles. A fatal snap resulted when the mandibles penetrated the head, thorax, or abdomen. Snaps which severed only an antenna or leg were not fatal. Soldiers that had delivered a fatal snap made several additional contacts, an occasional snap, and moved away as if no longer considering the "enemy" a threat. There were further contacts by the victorious soldier but no snaps. The mechanism by which the soldier made this decision is unknown.

Soldier vs. worker interactions: arena size

Intracolonial termite pairs of soldier and worker had a mean number of encounters/minute ($\pm$ standard error) of 3.0 ± 0.2 at 1.5 cm^2, 2.5 ± 0.2 at 3.0 cm^2, 2.2 ± 0.2 at 4.5 cm^2, and 1.6 ± 0.2 at 6.0 cm^2 (Figure 2a). Intercolonial encounters between soldier and worker also decreased with an increase in arena size. The mean number of encounters/minute ($\pm$ standard error) for intercolony pairings was 2.0 ± 0.2, 2.2 ± 0.2, 1.7 ± 0.2, and 1.4 ± 0.1 at arena sizes of 1.5, 3.0, 4.5, and 6.0 cm^2 respectively (Figure 2a). While there was no aggression during intracolony pairings, most intercolony pairings resulted in soldier displays of aggression, including attack posture (open mandibles against the substrate), numerous snaps of the mandibles, and rapid retreats. At every arena size more

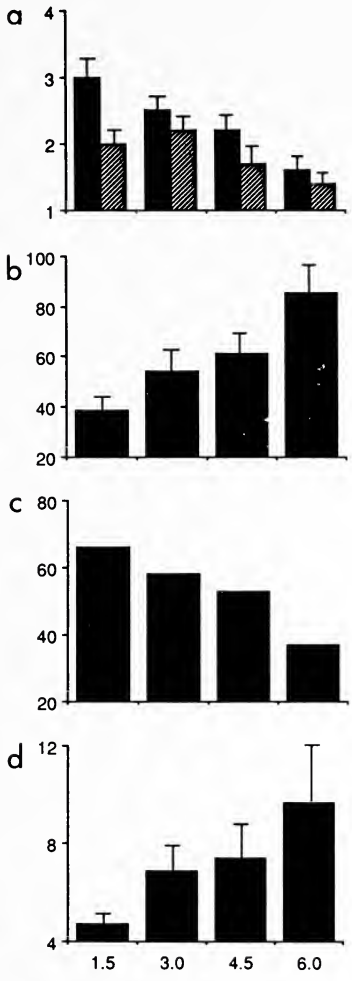

Figure 2. *Heterotermes aureus* encounters in an arena. The horizontal axis represents increase in arena size (cm^2). Vertical lines on each column represent standard error. a) Intracolonial (hatched) vs intercolonial (solid) mean number of encounters per minute. b) Mean time soldiers require to inflict fatal snaps on alien workers (seconds). c) Percentage of soldier encounters following a fatal snap against a worker. d) Mean number of snaps a soldier requires to inflict a fatal snap on a worker.

than 50% of the workers were fatally wounded. Only the soldier made additional contacts following a fatal snap while both the soldier and the worker participated in encounters if there was no fatal snap. Again, soldiers refrained from further snaps during contacts after a fatal snap. Soldiers delivered a fatal snap in a mean time (± standard error) of 37 ± 7 seconds in a 1.5 cm^2 arena, 51 ± 10 seconds in a 3.0 cm^2 arena, 62 ± 8 seconds in a 4.5 cm^2 arena, and 80 ± 13 seconds in a 6.0 cm^2 arena (Fig. 2b). The percentage of soldier encounters following a fatal snap decreased as the arena size increased and was 66% at 1.5 cm^2, 58% at 3.0 cm^2, 53% at 4.5 cm^2, and 37% at 6.0 cm^2 (Fig. 2c). The number of encounters following a fatal snap by a soldier was higher at smaller arena sizes since the encounter rate was higher and more than 80% of the fatal snaps were delivered by the third encounter. The soldier also required fewer snaps to deliver a fatal snap as arena size diminished (Figure 2d).

Even though the response of a soldier to an alien worker was more rapid as arena size decreased, not all workers were killed. Some avoided a fatal encounter with a soldier; escape was most frequent at the largest arena size (Table 1). In fact, 25% of the workers behaved aggressively and attacked a soldier. Aggressive workers were usually slashed by the sharp and powerful soldier mandibles but a few workers were able to evade the soldier defenses. During these encounters the soldier became the victim, having one or both antennae removed just above the scape. The behavior of workers when confronted with an aggressive soldier was grouped in two categories: 1) the worker responded actively (ran away or became aggressive), or 2) the worker remained stationary (no motion). Each category had a nearly equal probability but more workers survived if their behavior was active (Table 2).

Soldier vs. worker interactions: immobilization of soldiers or workers

Worker behavior toward a soldier and soldier behavior toward a worker were distinguished when one of the individuals was immobilized while the other moved freely. Soldier snaps to the worker abdomen were less frequent and less violent than snaps to the worker head (Table 3). Workers approached the abdomen of an immobilized soldier, made brief touches with the antennae and retreated. The worker attacked vigorously until the cuticle was

Table 1. The evasion of soldier aggression by workers during all intercolony pairings of workers and soldiers.

	Worker evasion	
Arena size (cm^2)	no.[a]	%[a]
1.5	4	20
3.0	3	15
4.5	4	20
6.0	9	45
	Total	
	20	25

[a]Each value based on 20 pairs of termites

Table 2. Comparison of worker behavior and survival during all intercolony pairings of soldiers and workers.

	Worker response	
	no.	%
	active	
Initial behavior	44/80	55
Within group survival	17/44	39
Total survival	17/80	21
	passive	
Initial behavior	36/80	45
Within group survival	3/36	8
Total survival	3/80	4

Table 3. The aggressive response of soldiers to immobilized workers and the aggressive response of workers to immobilized soldiers.[a]

	Immobilized workers		Immobilized soldiers	
	Abdomen exposed	Head exposed	Abdomen exposed	Head exposed
Aggressive response on first encounter	3[b]	5	3	7
Aggressive response after 3 encounters	3	5	10	9

[a]Aggressive responses followed encounters of individuals of different colonies and resulted in a snap of the mandibles by the soldier or a worker attack

[b]Each column represents the actual number of individuals responding of 10 pairs of termites

penetrated if there was a second encounter. When the worker contacted the head of an immobilized soldier there was repeated movement of the worker's mandibles but no penetration of the heavily armored soldier head capsule. Eventually the soldier's antennae were snipped off just above the scape or the labrum was damaged.

Simulated foraging experiments

Four experiments were completed. Experimental and control trials were made on October 1, 1986. The experimental group contained 300 workers and 15 soldiers (undyed) on one side of the balsawood barrier and 500 workers and 15 soldiers (dyed) from another colony on the other. A similar control group contained 500 workers and 15 soldiers from the same colony on each side with one of the groups dyed. The soldier/worker ratio in these experiments was similar to soldier/worker ratio of *H. aureus* foraging groups in the field (Haverty, 1977). After the normalization period, workers of both experimental groups began removing bits of the wood partition. Upon antennal contact with alien workers, some workers abandoned their activity, retreated backwards out of the hole, and began Vertical Oscillatory Movement (V.O.M.) (Howse, 1964). Many termites became agitated, moved rapidly, and soldiers clustered around the breach in the barrier (Figure 3). The soldiers in the hole impeded tunneling, but a few workers excavated more wood. Some soldiers arched the abdomen, perhaps releasing a sternal gland substance. After 30 minutes, 2 dyed workers penetrated to the side of the undyed colony and within 15 minutes more than 100 dyed termites (both workers and soldiers) had migrated to the undyed termite side while only 55 undyed termites moved to the dyed termite area. After 24 hours only 5 dyed individuals remained alive. Meanwhile, control groups had penetrated at about the same time as the experimentals but no agonistic behavior was observed. After 24 hours, members of the dyed and undyed control groups were completely mixed. These results demonstrated that intercolony contact of large foraging groups led to aggression which was not terminated at colony boundaries. The soldier's contribution to the successful invasion was not clear, so two more tests were made on November 1, 1986. One test contained 500 workers from different colonies on either side, with no soldiers. All the termites were dead after 24 hours. The coincident trial contained 500 workers on either side but one side contained 8 soldiers (dyed) while the other side contained 25 soldiers (undyed). When the hole was large enough,

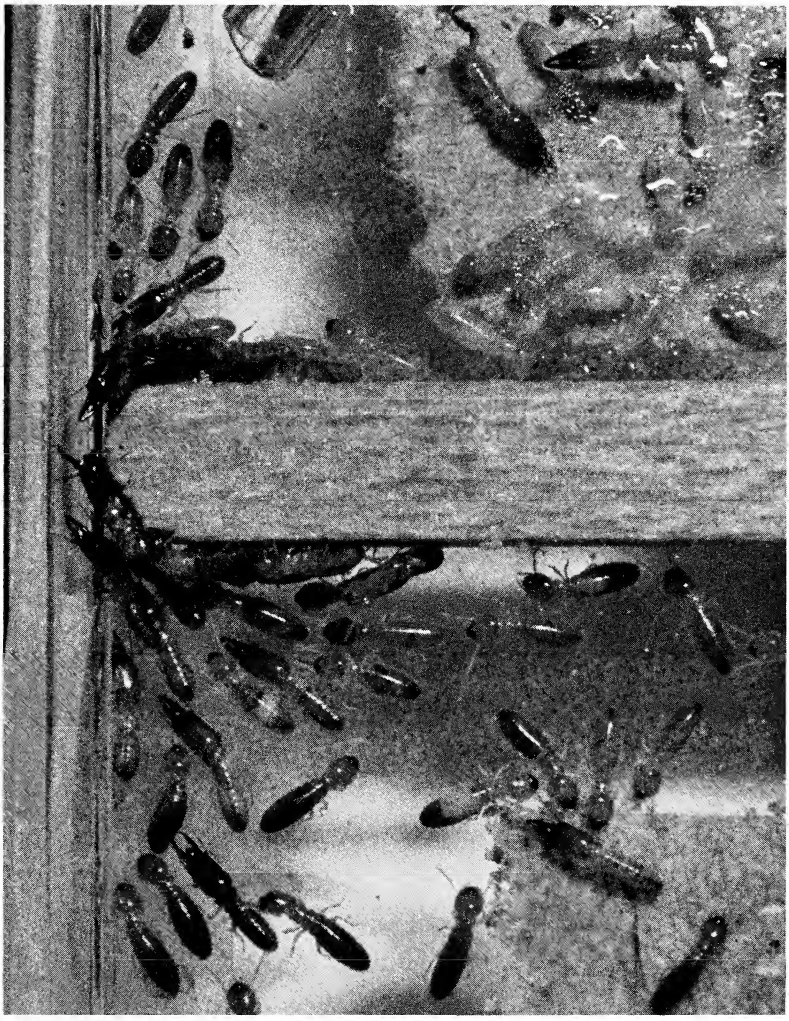

Figure 3. Soldier aggregation at orifices between groups during simulated foraging of *Heterotermes aureus.*

several undyed workers immediately penetrated to the side of the dyed termites. The invasion resulted in vigorous attacks by the dyed termites but after 24 hours all of the dyed termites were dead while there were still numerous undyed termites searching the arena.

Discussion

Both workers and soldiers of *H. aureus* were able to distinguish individuals of their own colony from those of an alien colony and recognition always followed some type of body contact. Intercolony pairings of soldiers or soldiers and workers resulted in aggression with the death of one individual while in similar intracolony pairings there was no aggression or mortality. Recognition after body contact was especially evident when several intra- and intercolony switches were made sequentially. The contacts were probably the result of random movement and not a response to a pheromone, because the number of encounters/minute decreased for both intra- and intercolonial pairings with an increase in arena size. Moreover, workers were not alarmed until there was contact of the antennae during simulated foraging. Body contact is also part of alarm communication of *Zootermopsis angusticollis* and *Z. nevadensis* (Stuart, 1970).

Repeated contacts in small arenas intensified aggression between individuals of *H. aureus* resulting in more encounters and fewer encounters to a fatal snap. The termites could have been stimulated by contact behavior or increased exposure to cuticular and/or glandular substances. Cuticular hydrocarbons are associated with interspecific and caste recognition cues in the termite, *Reticulitermes virginicus* (Howard *et al.*, 1982a, 1982b). The role of cuticular hydrocarbons in the conspecific intercolonial interactions of *R. virginicus* is unclear because pooled extracts of termites from widely separated locations (>1.6 km apart) were used. These termites were almost certainly from separate colonies, and some agonistic behavior would be expected which could not be conclusively evaluated by a behavioral assay (Howard *et al.*, 1982a). Nevertheless, cuticular hydrocarbons could be an important factor for communication during *H. aureus* encounters, since workers and soldiers became excited after body contact. Furthermore, there was recognition and alarm after contact of only the antennae during simulated foraging. Soldiers also became excited and moved into the orifice between groups; some of the soldiers arched the abdomen and may have released an abdominal sternal gland substance which helped excite both soldiers and workers. Soldier sternal gland pheromone is important for recruiting soldiers and workers to areas of interspecific confrontation in *Nasutitermes costalis* (Traniello, 1981). Soldierless foraging

groups of *H. aureus* penetrated, invaded, and attacked another colony similarly to foraging groups with soldiers, so that the actual contribution of a soldier's cuticular or glandular substance to the increased excitement of the termites is uncertain.

Complex behavior followed paired and multi-termite contacts in *H. aureus*. After encounters of paired termites from the same colony, the soldier or both the soldier and the worker made a few V.O.M.'s. Most V.O.M.'s, however, occurred during intercolony pairings, so it may be an alarm signal as suggested by Howse (1965). Workers were responsible for the initial intercolonial discrimination in simulated foraging experiments and then transmitted a warning via vibrational signals (V.O.M.'S) to the remainder of the colony. Worker V.O.M.'s are probably important cues to "call" soldiers to the area of contention. The source and the identity of the discrimination cue (i.e. cuticular chemicals or complex behavior) is still unknown.

Soldiers and workers behaved differently when given similar experimental treatments. A worker confronted with an immobilized alien soldier attacked. A soldier confronted with an immobilized alien worker did not immediately respond aggressively. The soldier may not have recognized the worker as "different" or immobilization prevented worker behavior critical for discrimination. Soldiers respond to cuticular and/or secretory substances in paired encounters but were more likely to acknowledge vibrational cues during simulated foraging. *H. aureus* soldiers in normal foraging conditions may be relegated to a defensive/offensive role as observed in other termites (Prestwich, 1984; Stuart, 1969; Thorne, 1982) and may not participate in intercolonial encounters until summoned by the workers giving vibrational signals.

Workers and soldiers have different roles in overall colony aggression. Workers made initial contact with other colony members in simulated foraging experiments. They then triggered a sequence of events which recruited soldiers to the area of confrontation, widened the orifice between colonies, and were first to invade new territory. Workers were also aggressive in the absence of soldiers. The worker's primary role in intercolony contacts, agonistic behavior, and defense has been described in *Nasutitermes corniger* (Thorne, 1982). The *N. corniger* workers attack soldiers vigorously, biting the legs and abdomen and *H. aureus* workers behave similarly. Soldiers that penetrated to the other colony area in simulated

foraging experiments, were immediately confronted by a squad of both soldiers and workers. Instead of retreating, the workers attacked the soldier's abdomen, legs, and head. Many workers were killed by the soldier but it was eventually subdued. The worker's behavior helped increase its survival and might be important in securing and protecting territory. How worker behavior is integrated in the foraging dynamics of natural groups of termites is unclear.

The role of the soldier was also important in simulated foraging. The number of soldiers participating in the interactions was critical to the successful invasion of one colony by another. When the number of soldiers was equivalent, there was nearly complete decimation of both simulated foraging groups regardless of the number of workers. When the number of soldiers was disproportionate, the group with the larger number of soldiers successfully invaded. Since soldiers migrate into areas of conflict between groups, the soldier density may be substantially greater in natural foraging groups where intercolonial or interspecific confrontations are frequent. Locations in the colony interior may have few soldiers, so the soldier ratios suggested by Haverty (1977) could be an artifact of the collection procedure. Unfortunately, *H. aureus* colonies are difficult to excavate, so the absolute numbers of different caste members and their distribution is not known. The number of soldiers available for protection is important for colony preservation and may even contribute to territory expansion. Therefore, the number of soldiers in *H. aureus* colonies under natural conditions is probably highest in the aggravated parts of the colony or at intercolonial (interspecific and intraspecific) boundaries.

Actual aggressive interactions between natural colonies of *H. aureus* have never been observed. Large colonies may invade and destroy smaller colonies of *H. aureus* or other termites to secure and control additional resources (i.e. nesting areas, moisture) and food. Foraging populations attack areas providing ample vegetation, although foraging is random once a suitable site is located (Jones *et al.,* 1987). If colony aggression helps stabilize (Haverty *et al.,* 1975) or enlarge territories of *H. aureus,* I would expect large dominant colonies with infrequent small colonies. Large colonies would increase the ecological and/or economic impact of this species in areas with few competitors and predators. The aggressive behavior

of *H. aureus* could also have an important influence on the intra- and interspecific associations of various termite populations in the Southwest.

Summary

Aggressive behavior of individuals and groups of *Heterotermes aureus* was studied in the laboratory. Intracolony pairing of soldiers resulted in no aggression. Intercolony pairing of soldiers always resulted in aggression and the mortality of one soldier. Similarly, intercolony pairing of a soldier and a worker resulted in aggression and a high rate of worker mortality, while intracolony pairing of a soldier and a worker resulted in no aggression.

The number of encounters between paired soldiers and workers decreased with increase in arena size. Soldiers had fewer opportunities for aggression, required more time to inflict a fatal snap of the mandibles, and more snaps to kill a worker with increase in arena size. Consequently, fewer workers had fatal encounters at the largest arena size. Workers also had a greater chance for survival by behaving aggressively or running away and were more likely to attack soldiers after multiple encounters.

Foraging of large groups of termites was simulated in the laboratory to study intra- and intercolony dynamics. Intercolonial groups, each with the same number of soldiers, maintained continuous agonistic engagements, established no common boundaries, and the death of all termites resulted. A foraging group with more soldiers, however, was able to invade another group's territory. Workers were first to recognize foreign colony members and recruit more termites, while soldiers crowded into the orifice to protect existing territory. The impact of conspecific, intercolony aggression in natural termite communities is discussed.

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CONTENTS

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CHEMICAL COMMUNICATION IN *MERANOPLUS* (HYMENOPTERA: FORMICIDAE)*

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Introduction

The chemical communication systems of social insects, and in particular of ants, has been intensively studied by many research groups during the past 25 years. These studies included the identification and description of exocrine glands involved in pheromone production (see Hölldobler and Engel, 1978; Hölldobler, 1982; Jessen et al 1979; Billen, 1987), the investigation of the natural product chemistry of pheromones (see Blum, 1982; Morgan, 1984; Attygalle and Morgan, 1985), and the study of the underlying behavioral mechanisms and evolution of chemical communication (see Hölldobler, 1978; 1984; Buschinger and Maschwitz, 1984). Nevertheless, there are some groups of ants that have been almost completely neglected by behavioral biologists in spite of the fact that they are relatively abundant and probably ecologically important. One such group is the genus *Meranoplus,* which is very common in Australia. In this paper I report the results of my experimental studies of the communication behavior of several Australian *Meranoplus* species.

*Manuscript received by the editor October 27, 1988.

Material and Methods

The work was conducted in the laboratories of the Division of Entomology of CSIRO in Canberra, Australia, during a research year in 1980. Colonies of *Meranoplus* were collected near Canberra (ACT), near Poochera, South Australia, and near Lake Eacham and Eungella, Queensland. A total of seven species were investigated. They are listed in table 1 with my acquisition number and the species number of the Australian National Insect Collection (ANIC)/ (assigned by R. W. Taylor), where voucher specimens have been deposited.

Colonies or groups of workers with brood have been housed in moist gypsum nests, or in test tubes containing water held in by a cotton plug, and fed honeywater, freshly killed cockroaches and a specially prepared diet (Bhatkar and Whitcomb, 1970). The nest of each colony was placed in plastic boxes (30 × 75 × 10 cm) which served as foraging arenas.

Glandular dissections were performed in distilled water on ants killed by placing them for a few minutes in a freezer. Additional information concerning procedures will be given with the description of the individual experiments.

Results

Recruitment to nests and food

The most detailed results were obtained with *Meranoplus* sp. no. 11. Two colonies of this species were collected in the Corin Dam area, near Canberra. Each of the colonies had one queen, approximately 200 workers and larvae. In addition, in the same area, I collected two queenless worker groups each containing approxi-

Table 1. Species of *Meranoplus* investigated in this study.

Species	Acquisition number	ANIC number	Locality
Meranoplus hirsutus	135		Near Lake Eacham, Qld
	177		Eungella, Qld
Meranoplus sp.	32	11	Near Canberra, ACT
Meranoplus sp.	70	11	Near Canberra, ACT
Meranoplus sp.	150	12	Near Monga Forest, NSW
Meranoplus sp.	194	13	Near Poochera, SA
Meranoplus sp.	195	14	Near Poochera, SA
Meranoplus sp.	246	15	Near Canberra, ACT

mately 50–60 workers. Although the queenless worker groups were found at least 50 m away from both queenright colonies, when they wer joined with a queenright colony, they readily merged without any sign of aggression or aversion.

The first indication that *Meranoplus* communicates by chemical trails was obtained when I dumped a field-collected colony inside the arena where I also provided a dark, moist test-tube nest. The colony first gathered in clusters along the arena wall. A few workers explored the surroundings of the arena, until after 43 minutes the first scout discovered the test tube nest. A few minutes later 3 more workers entered the nest. When leaving the nest the workers clearly exhibited trailing behavior, tapping their gaster tips repeatedly to the gound and sometimes even dragging them on the floor for distances of 0.5–1.0 cm (Fig. 1). This behavior was especially conspicuous near the entrance of the nest tube. Subsequently, the number of workers moving toward the nest increased markedly, although no clear trail following could yet be noticed. However, after an additional period of approximately 30 minutes, a continuous trail, leading from the cluster of ants to the nest, began to be established (Fig. 2a). Scouts, which returned from the newly discovered dark nest,

Figure 1. A worker of *Meranoplus hirsutus* dragging its abdominal tip over the ground during trail marking. The arrow points to the extruded sting.

often exhibited a vigorous shaking behavior when encountering nestmates. This seemed to stimulate the nest mate to follow the trail. The shaking behavior was especially strong and persistent when recruiting workers encountered the queen. Often 3 to 6 workers approached the queen simultaneously, alternately gnawing with their mandibles on her cuticle or vigorously shaking their bodies toward the queen. This behavior was primarily aimed at the queen's gaster as if the workers were attempting to push the queen forward. At the beginning the queen moved very haphazardly, but once she contacted the trail, she walked straight to the nest. There was no pulling or dragging behavior, but occasionally I observed adult transport in the typical myrmicine mode, with the carried ant curled over the back of the carrier. The carried ant assumes the "pupal" position, with antennae and legs tightly folded to the body. *Meranoplus* workers often take this same position when mechanically disturbed. In addition I have seen them inside the nest in this position, lying on their sides as if they were sleeping.

Once the colony had settled inside the new nest I replaced the paper cover of the arena floor and offered honey water in the arena in approximately 15 cm distance from the nest entrance. As soon as the first forager discovered the food source it imbibed the liquid and returned to the nest. In order to observe the colony inside the nest I removed the aluminum foil cover from the nest tube. The ants did not show any sign of disturbance. The returning scout exhibited a vigorous shaking behavior when encountering nestmates. This behavior did not noticeably differ from that performed during colony movement. The scout engaged in frequent oral trophallactic exchanges, sometimes with 2 to 3 nestmates simultaneously. This behavior was frequently interrupted by renewed shaking behavior. When the scout finally left the nest again to return to the food source, it repeatedly dragged its abdominal tip on the ground for short intervals. The scout was usually followed by 5–15 ants (Fig. 2b). When encountering nestmates in the arena, the scout also displayed the shaking which clearly appeared to stimulate the nestmates to follow along the trail to the food source. Occasionally I even observed recruiters moving repeatedly back and forth on the trail without even entering the nest, vigorously shaking their bodies whenever they encountered nestmates. This behavior resulted in a relatively quick establishment of a trail between food source and

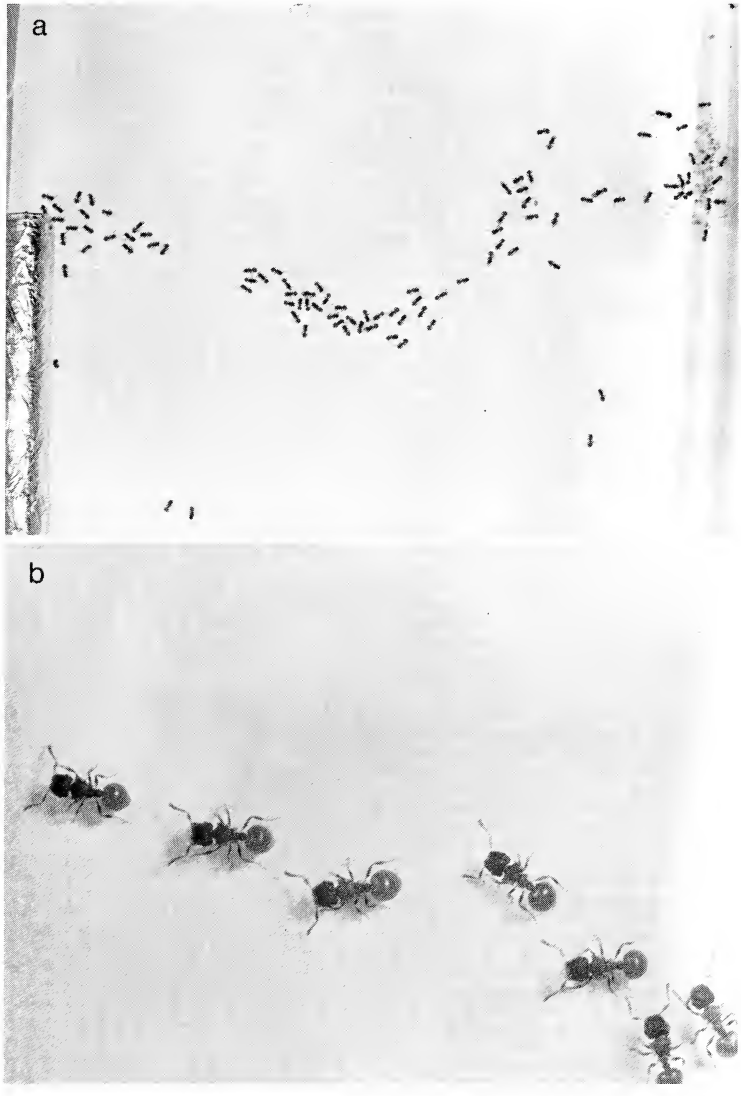

Figure 2. Trail following behavior in *Meranoplus*. a. During colony movements the ants move along a well established route to the nest provided in the test tube (covered with an aluminum foil). b. A trail laying recruiter moves from the nest to the food source and is followed by 6 nestmates.

nest, because in this initial phase almost each worker returning from the feeding site to the nest appeared to lay a trail.

The anatomical sources of the trail pheromones

The fact that recruiting *Meranoplus* workers frequently tap with their abdominal tip the ground, suggests that either one of the major sting glands (Poison gland and/or Dufour's gland) or the rectal bladder are involved in trail communication. Each of the three organs were dissected out of freshly killed workers, crushed on hardwood applicators and rubbed along a line of 25 cm length. Each test trail was offered to the ants simultaneously with a control trail, which consisted either of water, or of the secretions of one of the other organs. Both trails originated in the same circle of 0.5 cm in diameter directly at the nest entrance, but diverged in an angle of 40°. The sides of control and test trails were changed in irregular sequence.

All *Meranoplus* species investigated have unusually large Dufour's glands. In the species *Meranoplus* sp. 11 the Dufour's gland stretches almost the whole length of the gaster, whereas the poison gland is relatively small, with a pair of bulging glandular filaments (Fig. 3). In a series of pilot tests it quickly became apparent that secretions from both the poison and Dufour's glands elicit trail following behavior in *Meranoplus* workers, whereas the contents of the rectal bladder had no effect as a trail substance. There was, however, a significant difference between the ants' responses toward the two trail substances: Trails drawn with crushed poison glands elicited a much stronger initial response than those drawn with Dufour's glands. The poison gland trails, however, were only effective for a few minutes, whereas Dufour's gland trails had an orienting effect for at least 7 hours and possibly even longer. Table 2 shows the quantitative results of the trail tests. It is interesting to note that considerably more ants followed the Dufour's gland trail when it was presented simultaneously with a poison gland trail, probably due to the stimulating effect of the poison gland secretions (independent samples t-test: $p = 0.067$). This is further supported by the following results.

Dufour's gland secretions alone did not elicit a substantial trail following response in *Meranoplus* workers. But when a crushed poison gland on the tip of an applicator stick was offered simultaneously at the nest entrance, a significant number of ants emerged

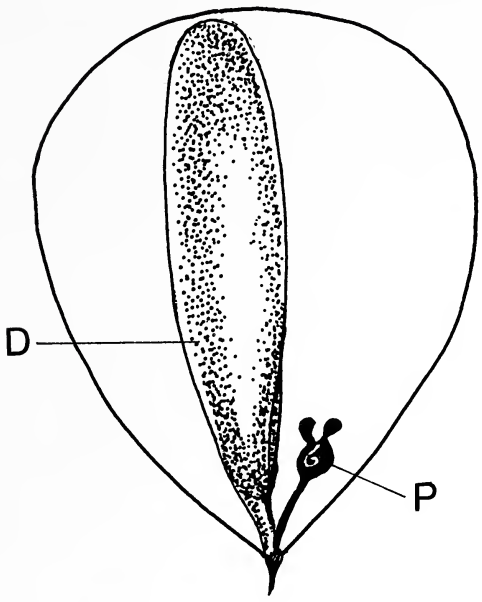

Figure 3. Schematical illustration of the outline of the gaster of a *Meranoplus* worker showing the large Dufour's gland (D) and the poison gland (P) with its bulging filaments.

from the nest and followed the Dufour's gland trail. From these experiments one can conclude that both the poison and the Dufour's gland serve in chemical trail communication. The poison gland secretions appear to function as relatively short lived recruitment signals. The Dufour's gland secretions do not elicit a strong recruitment response, but they appear to be much longer lasting, and motivated ants follow a Dufour's gland trail. This conclusion was further supported by the following experiments:

Meranoplus workers were stimulated to leave the nest along a 5 cm long trail drawn with a freshly crushed poison gland. After 5 cm this trail was continued with a trail drawn 60 minutes previously with Dufour's gland secretions. Almost 83% (24) of the ants arriving at the transition point continued to follow the Dufour's gland trail through at least 10 cm. Additional observations in the laboratory and in the field confirm that *Meranoplus* establish trails which are very long lasting so that they function as trunk routes. From my

Table 2. Number of workers of *Meranoplus* sp. no. 11 following artificial trails drawn with crushed poison and Dufour's glands. All ants following the trail at least through 10 cm during a 2 minute observation period were counted. The means and standard deviations of a total of 6 experiments for each combination are given.

Poison gland vs water		Dufour's gland vs water		Poison gland vs Dufour's gland	
26.17 ± 8.80	0	4.17 ± 1.72	0	24.00 ± 6.13	8.33 + 4.32

experimental results I conclude that these long lasting routes are marked with Dufour's gland secretions.

Finally, I could not find evidence that the trail pheromones of *Meranoplus* are species specific. *Meranoplus* sp. no. 11 readily responded to poison gland trails of *Meranoplus hirsutus.* When glandular secretions of both species were offered simultaneosuly in a choice test, there was no preference for the conspecific poison or Dufour's gland trails. *Meranoplus* sp. no. 11 followed the poison gland and Dufour's gland trails of *Meranoplus* spp. no. 12, 13, 14, and 15. Similarly, *Meranoplus* sp. no. 14 followed trails drawn with poison or Dufour's gland secretions of *M. hirsutus,* M. spp no. 11 and 14.

Repellent secretions in the Dufour's glands

Most *Meranoplus* species studied became motionless and assumed a pupal position when they were mechanically disturbed. In contrast, *M. hirsutus* workers arched their gasters upright and extruded a whitish, sticky substance at the tip of the exposed sting (Fig. 4a). The same defense behavior could be observed when *M. hirsutus* foragers encountered other ant species, especially at a food source (Fig. 4b). The secretions, which originate from the Dufour's gland, elicit a strong repellent effect in other ant species such as *Camponotus consobrinus, Polyrhachis* sp. and *Rhytidoponera* sp. I was unable to test whether the Dufour's gland secretions of the other *Meranoplus* species studied have a similar defensive function in interspecific interactions.

Nest site marking

In the laboratory nests of *Meranoplus* sp. no. 11 I noticed that within a few days the paper floor of the foraging arena was marked with fecal droplets. These markings increased in density near the nest and were especially conspicuous directly at the nest entrance (Fig. 5a).

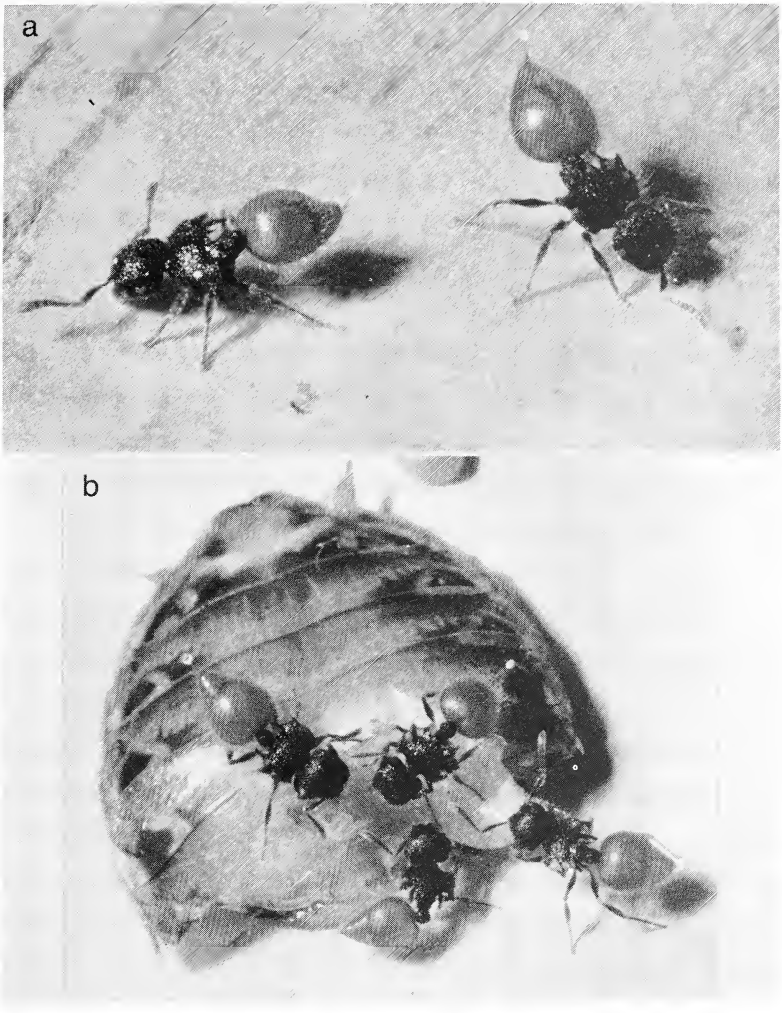

Figure 4. *Meranoplus hirsutus* workers in defensive posture. a. Workers which were mechanically disturbed, immediately arch up their gaster and extrude a droplet of Dufour's gland secretions on the exposed sting. b. The same behavior can be observed in workers guarding a piece of prey.

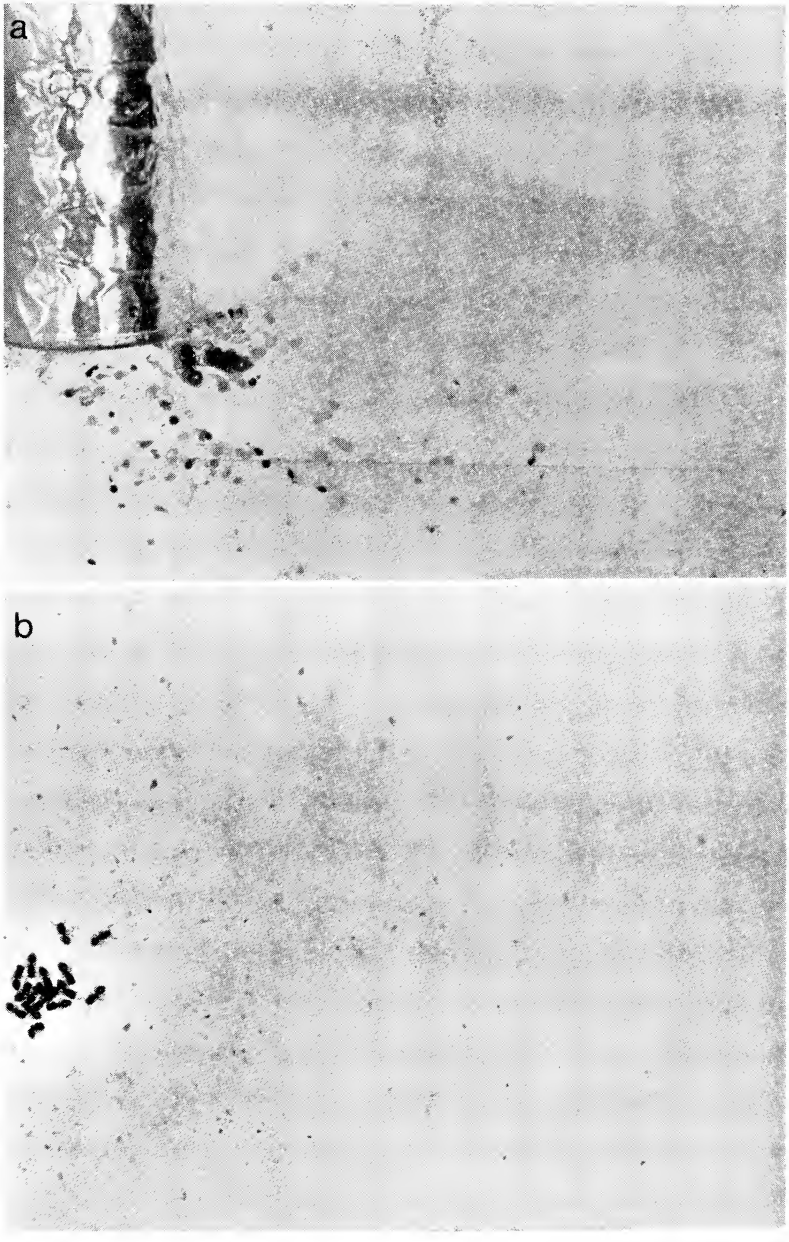

Figure 5. Nest area making in *Meranoplus*. a. The fecal spots are especially dense near the nest entrance. b. On a marked paper the *Meranoplus* workers gather directly at the spot where the nest entrance of a previously removed nest was located.

To investigate whether these markings can serve as homing cues, the paper floor was placed into another arena and 20 ants, taken from the nest tube, were released in the new arena. In all five replicas of the same test, most of the displaced ants had gathered within 15 minutes at the exact spot on the paper floor where the nest entrance was previously located (Fig. 5b).

In a second series of tests the colony *Meranoplus* sp. no. 11 was transferred into a new arena with a new paper floor and two pieces of paper (5 × 5 cm) were placed approximately 5 cm from the nest entrance. The centers of both papers were approximately 10 cm apart. Papers marked by the test colony, by a conspecific foreign colony, by a colony of another *Meranoplus* species and unmarked papers were tested in different combinations (Tab. 3). Approximately 40 ants were released into the arena, and subsequently the nest tube was removed. After an adjustment period of 15 to 20 minutes, I counted the number of ants on each paper. At least one hour elapsed before another test was conducted and the left-right arrangement of the pairs of test papers was alternated from test to test to take into account possible artifactual preferences for one side or another. As can be seen from table 3 workers of *Meranoplus* sp. no. 11 appear to be able to differentiate the markings from their own colony from those of conspecific foreign colonies and colonies of other *Meranoplus* species. Interestingly, when encountering foreign markings the ants did not exhibit a particular aggressive behavior or avoidance. This suggests that the markings do not function as territorial signposts, but rather as homing and colony recognition cues.

Table 3. Number of ants of the test colony (*Meranoplus* sp. no. 11) counted on papers marked by different *Meranoplus* colonies. The means of 7 experiments and standard deviations are given.

Test colony vs unmarked paper	
6.57 ± 2.51	0.71 ± 0.95
Test colony vs foreign conspecific colony	
9.00 ± 2.94	1.43 ± 1.27
Test colony vs colony of *Meranoplus hirsutus*	
8.14 ± 3.72	1.43 ± 2.15

Summary

The communication behavior of seven Australian species of the genus *Meranoplus* was studied in the laboratory. All species exhibited basically the same recruitment communication during nest movements and recruitment to food sources. Scouts stimulate nestmates by a vigorous body shaking behavior. They lay short lasting recruitment trails with secretions from the poison gland. Long lasting trunk routes are apparently marked with relatively non-volatile secretions from the Dufour's glands. All *Meranoplus* species studied have very large Dufour's glands, stretching the whole length of the gaster. In comparison the poison gland is small. In at least one species the secretions of the Dufour's gland also function as defensive secretions against enemies and predators. The nest area of *Meranoplus* is marked with colony specific chemical cues, which are probably contained in the fecal droplets.

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MINDAZERIUS DOMINICANUS NOV. GEN., NOV. SP., A FOSSIL APHID (HOMOPTERA, APHIDOIDEA, DREPANOSIPHIDAE) FROM DOMINICAN AMBER

By Ole E. Heie[1] & George O. Poinar, Jr.[2]

Introduction

A range of animals—insects, spiders, frogs, lizards and mammalian hair—have been represented in Dominican amber (Poinar & Cannatella 1987, Poinar 1988), but until now no aphids. One of us (G. O. Poinar) found a single remarkable specimen after sorting through some 20,000 pieces. It is placed in a new genus within the tribe Lizerini.

The fossil resembles species of *Mindarus* Koch, a genus represented by more Tertiary than extant species. However, it also shares characters with *Lizerius* Blanchard and *Paoliella* Theobald, both recent, but presumably primitive genera of the family Drepanosiphidae.

The present fossil originated from mines located either in the northern or eastern portion of the Dominican Republic. Sedimentary and geological evidence indicates a range from Upper Eocene to Lower Miocene for the amber mines in these regions (Lambert et al. 1985, Poinar & Cannatella, 1987). Dominican amber originated from leguminous trees of the genus *Hymenaea* (Hueber & Langenheim, 1986). Chemical and physical tests (Poinar 1982) performed on the piece verified that it was authentic amber.

The aphid occurred in a small piece of transparent yellow amber with several small air bubbles. Its body and appendages were undamaged and easily observed (except for the anterior part of the abdominal dorsum, which was covered by parts of the wings and a narrow film of air) (Fig. 1). Antennae, wings, and some of the legs were stretched out, so that measurements could easily be made. A binocular Zeiss-Winkel microscope with a 10× objective was used

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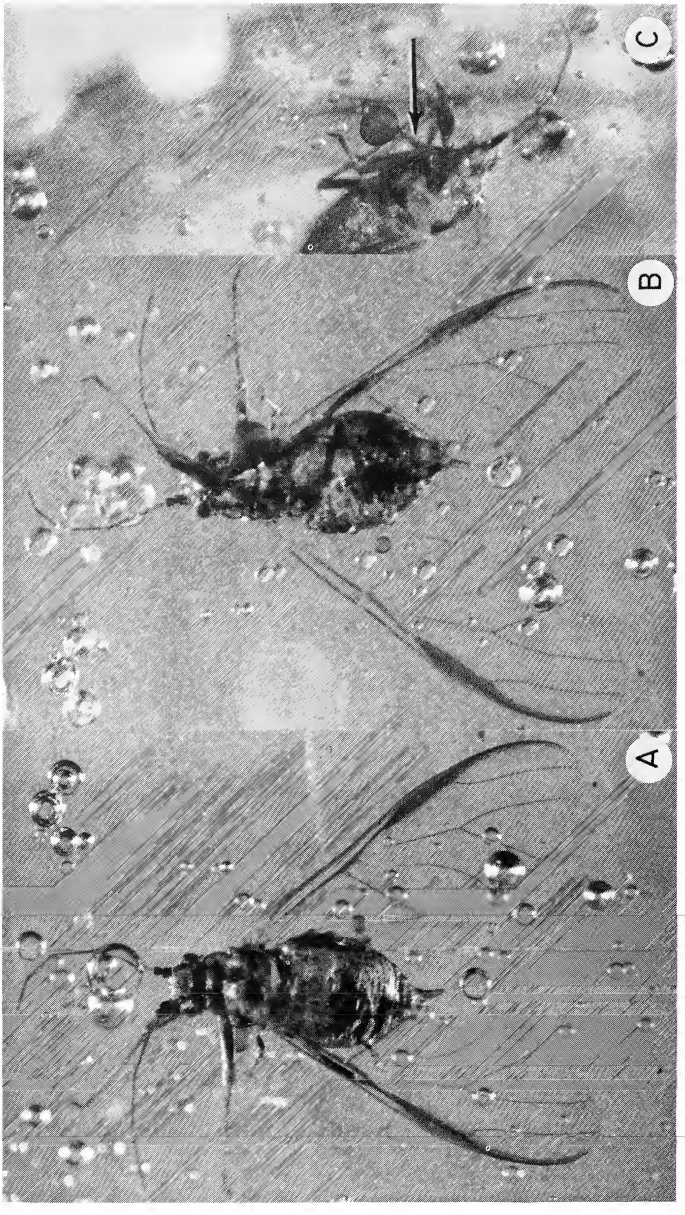

Fig. 1. *Mindazerius dominicanus* n. sp. A: In a dorsal view, B: In a ventral view, C: In antero-lateral view. Arrow = rostrum (G. O. Poinar phot.).

for the description. Placing the amber piece in mineral oil facilitated microscopic observation.

Description

Mindazerius gen. nov.

Wing venation as in *Mindarus* Koch (Fig. 3). Pterostigma long, slender, reaching apex of the fore wing; radial sector long and nearly straight, leaving the proximal half of pterostigma; media with one fork; cubitus branches leaving main vein at separate points, the distal one curved backwards; siphunculi present, short, but rather well developed, truncate, broad at base; cauda rather long and slender; processus terminalis of antenna about half as long as basal part of ultimate antennal segment; fore femur much thicker than hind femur.

Main differences from *Lizerius* and *Paoliella:* Anal plate not biolobed; cauda not distinctly knobbed.

Monotypic. Type-species: *Mindazerius dominicanus* sp. nov.

Mindazerius dominicanus sp. nov.

Body length 1.6 mm (Fig. 2). Largest width of abdomen 0.68 mm. Frons with three small tubercles placed between antennal bases; width of head across eyes 0.37 mm, indistinct lines on the underside of the head may be interpreted as part of the epicranial suture (Fig. 11). Eyes very large, semiglobular, with distinctly separated, rather large ocular tubercles; longitudinal diameter of eye 0.11 mm excluding the tubercle, 0.13 mm including the ocular tubercle. Ocelli with dark rims. Antenna 6-segmented, 0.7 × body; lengths of segments in mm: I–0.07, II–0.07, III–0.35, IV–0.26–0.27, V–0.21–0.22, VIa–0.11, VIb–(processus terminalis) 0.055–0.065; processus terminalis 0.5–0.6 × basal part of VIth segment (VIa), 0.16–0.19 × segm. III; segm. IV–0.74–0.78 × III; V–0.61–0.62 × III; VI–0.47–0.49 × III; segm. III with 7 subcircular secondary rhinaria in a row on the slightly thickened proximal two-thirds (Fig. 6); the other segments without secondary rhinaria. Rostrum rather short, about 0.4 mm long (0.3 in an oblique view from the polished plane of the amber piece; 0.3 × square root of 2 = 0.42), nearly reaching to middle coxae, rather slender; apical segment about 0.07 mm, of about the same length as segment II of hind tarsus.

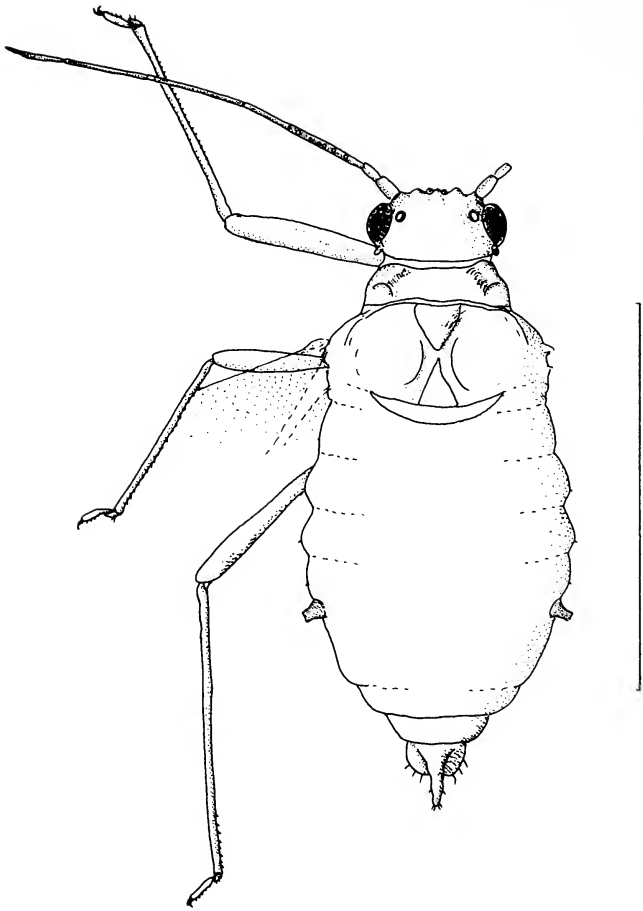

Fig. 2. *Mindazerius dominicanus* n. sp. Body (wings not drawn) in a dorsal view. Reconstruction. Scale: 1 mm.

Posterior margin of pronotum slightly curved, nearly straight; mesothoracic lobes well developed, indicating roof-like position of wings in repose; triangular field between the posterior parts of these lobes (but it is impossible to see if it is membranous); fore femora as long as hind femora, thicker than middle and hind femora, about 1.8 × width of hind femora (Figs. 7 and 8); lengths in mm: fore femur 0.46, hind femur 0.45–0.46, fore tibia 0.53, middle tibia 0.47, hind tibia 0.75, tarsi (tarsal claws excluded) 0.09–0.10, segment II of

hind tarsus about 0.062; widths in the middle in mm: fore femur 0.072, middle femur 0.060, hind femur about 0.04, fore tibia about 0.02, middle and hind tibiae 0.025. Hairs on tibiae short, as long as basal diameter of antennal segment III or shorter. First tarsal segments with several hairs (more than 3). Fore wing (Fig. 3) 2.28 mm long; length of the slender pterostigma about 1.13 mm; radial sector nearly straight, leaving the basal part of pterostigma 0.74 mm from its apex, reaching the apex of the wing 0.09 mm below the apex of the pterostigma; media about 1.0 mm long, with invisible proximal part and one fork, the proximal branch of the fork being 0.53 mm long; cubitus-branches leaving the main vein from points 0.13 mm apart, the distal branch strongly curved, the proximal branch nearly straight and more strongly pigmented. Hind wing (Fig. 4) about 1.3 mm long, with two oblique veins.

Dorsum of the anterior abdominal segments covered by parts of the wings and a film of air. Sclerotization and pigmentation of abdomen unknown. Presence or absence of dorsal body hairs and wax glands impossible to detect. Tergites I–IV with low, broad, rounded marginal tubercles, each carrying a very short hair or spinule (Fig. 2). Siphunculi truncate, about 0.05 mm long, about 0.085 mm broad at base, 0.037 mm broad at apex, situated rather far from each other in nearly lateral positions and rather far ahead, near the middle of the margins of abdominal segment V, and without distinct flanges (Fig. 2). Drops of fluid from the siphunculi present at their apices. Cauda finger- or sausage-shaped, nearly cylindrical, about 0.14 mm long, about 0.04 mm broad in the middle, with at least 6 rather short, pointed hairs, two pairs being placed at the blunt apex and the remaining two hairs placed closer to the middle in lateral positions (Figs. 9 and 10). It is impossible to see if the cauda is slightly constricted at base or not constricted at all. Anal plate apparently with nearly straight posterior margin or slightly emarginated (partly covered by an air bubble) (Fig. 9).

Holotype

The holotype is included in an amber piece labelled "No. HO 4–7, *Mindazerius dominicanus* Heie & Poinar, Holotype" in the Poinar collection of Dominican amber housed at the University of California, Berkeley, California, USA.

Type-locality

Amber mine in the Dominican Republic.

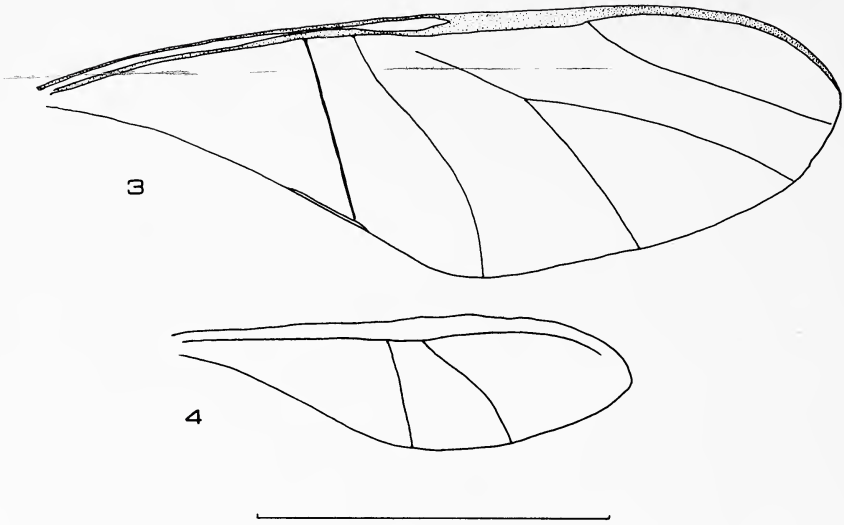

Fig. 3 and 4. *Mindazerius dominicanus* n. sp. Fore wing (3) and hind wing (4). Scale 1 mm.

Taxonomic and Phylogenetic Considerations

The wing venation of the fossil is similar to that of *Mindarus* Koch (Mindaridae) and some species of *Lizerius* Blanchard, *Paoliella* Theobald and *Israelaphis* Essig (Drepanosiphidae). A long, pointed pterostigma reaching the apex of the fore wing and a nearly straight radial sector leaving the proximal part of the pterostigma are regarded as archaic or plesiomorphous characters (Baker 1920, Quednau 1974) and were probably present in the common ancestor of the families Mindaridae and Drepanosiphidae, whereas the once-branched media is a derived or apomorphous character developed from a two-branched media in several aphid groups by parallel evolution or convergency.

Other characters show that the fossil is closer related to *Lizerius* than to *Mindarus*. Some of the similarities to *Lizerius* are probably symplesiomorphies and consequently do not prove relationship, viz. the long cauda and the presence of siphunculi and low tubercles on head and margins of abdomen. Some others must be regarded as synapomorphies, viz. the saltatorial fore legs (thickened fore

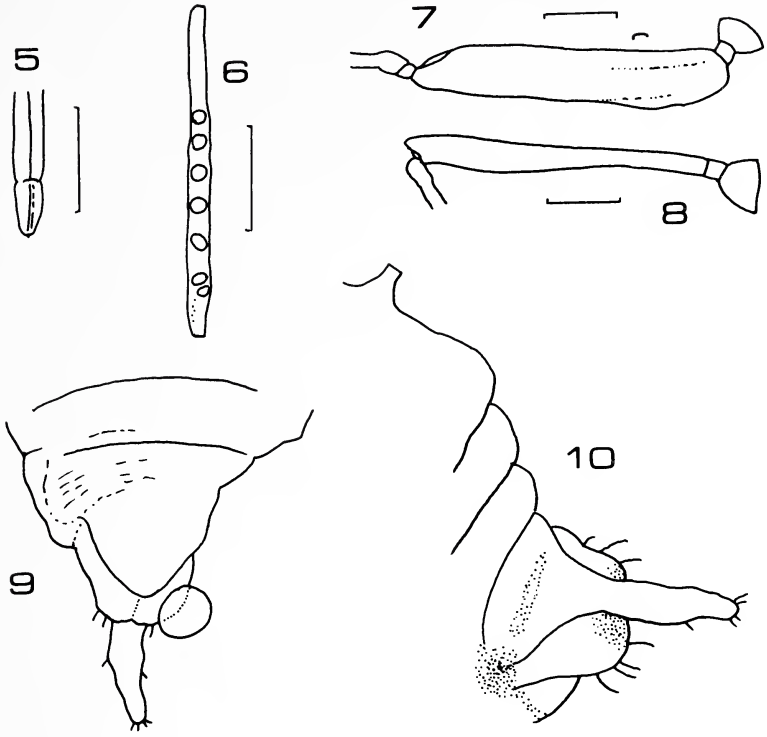

Fig. 5–10. *Mindazerius dominicanus* n. sp. Distal part of the rostrum (5), antennal segment III with secondary rhinaria (6), fore femur (7), hind femur (8), posterior part of abdomen with cauda and anal plate in an oblique ventral view (a = air bubble) (9), posterior part of abdomen in a dorsolateral view (10). Scales for figs. 5–8 0.1 mm. (Free-hand drawings).

femora) and perhaps also the triangular field between the posterior parts of the mesothoracic lobes.

The tribe Lizerini was established by Blanchard in 1923, and Paoliellini Takahashi, 1930 is a synonym (Quednau 1974). The diagnostic characters have been listed by Ilharco (1966) and Quednau (1974). Some of them are not visible in the fossil, but the combination of others show its relationship to the Lizerini. Such characters include the presence of frontal tubercles, apparent presence of an epicranial suture, ocular tubercles prominent, fore femora enlarged, apparent presence of membranous triangle be-

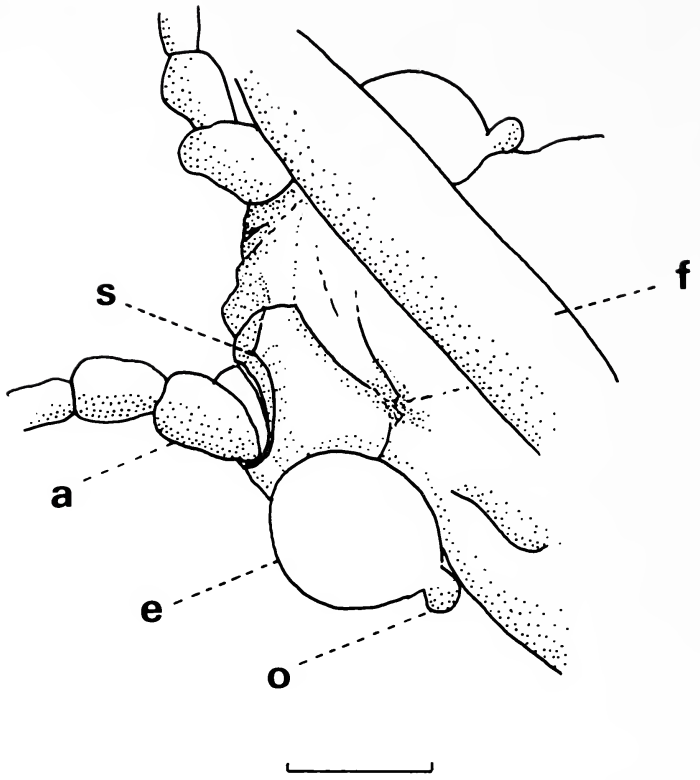

Fig. 11. *Mindazerius dominicanus* n. sp. Underside of head. Abbreviations: a = ant. segm. I, e = eye, f = part of fore femur, o = ocular tubercle, s = supposed part of epicranial suture. Scale 0.1 mm.

tween the mesothoracic lobes, *Mindarus*-like venation of wings, abdominal segments I–IV with low and broad marginal tubercles, each with an apical seta, short flangeless siphunculi placed on margins of abdominal segment V, and a long nearly cylindrical cauda.

Mindazerius differs from the two recent genera of Lizerini (*Lizerius* and *Paoliella*) in the following characters: cauda not knobbed (it is impossible to see if the cauda is slightly constricted at base or not) and anal plate not deeply incised or bilobed.

Mindazerius resembles *Lizerius* more than *Paoliella.* The processus teminalis is short as in *Lizerius,* while it is prolonged in *Paoliella,* and the posterior margin of the pronotum is not deeply

emarginated as in *Paoliella,* but both similarities between *Mindazerius* and *Lizerius* are plesiomorphies, so that they do not indicate that *Mindazerius*+*Lizerius* is the sister group of *Paoliella.* The bilobed anal plate and the knobbed cauda of the recent genera of Lizerini are to the contrary probably synapomorphies showing that *Mindazerius* is the sister group of *Lizerius* + *Paoliella.*

Quednau (1974) discussed the phylogenetic relationships of the Lizerini and concluded that the tribe can be placed nearer some other tribes of Drepanosiphidae (Neophylladini, Neuquenaphidini) than to *Mindarus.*

Biology and Zoogeography

It is impossible to determine the host plant of *Mindazerius dominicanus,* but it is reasonable to assume that it was a woody angiosperm.

Until the Cretaceous, aphids probably lived exclusively on gymnosperms. The fossil record shows that an evolutionary radiation or "explosion" took place as soon as the angiosperms became the dominant group of higher plants. Most recent aphid families are represented in the Cretaceous and Early Tertiary. The Adelgidae, the Mindaridae and some of the Drepanosiphidae, e.g. *Neophyllaphis,* did never give up gymnosperms (conifers) as their food sources and *Prociphilus* (Pemphigidae) retained conifers as secondary hosts, but the majority became associated with angiosperms. Some recent genera feeding on conifers today are descendants of aphids, which lived on angiosperms in the past, e.g. *Elatobium* (Aphididae) and *Cinara* (Lachnidae).

The first Lizerini, among these *Mindazerius,* may have lived on conifers. Although no remains of conifers have yet been described fom Dominican amber, a pine (*Pinus occidentalis*), juniper (*Juniperus gracilior*) and *Podocarpus Buchii* are indigenous species present today in the Dominican Republic (General Secretariat, 1969). The former species covers some 215,500 hectares or 4.5% of the country with the heaviest stands in the Cordillera Central and Sierra de Bohoruco.

It is, however, more reasonable to assume that the host plant was a woody angiosperm because most recent groups of Drepanosiphidae feed on angiosperms, which are known from the Early Tertiary. The Drepanosiphidae was a dominant family in Early Tertiary, and

some of the fossil species resemble modern drepanosiphids living on *Acer* and other angiosperms (Heie, 1967). Recent Lizerini feed on various families of angiosperms, including Combretaceae, Lauraceae, Nyctaginaceae and Burseraceae. Remains of angiosperm families which have been found in Dominican amber include representatives of the Leguminosae, Meliaceae, Myristiaceae, Actinidiaceae, Bombaceae and Hippocrateaceae (Poinar, unpublished data). The amber-producing plant, *Hymenaea,* need not be the host of the aphid since the latter is winged and could have flown or been blown into the resin.

The climate of the locality in the Miocene-Eocene period was tropical, warmer than the regions where *Mindarus* spp. occur today, but much like the climate where species of *Lizerius* and *Paoliella* live. It is interesting that the present distribution of *Lizerius* is Neotropical, since the continuous tropical climate may be the reason why *Mindazerius* and most other groups of fossils in Dominican amber still have relatives in South America today.

The geographical distribution of *Lizerius* (South America) and *Paoliella* (Africa, India and South America) suggests that Lizerini originated in the southern hemisphere in the Late Mesozoic, when the Atlantic Ocean did not represent an obstacle to dispersal. The occurrence of a fossil relative in Dominican amber does not invalidate this idea.

Affinities

The oldest known fossil aphid with a similar wing venation to *Mindazerius* is *Nordaphis sukatchevae* Kononova from the Cretaceous Taymyrian amber in the USSR. Kononova (1977) placed it in Lizerini, but her drawing suggests that it could also belong in the Mindaridae (Heie 1987). With *Mindazerius,* which is more similar to *Lizerius* than to *Mindarus, Nordaphis* could well be a relative of *Lizerius* and of *Mindarus. Nordaphis* may be a specialized representative (with an extremely long rostrum) of a group related to the ancestor of Lizerini or the ancestor of both Drepanosiphidae and Mindaridae.

If *Mindazerius dominicanus* had had the fore legs, the siphunculi and the long cauda missing—then it probably would have been placed in the Mindaridae. All Tertiary aphids with that kind of wing

venation have been described as species of *Mindarus,* but could some of them belong to the Lizerini?

Five fossil *Mindarus* species have been described, viz. three from Baltic amber, *M. magnus* Baker, *M. parvus* Heie and *M. transparens* (Germar & Berendt) (Heie, 1968; 1971), and two from the Oligocene clay at Florissant, Colorado, *M. recurvus* (Buckton) and *M. scudderi* (Buckton) (Heie, 1967; 1985).

The three amber species belong without doubt to *Mindarus.* None of them have saltatorial fore legs. The cauda is visible in *parvus* (Heie, 1967) and one specimen of *magnus* (Heie, 1969), and is short as in recent *Mindarus* spp. *M. parvus* shows on one side a short, cylindrical structure partly covered by an impurity. It is, however, not a siphunculus, but probably the border of a drop of secretion from a siphuncular pore. The differences between *parvus* and the recent species *abietinus* are so small that *parvus* in fact may be regarded as a dwarf form of *abietinus* or one of the other still living species.

The siphuncular pores and cauda of the two species from Florissant are invisible. The legs are badly preserved, but the general appearance is much like *Mindarus.* Both are very large, body length being about 3 mm in *scudderi* (Buckton) and 4 mm in *recurvus* (Buckton). Some of the *Mindarus* specimens in Baltic amber are of similar size, while all Lizerini are rather small aphids.

Mindaridae is the only extant aphid family containing more fossil than recent species. The family has apparently changed very little since the Eocene since the differences between the fossil and recent species are small, although representatives showed greater diversity in the Early Tertiary than they do now. The three or four recent species which now occur in temperate North America and Eurasia, are "living fossils." They include *M. obliquus* (Cholodkovsky) on *Picea* in Eurasia, *M. abietinus* Koch on *Abies* in Europe and North America, *M. japonicus* Takahashi on *Abies* in East Asia, and *M. victoria* Essig on *Abies* in North America. Some of these names are probably synonyms. The difference between *M. abietinus* and *M. japonicus* is so small that they may be geographical races of one species (Heie, 1967, p. 34). The former has 12–27 secondary rhinaria on antennal segment III, while the latter has 24–37 secondary rhinaria. We have not seen material of *M. victoria.*

Sigmacallis pilosa Zhang from *Populus* in China perhaps belongs to the Mindaridae according to Zhang & Zhong (1981) although its pterostigma is rather short, not reaching to the tip of the wing.

Lizerini is a tribe within the subfamily Drepanosiphinae, family Drepanosiphidae (Heie, 1980). Among its archaic characters is the presence of scent plaques ("pseudosensoria") on all tibiae of the oviparous morph, not only the hind tibiae. The apterous morphs carry "chamois-horn-like" processes as the extinct *Palaeosiphon hirsutum* (Germar & Berendt) (the oviparous female of which also has scent plaques on all tibiae) from Baltic amber (Heie, 1967) and some recent representatives of various tribes of Drepanosiphinae, e.g. *Eonaphis* Quednau from Africa and *Neuquenaphis* Essig from South America. Until now 30 recent species of Lizerini have been described, 9 species of *Lizerius* and 21 species of *Paoliella*. Not all Lizerini have wings like *Mindarus*. The pterostigma does not quite reach the apex of the wing in *Lizerius intermedius* Quednau, *L. costai* Quednau and some others. *Mindazerius dominicanus* resembles *L. cermelii* Quednau (on *Bougainvillea* in Brazil) very much in respect to wing venation and some other characters.

Summary

The first fossil aphid from the Neotropics, *Mindazerius dominicanus* nov. gen., nov. sp., is described from Dominican Republic amber. It is placed in the tribe Lizerini of the family Drepanosiphidae (Aphidoidea) and shares characters with the genera *Mindarus* and *Lizerius*. Major features of the fossil include the long pterostigma of the fore wing the truncate siphunculi, long cauda and strongly thickened fore femora. Biological and zoogeographical implications, as well as affinities with both fossil and recent relatives, are presented.

Key words: Aphid, Lizerini, Drepanosiphidae, Mindaridae, fossil, phylogeny, palaeontology, Dominican amber.

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THE AMERICAN BURYING BEETLE, *NICROPHORUS AMERICANUS:* STUDIES ON THE NATURAL HISTORY OF A DECLINING SPECIES*

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Introduction

Nicrophorus americanus (Coleoptera: Silphidae), the American burying beetle, was once widespread in its distribution in North America, but has apparently suffered a severe decline in this century and is presently known to occur only on Block Island, Rhode Island and in eastern Oklahoma. Although the natural history, ecology, and reproductive biology of North American and European burying beetles has been described (Pukowski 1933, Milne and Milne 1976, Anderson 1982a, Wilson and Fudge 1984, Wilson and Knollenberg 1984, Wilson et al. 1984, Scott and Traniello 1987, Scott 1988), there is very little information on *N. americanus* except documentation of its past distribution and decline (Davis 1980, Anderson 1982b).

We recently were able to assess the size of the *N. americanus* population on Block Island, and determine the resource requirements for reproduction of this potentially endangered species. In addition, we present information on reproductive behavior, interspecific competition, and correlates of reproductive success.

Methods

Study Sites

Studies were conducted on Block Island, Rhode Island. Block Island is located approximately 26 km southwest of Point Judith, Rhode Island at 71.34° W longitude and 41.11° N latitude. The habitat occupied by *N. americanus* on Block Island consists of maritime shrub thickets, coastal moraine grassland and agricultural pastures.

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marginatus, N. orbicollis, and *N. tomentosus.* Additional trapping was conducted on the coastal mainland of Massachusetts and Rhode Island and on the islands of Martha's Vineyard and Nantucket, but yielded no *N. americanus.* Trapping in Michigan, Arkansas, Missouri, North Carolina, Tennessee, Florida, Pennsylvania, New Jersey, and New York also gave negative results (L. Master and D. Schweitzer, personal communication).

Trapping Methods

N. americanus population size was estimated by three methods of live trapping. First, pitfall traps, baited with aged beef kidney placed along a transect at 25 meter intervals; second, a blacklight trap, which was moderately effective in attracting beetles to the ground near the light, and third, whole vertebrate carrion of various types, placed in the field for burial. A total of 467 pitfall trap-nights were logged, in addition to 16 hours of blacklight trapping, and 44 carrion burial traps in five four-day trapping sessions between May 26 and August 1, 1986. Carrion used for burial studies ranged in size from 20 grams to 500 grams and included mice, rats, starlings, chicks, squirrels, snakes, turtles, skates, Japanese quail, and hamsters. For each of these carrion types, a 1.5 meter piece of dental floss was attached to the carcass so it could be located and exhumed after burial. The surrounding vegetation and soil surface were also examined for beetles because unsuccessful competitors are often found near the area of burial (Wilson and Fudge 1984; personal observation). All *Nicrophorus* individuals captured were identified to species, sexed, measured, and released. Pronotal width was used as an index of an individual's size because it is highly correlated with weight ($r = 0.96$, $N = 150$). Each *N. americanus* was individually marked by lightly sanding the pronotum, painting it with a unique pattern and color(s) of enamel paint, and covering the paint with cyanoacrylate glue.

Population Size Estimation

A sequential Bayes algorithm (Gazey and Staley 1986) was used to estimate the population size of *N. americanus* on Block Island. This method was used because it was designed specifically for multiple mark-multiple recapture studies with relatively small sample sizes.

Prey Choice and Competition in Enclosures

In order to conduct studies on prey choice and interspecific competition, a square screened enclosure measuring 1.3 m^2 and 25 cm high was sunk into the ground to a depth of 10 cm. A 20-liter bucket filled with potting soil was sunk into the ground inside the enclosure and a single carcass was placed on top. To investigate interspecific competition, a male and female *N. americanus* and a male and female *N. orbicollis* were introduced into the enclosure at dusk with a single carcass. The following morning all beetles were collected from the enclosure and the carcass was exhumed to determine which beetle(s) had buried it. Prey choice studies were conducted in a similar manner. A male and female *N. americanus* were placed in the enclosure, and avian and mammalian carcasses were simultaneously available for burial.

Laboratory Studies

Ten of twenty broods monitored in the laboratory originated from burials in the field enclosure studies on Block Island. The other ten were initiated at Boston University using adults eclosed from laboratory broods. The size of prey used in the laboratory ranged from 60–206 grams. All broods were maintained at a constant temperature of 21°C with a 14:10 light:dark cycle. Nine broods were exhumed on the tenth day after burial and all larvae were counted, weighed, and returned to the brood chamber with the carcass and parent(s). Individuals were sexed, measured, and weighed on the day of eclosion.

Results

A total of 147 *N. americanus* (84 males, 63 females) were captured on Block Island (Table 1). The sex ratio of males:females captured did not differ significantly from 1:1 (χ^2 test, $p > 0.05$). One hundred thirteen *N. americanus* were captured in pitfall traps, 19 at blacklight traps, and 15 on carrion set out for burial. *Nicrophorus* beetles were trapped repeatedly and successfully on both rainy and windy nights provided the temperature was above 15°C. Seventeen of 147 (11%) *N. americanus* were recaptured; 15 individuals (eight females and nine males) were recaptured once and two (females) were recaptured twice. Eight of 17 recaptures occurred within four days of the

Table 1. *Nicrophorus* spp. captured on Block Island

Dates	Na	No	Nm	Nt
5/26–5/30	2	16	10	0
6/9–6/12	15(2)	20	0	0
6/24–6/28	43(5)	68	14	2
7/14–7/18	80(8)	35	8	17
7/28–8/1	26(4)	34	24	13

Na = *N. americanus*, No = *N. orbicollis*
Nm = *N. marginatus*, Nt = *N. tomentosus*
The numbers in parentheses indicate the number of total captures which had previously been captured and marked. Recapture information is available only for *N. americanus*.

original capture and 15 of 19 recaptures were made in the same location where the individual was originally marked. The population estimate was based on 19 recapture events in five sampling intervals and yielded a mean estimated total population size of 391.4 individuals. The 95% confidence intervals for the estimated mean were 258, 600.

N. americanus showed no significant preference for avian or mammalian carcasses ($G = 1.061 < \chi^2_{.05(2)} = 5.99$). In our experimental choice situation, the male and female did not always cooperate in burial. The mammalian carcass was chosen by 44% of the individuals and the avian carcass was chosen by 25% (N = 16). In the laboratory, *N. americanus* buried both avian and mammalian carcasses and successfully reared broods on both types of carrion.

In three trials, *N. americanus* outcompeted *N. orbicollis* for prey. In one trial, the male and female *N. americanus* buried the carcass together, and in the other two the male buried the carcass alone while the female remained in the enclosure but was not found with the male in the burial chamber. These results are not surprising, as in *Nicrophorus* species, size has been shown to be the single most important determinant of success in interspecific competition (Wilson and Fudge 1984; personal observation) and there is almost no overlap in size between *N. americanus* and *N. orbicollis*.

In the field, of 44 carcasses provided for burial, nine were buried by *N. americanus* (20%), four by *N. orbicollis* (9%) and three by *N. marginatus* (7%). The remaining carcasses were not buried. *N. orbicollis* primarily buried carcasses ranging from 20–25 grams on Block

Table 2. Carrion Burials—Field Studies

Prey Size	N	Buried By Na	Nm	No
20–25	14	0	0	3
60–80	5	2	1	1
80–100	10	6	2	0
100–200	6	0	0	0
200–300	2	1	0	0
>300	7	0	0	0

Species abbreviations are same as those for Table 1.
N = sample size.

Island. *N. americanus* showed a preference for prey ranging from 80–100 grams. *N. marginatus* also buried prey in this size category (Table 2).

Sixteen of the 20 broods reared in the laboratory resulted in eclosed tenerals. There was a significant positive correlation between carcass weight and total brood weight ($r = 0.60$, $p = 0.01$, Fig. 1). There was also a significant positive correlation between the number of tenerals eclosed and carcass weight ($r = 0.69$, $p = .007$) but no significant correlation between carcass weight and either mean weight or mean pronotal width of tenerals eclosed. A partial correlation analysis removing the effect of total brood weight indicated a highly significant negative correlation between the number of adults eclosed (per brood) and their average weight ($r = -0.77$, $p = .0001$).

Discussion

N. americanus is considered to be a potentially endangered species because its distribution may have declined to only two known populations. It is difficult to predict whether the estimated population size of *N. americanus* on Block Island alone is viable for the survival of the species. Fluctuations in environmental factors such as weather, resource availability, changes in vegetation and the presence of parasites or predators can cause natural oscillations in the size of insect populations (New 1984). Human activity can also have a major impact on insect populations.

The Gazey and Staley (1986) population estimate appeared to be the best one to use for *N. americanus* because sample sizes were

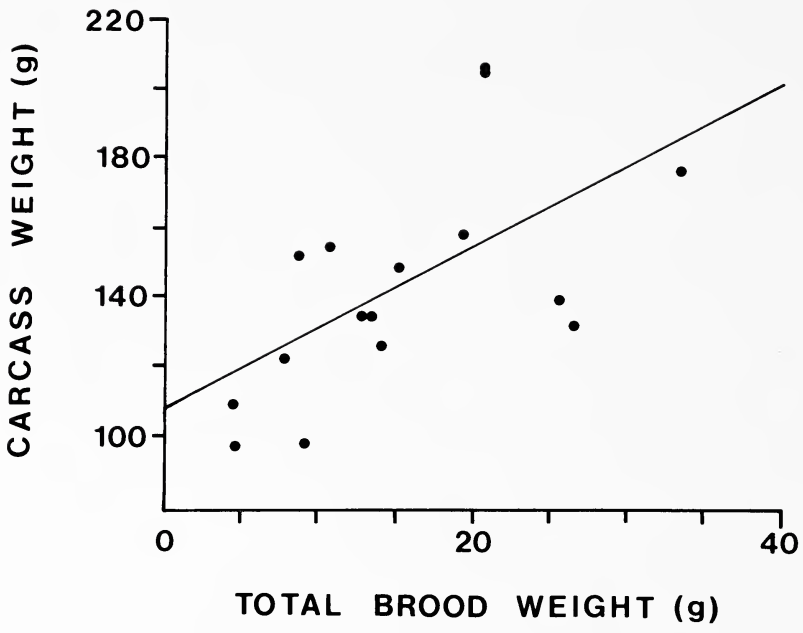

Fig. 1. Relationship of carcass weight to total brood weight.

small and a reasonably narrow confidence interval was desired. However, it should be noted that *N. americanus* violates two assumptions common to virtually all population estimate analyses: 1) that the population size remains constant for the duration of the experiment and 2) that all individuals are equally available for recapture. Because the estimate was made during a two month period, normal mortality and a pulsed recruitment of newly eclosed individuals could have resulted in fluctuations in the size of the population. In addition, at any one time, a proportion of *N. americanus* in a given population will be unavailable for recapture as they will be underground rearing a brood. The latter factor can potentially yield an overestimate of mean abundance if the number of animals actually available for recapture in any one sampling interval is less than the total population because the number of total recaptures may be underestimated.

Maximum numbers of *N. americanus* were captured in pitfall traps in June and there was a decrease in pitfall captures in late July. This is a common pattern for *Nicrophorus* species (Anderson 1982a,

Scott unpublished data) although some species have a second population peak in mid to late summer when tenerals emerge. In late July and early August *N. americanus* were still readily captured at carrion. Wilson and Knollenberg (1984) have suggested that pitfall traps provide biased samples as they represent a feeding opportunity rather than a reproductive opportunity. This may explain the decrease in pitfall captures observed on Block Island.

As is generally true of *Nicrophorus* spp., *N. americanus* require carrion to bury and use as a reproductive resource and their reproductive behavior is similar to that described for other *Nicrophorus* species (Pukowski 1933, Wilson and Fudge 1984, Scott and Traniello 1987). Male and female *N. americanus* are attracted to fresh carrion and intrasexual competition occurs within each sex until usually only one male and female remain. Interspecific competition may also occur for possession of a carcass. In one case on Block Island, an *N. marginatus* female was found burying a 60 gram quail on July 30. The female was found with a male *N. marginatus* on the following day, although the carcass was still not completely buried. The quail was exhumed on August 1 and a male and female *N. americanus* were the only beetles collected with the carrion.

N. americanus may cooperate in burying carrion, but individuals of both sexes are capable of burying a carcass alone. Three carcasses (a 90 gram rat, an 87 gram hamster, and a 229 gram chick) were buried by a lone female. Two carcasses were buried alone by a male *N. americanus,* a 70 gram rat and a 90 gram rat. In the former, the male was still alone on the second day after burial, while in the latter, the male was found with a female two days after he had buried the carcass. In all the above examples, the carcasses had been prepared by the parent(s) for the larvae in a fashion similar to that described for other *Nicrophorus* species (Pukowski 1933, Wilson and Fudge 1984, Scott and Traniello 1987). The carrion is shaved, rolled into a ball, and treated with anal and oral secretions. The female lays eggs in the soil near the carcass and altricial, lightly sclerotized larvae hatch within a few days. The larvae are fed regurgitated food by both the male and female parents. Approximately two weeks after burial the larvae complete development and pupate in the soil nearby. Data from laboratory broods indicate that adults eclose from 48 to 65 days after burial and range in size (pronotal width) from 7.83 to 12.71 mm. The range in size of individuals

captured in traps on Block Island was 7.98 to 12.63 mm. Females are reproductively capable immediately upon leaving a brood.

Laboratory studies with *N. americanus* showed that reproductive success, measured by total brood weight and by the number of tenerals eclosed, is significantly correlated with carcass size as has also been demonstrated in laboratory broods of *N. orbicollis* (Wilson and Fudge 1984). The significant negative correlation between the number of adults eclosed per brood and their average weight suggests that *N. americanus* individuals rearing broods may make a tradeoff between a large number of small offspring or a small number of large offspring. The outcome of this tradeoff may depend on carcass size, prior reproductive history of the parents, and possibly a prediction of future reproductive opportunities for the offspring.

Collection records from the Museum of Comparative Zoology at Harvard University indicate that *N. americanus* was found in the following states at the early part of this century: Kansas, Illinois, Minnesota, Wisconsin, Virginia, New York, Pennsylvania, Connecticut, New Hampshire, and Massachusetts. Davis (1980) reported additional collections in Tennessee (29 individuals in 1952) and Kentucky (1974). Anderson (1982b) located collection records of *N. americanus* after 1950 only in Ontario, Arkansas, Illinois, Michigan, Missouri, and Tennessee. Ten *N. americanus* individuals have been collected at light traps in Oklahoma (near Tenkiller Ferry Resevoir and in Latimer County) between 1979 and 1988 (L. Master, personal communication). Why has *N. americanus* suffered such a severe decline in what appears to be a relatively short period of time? Studies in enclosures with another species suggest it is unlikely that *N. americanus* has been outcompeted at least in direct confrontation by congeners. Studies with *N. orbicollis* have shown that the preferred carcass size is 20–60 grams and that carcasses over 60 grams are difficult to bury (Scott unpublished data). *N. orbicollis* may not be a major competitor of *N. americanus* because of a lack of overlap in the size frequency distribution of suitable carcasses and frequent loss in contest competition.

Nicrophorus species diversity is highest at northern latitudes (Scott et al. 1987) and it is likely that congeneric competition would be greatest where species diversity is highest. Size appears to be the most important determinant of success in competition for securing carrion; the largest individuals invariably displace smaller burying

beetles. Because *N. americanus* are the largest carrion beetles in North America and even the smallest *N. americanus* overlap in size only slightly with the largest *N. orbicollis* and *N. marginatus,* it seems unlikely that *N. americanus* have been outcompeted by other *Nicrophorus* species. However, factors other than size that might affect the outcome of competition (such as temperature or patterns of activity [Wilson et al. 1984]) remain to be examined.

The decline of *N. americanus* then may be more likely related to the impact of human activity. The widespread use of pesticides has been cited as a potential factor in the decline of non-pest insect populations but there have been few documented losses caused by pesticide use (Pyle et al. 1981, New 1984). This hypothesis initially appears attractive to explain the survivorship of *N. americanus* on Block Island because the island was never sprayed heavily with broad spectrum insecticides such as DDT. However the evidence against this hypothesis includes the following. *N. americanus* has disappeared from numerous other areas where DDT was never sprayed. *N. americanus* was collected in the 1960's from areas which had been sprayed heavily with DDT and lastly, congeners such as *N. orbicollis* and *N. marginatus,* who have a very similar reproductive biology, have apparently suffered no decline in population size.

The habitat(s) occupied by *N. americanus* before its decline was not clearly described so it is very difficult to ascertain how severe an impact the loss of habitat has had on this species. However, the increasing use of land for urbanization and commercial agriculture and forestry has had a demonstrated negative impact on numerous insect species (Pyle et al. 1981). This hypothesis, though tentative, appears to be the most plausible. Although there is no data from this research thus far to draw any significant conclusions about causal factors in the decline of *N. americanus* it is recommended that the search for answers to these questions focus on factors related to changes in, or loss of suitable habitat, that have made it impossible for *N. americanus* to survive today in areas where it was once successful.

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FINAL OBSERVATIONS ON *PHEIDOLE MEGACEPHALA* AND *IRIDOMYRMEX HUMILIS* IN BERMUDA*

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Introduction

Pheidole megacephala (Myrmicinae) and *Iridomyremex humilis* (Dolichoderinae) are two well known invasive pest species of ants which, within approximately the last century and a half, have achieved almost worldwide distribution within the tropical to semi-tropical habitats available to them. Both are extremely aggressive and are capable of displacing native ant faunas on an impressive scale. Thus *P. megacephala,* originating probably in middle Africa, radiated extremely actively in both the Old and New Worlds as a "tramp" species, and by 1852, judging by Heer's vivid account (Heer, 1856) it had thoroughly occupied, among many other western European locations, the island of Madeira, exterminating a very large fraction (if not all) of the indigenous ant fauna.

Iridomyrmex humilis, the "Argentine Ant" was first reported from Buenos Aires in 1866, and described by G. Mayr in 1868 (Skaife, 1951, p. 7) (it may well have originally been indigenous to Brazil). By 1882 it had found its way (likewise as a "tramp" species exploiting human transport) to Madeira, which it occupied, in competition with the resident *P. megacephala.* It was a successful "occupation", and by 1898, according to Stoll (1898) *P. megacephala* had completely disappeared from the Island, leaving *I. humilis* as the sole ant reported. Nothing is known of further details of the explosive interaction between these species in this limited island environment.

P. megacephala reached Bermuda at least as early as 1902 (Dahl, 1902), where it behaved essentially as in Madeira, displacing the greater part of the indigenous ant fauna and "blanketing" the Islands. By the time that one of the authors made a survey in 1927, its situation as a ubiquitous field and house ant closely resembled Heer's account of it in Madeira seventy-five years earlier.

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It was therefore of particular interest when *Iridomyrmex humilis* was noted in Bermuda in 1953, the original focus having been reported at Waterville in Paget, where it was probably introduced with nursery stock. By late 1953 seven new foci had been identified, and the invader was well on its way to challenging *P. megacephala* for "possession" of the Island (Crowell, 1968). In 1955 the Bermuda Department of Agriculture officially recognized *I. humilis* as a "major economic pest", and roadside surveys were conducted by the Department, under the direction of I. W. Hughes, tracing its expansion from 1955 to 1959.

In 1959, and twice in 1963, Haskins and Haskins (1965) conducted "point surveys" which indicated that by that time *Iridomyrmex* had occupied a large part of the Island and was actively replacing *megacephala* in many districts widely dispersed throughout Bermuda. At that time these authors raised the question of whether the ultimate outcome of this competition would be complete elimination of one of the species (probably *P. megacephala*), as occurred in Madeira, or whether a long term "permanent" but shifting equilibrium would result.

The 1959/1963 survey was followed in 1966 by a more complete one by Crowell (1967), undertaken in the same basic mode as the previous ones, and including a summary of earlier surveys. Finally, the most complete survey to date was accomplished by Lieberberg, Kranz, and Seip (1975) in 1973, again using methods basically similar to those of the preceding censuses. Thus a fairly complete picture was achieved of the interactions of *humilis* and *megacephala* over nearly two decades. So far as we are aware, no detailed surveys were made, so it seemed that a final one should be undertaken, thirty-three years after the first official report of the arrival of *I. humilis*. That effort is the subject of the present note.

Methods and Results

In some respects this last survey was disappointing. So much land in Bermuda has been committed to building and to "artificial withdrawal" in other developments eliminating or greatly modifying many of the sites included in the earlier surveys, and the density of motor traffic has so much increased that any repetition of the surveys in the older "roadside observation" mode was not only deemed impracticable, but would have been unrepresentative, in our view.

Therefore, recourse was had to a different procedure. Ten specific sites were selected which has been censuses in the 1963 Haskins survey and in the surveys of Crowell and Lieberberg *et al.* and are still relatively unmodified physically, and a careful examination made of these. It was hoped that a survey of this kind would be adequate to answer at least the general questions posed above. In Table I the data for those sites are presented for the 1963, 1966, 1973, and the current surveys. The data from Crowell were by necessity under-represented, because, unfortunately, the early Department of Agriculture surveys which he reports proved difficult to compare reliably with later ones, and because the maps in his publication have been so reduced as to be difficult to interpret reliably, but the extensive accounts in his text are wholly consonant with the other material, and highly informative.

Table II presents a summary of the shifts in distribution of *P. megacephala* and *I. humilis* at the ten selected sites as recorded by the surveys, proceeding from east to west in the Islands.

Discussion and Conclusions

The first conclusion from these data is clear and unequivocal: Thirty-three years after the first reporting of *I. humilis* in Bermuda, *P. megacephala* and *I. humilis* still coexist in strength there. Secondly, the earlier surveys have noted a consistent slowing in the rate of expansion of *humilis* as the territory has become saturated, and an increasing tendency for the patterns of distribution of both species to form an interdigitating, mosaic-like pattern, reminiscent of the patterns of mosaic distribution of three species of *Lasius,* two of *Myrmica,* and one of *Formica* described by Brian (1977) for a long-occupied British garden site. This tendency, together with the slowing expansion of both species, was noted particularly in the survey of Lieberberg *et al.* Both developments appeared to have progressed further in 1986. They may well suggest an approach to "saturation " of the environment.

The "equilibrium", however, is clearly an uneasy and shifting one, with ground being continually lost and regained by both species: a feature also emphasized in the earlier surveys. It will be noted that, in the current tabulation of sites, only two, Spittall Pond Reserve and Ireland Island, have remained in consistent "possession" of one species (*P. megacephala*) throughout the whole period.

Table I. Combined surveys of ten sites occupied by *Pheidole* or *Iridomyrmex* (or both) between 1963 and 1986 (sites which have remained physically basically unmodified over that period) suggesting competitive shifts in occupation over that time.

SITE	1986	1973	1966	1963
1. ST. DAVID'S HEAD (GREAT HEAD PARK)	*I. humilis* only	Area where *I. humilis* and *P. megacephala* coexist		
2. MULLET BAY ROAD AND FERRY ROAD (ST. GEORGE'S ISLAND)	*I. humilis* only	Mixture of *I. humilis* and *P. megacephala*	*I. humilis* and *P. megacephala* shifting lines with greatest area occupied by *humilis*	*P. megacephala* (sparse)
3. LEAMINGTON CAVES	*I. humilis* only	Area where *I. humilis* was replaced by *P. megacephala*		*I. humilis* only
4. KNAPTON HILL INTERSECTION	*I. humilis* only	*P. megacephala*, replacing *I. humilis*		*I. humilis* only
5. KNAPTON HILL ROAD AND HARRINGTON HUNDREDS	*I. humilis* only	Area where *I. humilis* has been replaced by *P. megacephala*		*I. humilis* only
6. CHRISTCHURCH/ BRIGHTON HILL	*I. humilis* only	Area in which *P. megacephala* has replaced *I. humilis*		Mixture of *I. humilis* and *P. megacephala*
7. SPITALL POND RESERVE	*P. megacephala* only	*P. megacephala* only		*P. megacephala* only

SITE	1986	1973	1966	1963
8. HAMILTON: NEWSTEAD	*I. humilis; P. megacephala* (mosaic, predominantly *humilis*)	*I. humilis* only		*I. humilis* only
9. WRECK ROAD	*P. megacephala* only	New *I. humilis* focus. Area where *I. humilis* has been replaced by *P. megacephala*		Mixture of *I. humilis* and *P. megacephala*
10. IRELAND ISLAND	*P. megacephala* only		*P. megacephala* (sparse)	

*Of the ten localities recorded, only these two (Spittall Pond Reserve and Ireland Island) have remained unchanged (both with *P. megacephala* only) throughout the twenty-three-year observation period.

Table II. Representative shifts in distribution.

1. ST. DAVIDS HEAD:	1973: *megacephala* and *humilis* coexisting; 1986; *humilis* only
2. MULLET BAY ROAD AND FERRY ROAD (ST. GEORGE'S ISLAND)	1963: *P. megacephala* only (sparse); 1966: *humilis* and *megacephala*—shifting lines with greatest area occupied by *humilis;* 1973 mixture of *humilis* and *megacephala;* 1986: *I. humilis* only
3. LEAMINGTON CAVES	1963: *I. humilis* only; 1973: Area where *P. megacephala* has replaced *I. humilis;* 1986: *I. humilis* only
4. KNAPTON HILL INTERSECTION	1963: *I. humilis* only; 1973: *P. megacephala* apparently replacing *I. humilis;* 1986: *I. humilis* only
5. KNAPTON HILL ROAD AND HARRINGTON HUNDREDS	1963: *I. humilis* only; 1973: Area where *P. megacephala* has replaced *I. humilis;* 1986: *I. humilis* only
6. CHRISTCHURCH/BRIGHTON HILL	1963: Mixture of *P. megacephala* and *I. humilis;* 1973: Area where *P. megacephala* has replaced *I. humilis;* 1986: *I. humilis* only
*7. SPITTALL POND RESERVE	1963: *P. megacephala* only; 1973: *P. megacephala* only; 1986: *P. megacephala* only
8. HAMILTON-NEWSTEAD	1963: *I. humilis* only; 1973: *I. humilis* only; 1986: Predominantly *I. humilis,* but with small interspersed colonies of *P. megacephala*
9. WRECK ROAD	1963: Mixture of *I. humilis* and *P. megacephala;* 1973: New *Iridomyrmex* focus, bordering on area of *I. humilis* and *P. megacephala;* predominantly *I. humilis;* 1986: *P. megacephala* only
*10. IRELAND ISLAND	1963: *P. megacephala* only; 1973: *P. megacephala* only; 1986: *P. megacephala* only

*Of the ten localities recorded, only these two (Spittall Pond Reserve and Ireland Island) have remained unchanged (both with *P. megacephala* only) throughout the twenty-three-year observation period.

In sum, these accumulated results would seem to give a fairly highly probable answer to the questions posed in 1965: the situation would seem to be one of equilibrium rather than slow replacement, at least on the time-scale involved.

Certain ancillary observations are of interest. Despite the near-saturation of the environment by the "tramp" species, other ants have regularly been reported, often now as cryptic rarities, in all of

the earlier surveys. The genus *Odontomachus,* (*insularis* and *brunnei*), present in later surveys, was reported from Bermuda by Dahl (1902), together with *P. megacephala* and was relatively abundant in 1927. It is now a rare form. Other long-term survivors include the genus *Brachymyrmex* (still relatively abundant in niches unoccupied by either tramp species) and the genera *Paratrechina, Cardiocondyla, Hypoponera,* and *Wasmannia.* Several of these are well known West Indian species, some themselves relatively invasive. So a number could represent relatively recent arrivals or successive reoccupations. Thus *Paratrechina* was first described by Crowell in his survey. On the other hand, a number seem to have been in Bermuda on a long-continuing basis despite the disturbances around them. In addition to *Odontomachus insularis,* for instance, *Hypoponera opaciceps* seems to have been recorded as early as 1902, and *Wasmannia auropunctata* was recognized by the Department of Agriculture and Fisheries of Bermuda as early as 1950 (Crowell, 1968).

In the course of their 1963 survey, Haskins and Haskins visited a number of the small islands in the Great Sound, including Hinson, Darrell, Ports, Long, and Hawkins, all at that time undeveloped and unoccupied. In all of them, pure and dense stands of *P. megacephala* were found, with no trace of *I. humilis.* This is probably not surprising, given the "budding" mode of colony propagation typical of *I. humilis,* in which young queens in the polyginic communities, fertilized within the community, typically omit the nuptial flight and remain in the parental nest, migrating with worker groups to found new sub-associations. These islands in Great Sound and other similar ones do not seem to have been examined since. It would be interesting to do so again, especially in such a location as Five Star Island in Southampton Parish, lying very close to an area of the mainland heavily populated with *I. humilis.*

Finally, attention should be drawn to the fact that no account was taken in this last survey (nor perhaps in the others) of the possible effects of the use of insecticides on any of the sites. There seems no way to check this element with any certainty, but we believe it unlikely that it has been a significant factor, since none of the sites examined (with the possible exception of the immediate vicinity of Hamilton itself) included crop or garden areas. The great majority involved roadside verge-land or rough and unimproved brush areas.

a good part much exposed to wind and weather, especially in winter, which would be expected to minimize the effectiveness of sprays, especially against these largely subterranean insects.

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THE LARVA OF *LEPTANILLA JAPONICA*, WITH NOTES ON THE GENUS (HYMENOPTERA: FORMICIDAE: LEPTANILLINAE)

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We have previously described (1965) the larvae of three species of *Leptanilla: revelierei* Emery, *swani* Wheeler and *esheri* (Kutter). Now, thanks to the generosity of Dr. Keiichi Masuko, we are able to describe the fourth. We do not ordinarily describe and illustrate fully the larva of more than one species of a genus, but *Leptanilla* larvae are so extraordinary that we consider it advisable to describe as many species as possible. Perhaps by so doing we can convince skeptics (including us) that such creatures actually exist.

Dr. Masuko has not only provided us with specimens but also with his manuscripts, from which we quote briefly (with his permission). Dr. Masuko is the only myrmecologist who has seen living *Leptanilla* larvae. Furthermore, his observations necessitate changes in our previous descriptions. Hence we will begin with a complete revision of our generic characterization, which is also a characterization of the subfamily.

Genus Leptanilla Emery

Elongate and very slender; slightly constricted at the metathorax; remainder of body straight and clavate. With a curious structure projecting anteroventrally from the ventral surface of the prothorax. Spiracles minute. A hemolymph feeding pore on each side of abdominal somite III or IV. Body hairs smooth and unbranched, minute hairs very abundant and uniformly distributed; a few long hairs sparsely scattered. Cranium thin; subpyriform in anterior view, at least a third longer than broad. Head hairs lacking. Antennae small; each on the ventral end of a narrow ridge; each with 2 sensilla. Labrum large and thin; posterior surface spinulose; lateral surfaces with a few long slender sharp-pointed teeth. Mandible

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turned laterally (instead of medially as is usual with ant larvae); feebly sclerotized; with a long slender sharp-pointed apical tooth, which curves laterally; outer border furnished with several long slender sharp-pointed teeth; anterior surface with spinules in rows. Labium thin, flap-like and narrowed basally; each palp a ventrolateral cluster of five sensilla.

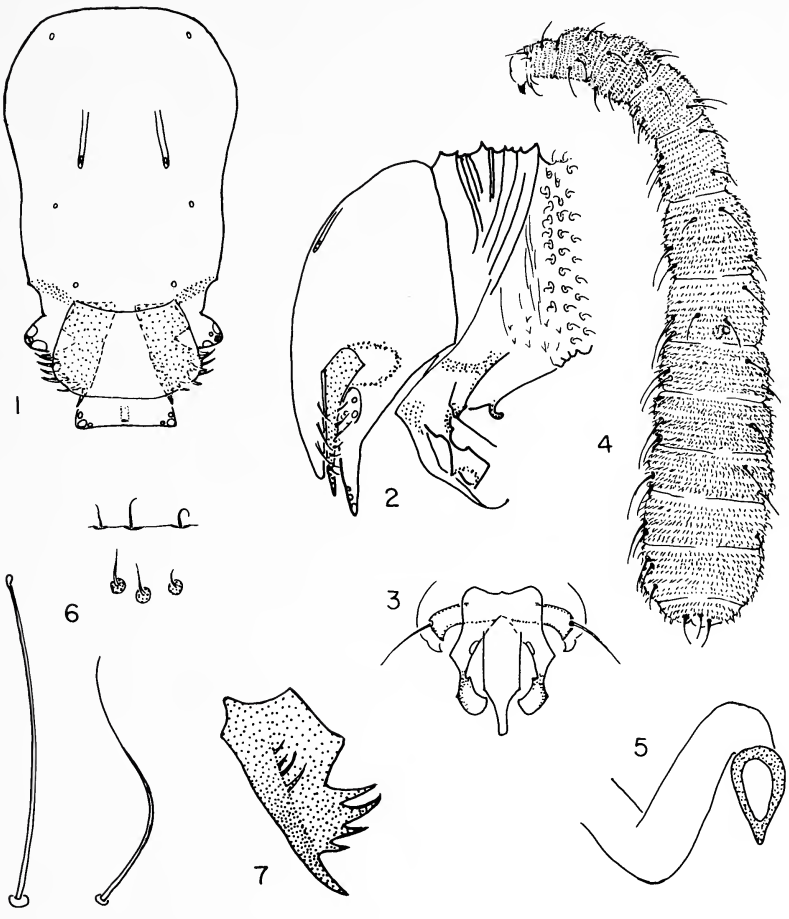
The larvae of *Leptanilla* are unique among the 200 known genera of ant larvae in 3 characters: The prothoracic projection, the hemolymph feeding pores and the mandibles. The most significant of the 3 is the hemolymph feeding pores. We considered them to be spiracles, because we could not find any structures that resembled spiracles. One reason why is now apparent: the spiracles of *L. japonica* are of the same diameter as the base of a minute hair. Therefore even if we had seen a spiracle we would have considered it as the base of a broken-off hair. Another reason: no one had ever studied a live colony of *Leptanilla.* The solution of the problem is Masuko's discovery of "larval hemolymph feeding (LHF)":—

Whenever the queen froze at the 4th abdominal segment, her mouthparts were placed near the posterior border on a side. "In this region a pair of strange structures is present. [Each] is externally a naked circular area bordered by a fringe of stiff hairs. ... In the center of this area, a slit-like opening is located. ... Histological sections were made [of] this region, revealing that this opening is internally attached to a short duct. ... This duct is strongly bent and opens directly into the larval body cavity."

"Since oral trophallaxis is totally absent in the species, LHF is the only way of obtaining nutrients by the queens. [The queens never feed on prey.] ... *L. japonica* workers ordinarily performed LHF even close to the queens, in addition to the prey feeding."

Leptanilla japonica Baroni-Urbani

Length (through spiracles) 1.2–1.7 mm. Elongate and very slender; slightly contricted at the metathorax; remainder of body straight and clavate. Anus posterior. With a peculiar complex structure on the anteroventral surface of the prothorax. Spiracles minute (sometimes vestigial or absent) on T2, T3 and AI-AVIII. On AIV there is a pair of "hemolymph feeding pores" (Masuko, in preparation). Integument of naked anterior portion of T1 with ridges and spinules; posterior portion with hairs similar to those on remainder



Figs. 1–7. Larva of *Leptanilla japonica*. 1, Head in anterior view, ×508; 2, head in side view, ×397; 3, prothoracic projection in anterior view, ×397; 4, larva in side view, ×59; 5, left hemolymph feeding pore, ×1042; 6, three types of body hairs, ×508; 7, left mandible in anterior view, ×962.

of body. Body hairs unbranched, smooth and slightly curved. Of 3 types: (1) 0.003–0.006 mm long, numerous, uniformly distributed (except lacking on anterior portion of T1 and posterior portion of AX) and in transverse rows, each hair set in a slightly sclerotized shallow depression; (2) 0.019–0.088 mm long, with pointed tip, a few

on each somite; (3) 0.069–0.088 mm long, with slightly enlarged flattened tip, on ventrolateral surfaces of AI-AVIII. Cranium thin; subpyriform in anterior view; a third longer than broad. Antenna minute; with 2 sensilla at end of a long ridge. No head hairs. Labrum a large thin flap, a third broader than long, widest ventrally; with 4 long slender sharp-pointed teeth on each lateral surface. Mandible turned laterally; apical half of medial surface heavily sclerotized; ending in a sharp-pointed apical tooth; anterior surface bearing about 4 long slender sharp-pointed teeth; with a wide blade bearing 4 long slender sharp-pointed teeth directed laterally. Maxilla (only partly visible) with a short base and a large lobate palp bearing 5 (1 apical and 4 subapical) sensilla; galea not seen. Labium a very thin flap, trapezoidal in anterior view, narrowed dorsally; palp represented by 5 sensilla on each ventrolateral corner; opening of sericteries a narrow slit on the ventral surface. (Material studied; 5 larvae from Kanagawa Pref., Japan, courtesy of Keiichi Masuko.)

Apologia

Of the 800 species of ant larvae we have studied, the leptanilline larvae are undoubtedly the most difficult to process. They are minute: 1.2–1.7 mm long. They are very slender: they must be punctured in several places with a minute needle; these minute openings retard the transfer of the processing liquids. If KOH does completely dissolve the internal tissues, the insoluble residue cannot be forced out without damaging the larval integument. Even when an integument is entirely cleaned the stain may never reach the head. After a stained integument is on a slide in balsam, it must be moved into the desired position for drawing. If the consistency of the balsam is not exactly right, the delicate integument will tear.

Another difficulty: we have had so few specimens (3, 3 and 5) that we dared not experiment.

Once a larva was stained and stably mounted we encountered difficulties of interpretation. The most exasperating was determining the limits of the prothorax (of this we were never certain). No orthodox insect larva or adult should have spiracles on the prothorax. But some insects do: the mesothoracic spiracles migrate forward during development. But the spiracles of *Leptanilla* are difficult to find because of their minute size. Furthermore Masuko has found by SEM photography that spiracles may be vestigial or

lacking on some somites of some larvae.

Even if one does determine the extent of the prothorax and does locate the 4th abdominal somite, he still has to find the hemolymph feeding pores. That is easy in *revelierei* because of the heavily sclerotized rim. This rim is lacking in *swani* and *japonica.* In fact, in the latter two we are unable to locate the pores in our preserved specimens.

Summary

The larva of *Leptanilla japonica* is described and illustrated. The structures on abdominal somite IV, which have heretofore been regarded as the only spiracles, have been shown by Masuko to be hemolymph feeding pores. The larvae of the genus are characterized on the basis of the four known species.

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GENETIC RELATEDNESS AMONG CO-FOUNDRESSES OF TWO DESERT ANTS, *VEROMESSOR PERGANDEI* AND *ACROMYRMEX VERSICOLOR* (HYMENOPTERA: FORMICIDAE)

By Robert H. Hagen[1], Deborah R. Smith[2], and Steven W. Rissing[3]

Cooperative colony foundation occurs in some social hymenoptera. Polistine wasp foundress associations are usually composed of close relatives (reviewed in Gamboa et al. 1986, Michener and Smith 1987) suggesting kin selection may play an important role in establishment of such groups. Cooperative colony foundation, however, may be advantageous even if cofoundresses are not related (Lin and Michener 1972, Pollock and Rissing 1988a). Indeed, several behavioral (reviewed in Rissing and Pollock 1988) and one electrophoretic (Ross and Fletcher 1985) study suggest ant foundress associations form without respect to relatedness. Here we report on an electrophoretic analysis of intra-group relatedness among co-foundresses of *Veromessor pergandei* and *Acromyrmex versicolor,* two common desert ants with cooperative colony foundation (Pollock and Rissing 1985, Rissing and Pollock 1986, Rissing et al. 1986).

Ideally, relatedness should be measured directly through pedigree analysis of interacting individuals (Hamilton 1972). Since this is impractical for most natural populations of social insects, the alternative is indirect estimation using neutral genetic markers (Pamilo and Crozier 1982, Pamilo 1984). We used polymorphic allozyme loci, detected by protein electrophoresis, for this purpose (Richardson et al. 1986). Allozyme loci offer the advantage that homozygous and heterozygous individuals are readily distinguishable; in addition, these loci are not likely involved directly in determining behavior patterns and thus can be treated as selectively neutral within the context of social evolution (Pamilo 1984).

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Materials and Methods

Foundress associations of *V. pergandei* were collected from two sites, "Main" and "Granite" (2 km apart) immediately south of the southeast corner of South Mountain Park, Phoenix, AZ during February–March 1988. Foundress associations of *A. versicolor* were collected from a site in North Scottsdale, AZ (described in Rissing et al. 1986) in September 1987. In each case, existence of a single characteristic mound of freshly excavated soil indicated a single foundress association. Live co-foundresses were air expressed immediately to Michigan State University where they were frozen at −80° C and stored until electrophoresed.

Electrophoretic methods. We prepared frozen ants for electrophoresis by grinding them individually in an extraction buffer at 4° C. We removed the gasters of *V. pergandei* queens before grinding in a pH 7.0, 0.1 M tris buffer (with 40 mg EDTA, 20 mg NAD, 10 mg NADP and 250 μl beta-mercaptoethanol per 100 ml: Buffer 1) or in an unbuffered detergent solution (with 100 μl Triton-X, 10 mg NADP and 100 μl beta-mercaptoethanol per 100 ml: Buffer 2). Buffer 2 gave superior results for esterases but was no better, and in some cases worse, than Buffer 1 for other enzymes. We ground whole *A. versicolor* in buffer 1. For each ant we adjusted the amount of buffer from 10 to 100 μl to give an approximately equal ratio of buffer to ant tissue.

We applied extracts from 12 ants (ca. 1 μl from each) to thin-layer cellulose acetate plates (Titan III: Helena Laboratories, Beaumont, TX). Plates were soaked for at least 30 min in a running buffer before sample application; we used the same buffer for the electrophoretic run. We used cellulose acetate running buffers "A", "B", "C", "D", and "I" of Richardson et. al. (1986); no single buffer gave good resolution for all enzymes tested. Run durations ranged 15–35 minutes, under constant voltage (200–300 V); durations and voltages were adjusted to optimize separation for each enzyme that showed clear activity. Combinations of running buffer, voltage and time giving best results are noted below. All electrophoresis was done at 4° C.

To visualize the allozymes we used enzyme-specific stains (Harris and Hopkinson 1978, Richardson et al. 1986), mixed 1:1 with 1.5% agar solution and poured onto the plates. When sufficient stain intensity was reached, we rinsed off the agar layer and soaked the

plate in tap water to remove unreacted dye. Precipitated dye remains in the cellulose acetate layer, so stained plates were preserved directly or photocopied. Genetic interpretations of variation in resulting bands was based on known enzyme quaternary structure (Harris and Hopkinson 1978, Richardson et al. 1986), supplemented by comparison of haploid males where possible.

We resolved allozyme products of 18 presumptive genetic loci from *V. pergandei* queens, 4 of which were polymorphic with 2 alleles each: *Est-1* and *Est-2* (general esterase; beta-naphthyl acetate as substrate), *Mdh-1* (malate dehydrogenase, EC 1.1.1.37) and *Pgm* (phosphoglucomutase, EC 2.7.5.1). Optimal separation for the *V. pergandei* esterase allozymes was given by buffer I (25 min at 250 V); for *Mdh-1* by buffer C (30 min at 250 V); and for *Pgm* by buffer I (25 min at 250 V). An additional polymorphism for *Idh-1* (isocitrate dehydrogenase, EC 1.1.1.42) was present in one small sample (buffer I, 20 min at 250 V). Banding patterns and allele designations for the esterase loci are shown in Figure 1; esterase genotypes could not be scored from all individuals.

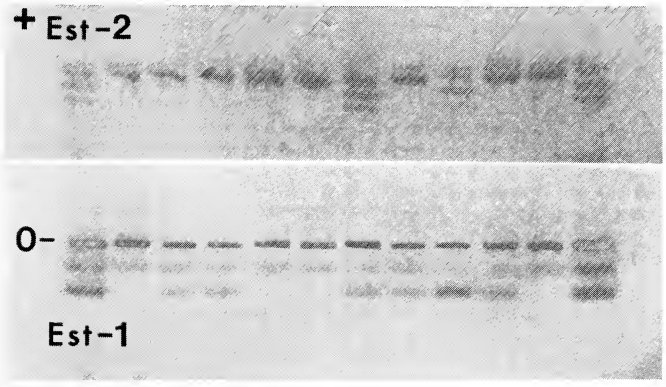

Figure 1. Zymogram of esterase loci in *V. pergandei.* Alleles for *Est-1* are designated "C" (cathodal) and "A" (anodal); the enzyme behaves as a monomer. *Est-1* CC and CA genotypes are distinguished by the relative intensity of each band, since an artifact band comigrates with the A allozyme. *Est-2* has alleles "F" (fast) and "S" (slow) and behaves as a dimer. "O" = origin; "+" = anodal. For *Est-1,* lanes, 2, 5, 6, and 11 are "A/A"; lanes 1, 3, 4, 7, 8 and 10 are "A/C" and lane 9 is "C/C". For *Est-2* lanes 2–6, 7, 10 and 11 are "F/F" and lanes 1, 7, 9 and 12 are "F/S".

An anamalous *Gpi* (glucose phosphate isomerase, EC 5.3.1.9) and *Ao* (aldehyde oxidase, EC 1.2.3.1) banding pattern was present in low frequency among *V. pergandei* queens (buffer I, 25 min at 250 V). Since we were unable to verify Mendelian inheritance of the variant pattern, which could not be interpreted easily in terms of known enzyme quaternary structure, we have omitted these loci from the analysis. The monomorphic loci resolved from *V. pergandei* were (enzyme trivial name, E.C. code and best running buffer are listed after each): *Aat-1* (aspartate aminotransferase, EC 2.6.1.1; I); *Ac* (aconitase, EC 4.2.1.3; C); *Dia* (diaphorase, EC 1.6.*.*; D); *G3p* (glycerol-3-phosphate dehydrogenase, EC 1.1.1.8; A); *G6pdh* (glucose-6-phosphate dehydrogenase, EC 1.1.1.49; A) *Hk* (hexose kinase, EC 2.7.1.1; I) *Lap* (leucine aminopeptidase, EC 3.4.11.1; I); *Ldh* (lactate dehydrogenase, EC 1.1.1.27; D); *Mdh-2* (C); *Pep* (peptidase, phenylalanyl-prolyl substrate; C); *Pgd* (6-phosphogluconate dehydrogenase, EC 1.1.1.44; D).

We resolved allozyme products of 30 presumptive genetic loci from *A. versicolor* queens. Only *Pgm* was polymorphic with 2 alleles designated F (fast migrating) and S (slow). Best resolution was given by buffer D, run for 30 min at 250 V. The monomorphic loci were (enzyme trivial name and EC code [if not listed above] and best buffer are listed after each): *Aat-1* and *Aat-2* (D); *Ac* (D); *Ada* (adenosine deaminase, EC 3.5.4.4; D); *Ak* (Adenylate kinase, EC 2.7.1.20; A); *Ald* (aldolase, EC 4.1.2.13; D); *Ao* (D); *Apk* (arginine phosphokinase, EC 2.7.3.3; D); *Dia* (I); *Est* (D); *Fum* (fumarase, EC 4.2.1.2; D); *Gapdh* (glyceraldehyde phosphate dehydrogenase, EC 1.2.1.12; C); *Gldh* (glucose dehydrogenase, EC 1.1.1.47; A); *Gpi* (C); *G3p* (A); *G6pdh* (B); *Hbdh* (hydroxybutyrate dehydrogenase, EC 1.1.1.30; D); *Hk* (C); *Idh-1* and *Idh-2* (C); *Lap* (C); *Ldh* (B); *Mdh-1* and *Mdh-2* (C); *Me* (malic enzyme, EC 1.1.1.40; A); *Pep* (glycyl-leucyl substrate; C); *Pgd* (A); *Sod* (superoxide dismutase, EC 1.15.1.1; D); *Sordh* (sorbitol dehydrogenase, EC 1.1.1.14; I).

Statistical analyses. The within group relatedness for foundress associations was calculated from the relationship:

$$r = 2*F_{st}/(1 + F_{it}),$$

where F_{st} and F_{it} are Wright's inbreeding coefficients (Hamilton 1972, Pamilo 1984, McCauley et al. 1988). The F_{st} and F_{it} were estimated for each polymorphic locus using Long's (1986) proce-

Table 1. Genotype and allele frequencies of *V. pergandei* queens from foundress associations, separated by subsite.

	EST-1			EST-2			PGM			MDH-1		
Group	CC	CA	AA	FF	FS	SS	FF	FS	SS	FF	FS	SS
Main:												
VF 1	2	2	6	7	3	0	10	0	0	8	2	0
VF 2	1	0	1	1	1	0	2	0	0	2	0	0
VF 3	0	3	1	4	0	0	2	2	0	4	0	0
VF 4	0	3	2	1	3	1	5	0	0	5	0	0
VF 5	0	0	2	2	0	0	2	0	0	2	0	0
VF 6	1	2	1	2	2	0	4	0	0	4	0	0
VF 7	0	3	0	1	2	0	3	0	0	3	0	0
VF 8	1	2	1	2	2	0	4	0	0	4	0	0
VF 9	0	2	3	4	0	1	3	1	0	4	1	0
VF 10	0	3	2	2	2	1	5	0	0	5	0	0
VF 11	0	3	0	2	1	0	3	0	0	3	0	0
VF 12	1	0	1	1	1	0	2	0	0	1	1	0
VF 13	0	2	0	1	1	0	2	0	0	2	0	0
VF 14	0	1	1	0	2	0	2	0	0	2	0	0
VF 15	0	0	2	0	2	0	2	0	0	2	0	0
VF 16	1	1	0	2	0	0	2	0	0	2	0	0
VF 17	-	-	-	3	2	0	5	0	0	4	1	0
VF 18	-	-	-	2	0	0	2	0	0	2	0	0
VF 19	0	2	4	5	0	1	6	0	0	5	1	0
VF 20	2	1	0	2	1	0	1	2	0	3	0	0
VF 21	-	-	-	6	1	0	7	0	0	5	2	0
VF 22	-	-	-	1	1	0	2	0	0	2	0	0
VF 23	-	-	-	2	1	0	2	0	1	3	0	0
	Freq. (A) = 0.66			Freq. (F) = 0.79			Freq. (F) = 0.96			Freq. (F) = 0.95		
Granite:												
VF 24	-	-	-	3	0	0	3	0	0	2	1	0
VF 25	1	3	0	2	1	1	4	0	0	4	0	0
VF 26	0	2	0	1	1	0	2	0	0	1	1	0
VF 27	-	-	-	0	1	1	2	0	0	2	0	0
VF 28	1	1	1	1	2	0	3	0	0	3	0	0
VF 29	1	1	1	2	1	0	3	0	0	2	1	0
VF 30	1	1	0	2	0	0	2	0	0	2	0	0
VF 31	0	4	0	3	1	0	4	0	0	3	1	0
	Freq. (A) = 0.44			Freq. (F) = 0.76			Freq. (F) = 1.00			Freq. (F) = 0.91		

dure, which is corrected for sample size bias. Since all of the polymorphic loci detected in this study had 2 alleles, the method is essentially identical to that of Pamilo (1984, Crozier et al. 1984, Pamilo and Rosengren 1984), when groups are weighted by the number of individuals. Weighting of groups by size appears preferable in the case of *V. pergandei* and *A. versicolor* foundress associations, which varied from 2 to 15 queens in these samples.

Standard errors (S.E.) for the relatedness estimates were obtained by a jacknife procedure over groups (Sokal and Rohlf 1981, Pamilo 1984, Crozier et al. 1984). Simulation studies have shown that S.E. estimated by this method tend to be overly conservative and can be unreliable when allele frequencies are highly unequal (Crozier et al. 1984, Wilkinson McCracken 1985). Because of this, use of these S.E. in formal statistical hypothesis testing is not justified with the present data. In the case of *V. pergandei* foundress associations, a more robust estimate of r is possible by combining estimates across the 4 informative loci (Wilkinson and McCracken 1985). For this pooled estimate we used the weighted means of F_{st} and F_{it} across loci (Long 1986).

Results

Veromessor pergandei. Relatedness within *V. pergandei* foundress associations does not differ from 0 (Table 1; mean estimate across loci = 0.033, Table 2). Allele frequencies of *V. pergandei* are similar between subsites (Table 1); therefore, we treat them as a single population. Pooling subsites would inflate estimated relatedness if subsites differed. *Pgm* and *Mdh-1* allele frequencies are highly unequal, which limits their usefulness as genetic markers for relatedness; they are most informative in combination with *Est-1* and *Est-2* alleles. None of the loci appear linked.

Acromyrmex versicolor. Genetic relatedness among *A. versicolor* co-foundresses is no greater than that expected from randomly associating queens (Table 2, 3). Negative value of the estimate (-0.125) is likely a statistical artifact resulting from unequal *Pgm* allele frequencies and relatively small numbers of queens in each foundress association (mean = 3.8) (Crozier et al. 1984, Wilkinson and McCracken 1985) rather than an indication that queens avoid kin (Hamilton 1972). The small standard error associated with the estimate (0.028) indicates little variation in relatedness among groups, consistent with purely random mixing of genotypes.

Table 2. Relatedness and F-statistics for *V. pergandei* and *A. versicolor* foundress associations. The S.E. is standard error of relatedness, r, based on jacknifing over N groups of foundresses or nestmates. The mean r for *V. pergandei* foundresses is calculated from the weighted mean F_{st} and F_{it} across loci.

	LOCUS	r	S.E.	F_{st}	F_{it}	N
V. pergandei	*Est-1*	0.043	0.106	0.0208	-0.0308	24
	Est-2	-0.009	0.093	-0.0049	0.0527	31
	Mdh-1	-0.117	0.043	-0.0554	-0.0561	31
	Pgm	0.174	0.158	0.1107	0.2685	31
	Mean	0.033		0.0176	0.0638	
A. versicolor	*Pgm*	-0.125	0.028	-0.0632	0.0077	26

Discussion

Foundress associations of *V. pergandei* and *A. versicolor* are not composed of close kin. *Veromessor pergandei* and *A. versicolor* foundresses do not deviate from random assortment of genotypes, precluding the operation of kin selection (Wilson 1977, 1983; Wade 1985). Similar random association of genotypes occurs in polygynous *Solenopsis invicta* colonies (Ross and Fletcher 1985), which are likely founded cooperatively. No other cooperatively founding ant species have demonstrated behavioral evidence of preferential association among relatives (Rissing and Pollock 1988), suggesting that results from the three species now studied electrophoretically are likely to be general. The genetic basis for cooperative behavior among co-founding queens, therefore, cannot be described as a direct consequence of kin selection.

Genetic diversity of many Hymenoptera is lower than found in other insect orders owing either to haplo-diploid sex determination (increasing selective pressure on deleterious alleles exposed in haploid males or decreasing effective population size) or behavioral/environmental peculiarities characteristic of many species, especially social ones (social structure lowering effective population size and providing a nest structure that buffers environmental variability) (reviewed in Graur 1985, Sheppard and Heydon 1986). The decreased variability of *A. versicolor* relative to *V. pergandei* may reflect differences in the mating systems of the two: while all *A. versicolor* colonies in an area release alates on a single day (Wheeler 1917, Rissing et al. 1986), *V. pergandei* colonies release alates over a three month period with little coordination of reproduction among

Table 3. *Pgm* genotype frequencies of *A. versicolor* queens from foundress associations. Groups are listed from largest to smallest in size; the frequencies among 14 solitary queens are given for comparison.

Foundress Group	*Pgm* Genotype		
	FF	FS	SS
FA 4	12	3	0
FA 6	11	2	0
FA 13	9	3	0
FA 5	9	2	0
FA 2	4	0	1
FA 1	3	1	0
FA 3	3	1	0
FA 17	4	0	0
FA 25	3	1	0
FA 34	4	0	0
FA 7	2	1	0
FA 8	3	0	0
FA 10	3	0	0
FA 11	3	0	0
FA 12	3	0	0
FA 14	3	0	0
FA 31	2	1	0
FA 32	2	1	0
FA 33	3	0	0
FA 35	3	0	0
FA 9	2	0	0
FA 15	1	1	0
FA 16	1	1	0
FA 18	2	0	0
FA 19	2	0	0
FA 21	1	1	0
Total:	98	19	1
Solitary:	13	1	0

adjacent colonies (Pollock and Rissing 1985). Under the latter system, small numbers of reproductives (especially males) released per day enhance sampling error associated with the distribution of genes with colonies, thus enhancing genetic variance within a population.

Starting colonies of four North American ant species (*Myrmecocystus mimicus, Solenopsis invicta, V. pergandei* and *A. versicolor*) have clumped starting nests, yet adult colonies of these species are highly territorial, leading to strong intraspecific competition among starting colonies in the form of brood raiding (reviewed in Pollock

and Rissing, 1988b.) Colonies initiated with more foundresses produce more workers and are more likely to succeed at brood raiding (Bartz and Hölldobler 1982, Tschinkel and Howard 1983, Rissing and Pollock 1987). Under such circumstances group life can be considered mandatory, and relatedness of a potential co-foundress is of little or no importance compared to her ability to contribute to an initial brood-raiding force (Pollock and Rissing, 1988a). While relatedness appears to play an important role in the formation of many wasp foundress associations (references above), this appears increasingly unlikely in most ant foundress associations.

Summary

Genetic relatedness among queens within foundress associations of two desert ant species was assayed with protein electrophoresis. Of 18 loci screened in the seed-harvester *Veromessor pergandei,* 4 were variable leading to a within-foundress-association relatedness estimate of $r = .03$ (i.e. random association of queens). Only one locus of 30 screened in the leaf-cutter *Acromyrmex versicolor* was variable. Relatedness within *A. versicolor* foundress associations was estimated at $r = -.12$, with the negative value likely a statistical artifact rather than an indication that kin avoid each other. These data are consistent with behavioral and electrophoretic observations of these and other ants and suggest kin selection plays little, if any, role in formation of most ant foundress associations.

Acknowledgments

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HINDGUT CHANGES PRECEDING PUPATION AND RELATED COCOON STRUCTURE IN *CHRYSOPERLA COMANCHE* BANKS (NEUROPTERA, CHRYSOPIDAE).

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Introduction

A blockage occurs between the midgut and hindgut of larval neuropterans in the suborder Planipennia (New 1986). Thus, the feces are stored in the midgut during larval life, enabling the hindgut to perform other functions. A compound stored in the hindgut of some larval chrysopid species is extruded from the abdominal tip and used as an adhesive during locomotion (Spiegler 1962) and for defense when the larvae are attacked (LaMunyon and Adams 1987).

This adhesive/defensive substance is produced by the malpighian tubules of chrysopid larvae. However, as pupation nears, the malpighian tubules produce silk precursors (Spiegler 1962), and undergo a dramatic histological change in the ca. 2 day transformation from mature larva to prepupa (the cocoon building stage) (McDunnough 1909, Spiegler 1962, Wigglesworth 1972). The silk precursors flow from the tubules into the hindgut and are extruded from the anus during cocoon construction.

The composition of chrysopid cocoons is not known. Larval silk does not have the solubility properties of protein (Lucas and Rudall 1968), and Rudall and Kenchington (1971) suggested it might be "a kind of nylon with condensation of dicarboxylic and diamino hydrocarbons." These authors also found that cocoons are composed of an outer fibrous silk, and an inner wall consisting of compact layers. Infrared spectroscopy suggested that the inner wall is composed of a polymerized molecule containing some alpha helical domains. They placed the cocoons in the category of the cuticulin silks, which are produced by epithelial cells.

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While performing a histological examination of the abdomen of *C. comanche* larvae, I found that the hindgut epithelium changes drastically prior to pupation. The work described here is a light microscopic examination of larval and prepupal *C. comanche* hindgut epithelium, and an electron microscopic investigation of cocoon structure.

Materials and Methods

Laboratory colonies of *C. comanche* were raised from adults collected in Orange Co., Ca. Rearing procedures followed those described earlier (LaMunyon and Adams 1987).

Mid-third instar larvae, prepupae spinning silk, and prepupae that had just spun cocoons, were prepared for light microscopy in

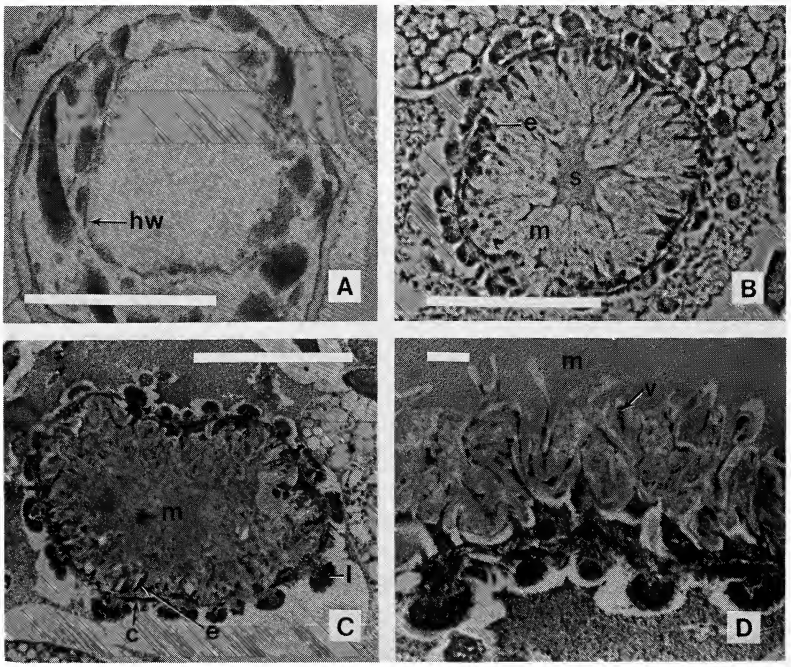

Figure 1. Light micrographs of cross sections through the abdomen of larval and prepupal *C. comanche*. (A) Mid third-instar larva (Bar = 100μ). (B) Prepupa spinning silk (phase contrast; Bar = 100μ). (C) Prepupa after spinning silk (Bar = 100μ). (D) Close-up of (C) (Bar = 10μ). c, circular muscle; e, epithelium; hw, hindgut wall; l, longitudinal muscle; m, epithelial associated material; s, silk precursors; v, epithelial villi.

two ways. Some were fixed in formalin, dehydrated in ethanol, embedded in paraffin, sectioned at 8 microns, then mounted and stained with hematoxylin and eosin. Others were fixed in 4% glutaraldehyde in 0.01M phosphate buffer (pH 7.2 at 5°C), post fixed in 2% osmium tetroxide in 0.01 M phosphate buffer (pH 7.2 at room temperature), dehydrated in ethanol, embedded in Epon-Araldite 502, sectioned at 1 micron, and mounted and stained with toluidine blue. In all, 12 larvae and 6 prepupae were sectioned and examined.

Empty cocoons were also examined microscopically. Some were embedded in paraffin, sectioned at 40 microns, then mounted and stained with eosin. Others were fractured after submersion in liquid nitrogen, mounted on stubs, sputter-coated with gold, and viewed with a scanning electron microscope.

Results

In mature third-instar larvae, the defensive substance is stored in the hindgut, which has a very thin epithelium (Fig. 1A). In prepupae spinning silk, the epithelium is greatly enlarged and villous, extending into the lumen (Fig. 1B). Two substances are visible in this section: an innermost eosin-staining material continuous with malpighian tubule-produced silk precursors, and an outer, non-staining substance associated with the villous epithelium. In prepupae fixed after spinning the outer layer of cocoon fibers, the epithelium is still unusually enlarged, and long, finger-like extensions into the lumen are visible (Fig. 1C & 1D). At this stage, only the epithelium-associated substance remains.

In the paraffin cocoon sections, there were two different materials present: the outermost silk which stained with eosin, and the non-staining substance making up the solid inner wall (micrographs not included). These two cocoon layers appear discrete in the electron micrographs. The inner wall is relatively thick, is surrounded by the fibrous silk, and is the major component of the cocoon (Fig. 2 A, B, C). Figure 2C also shows a pore through the inner wall; all pores observed were composed of two holes. The homogeneity of the inner wall is evident from Fig. 2D.

The abdominal musculature changes during transition from mature, third instar larvae to prepupae. Large, intersegmental muscles can be seen traversing the section of a younger larva (Fig. 1A). The defensive substance, being less viscous than cocoon precursors

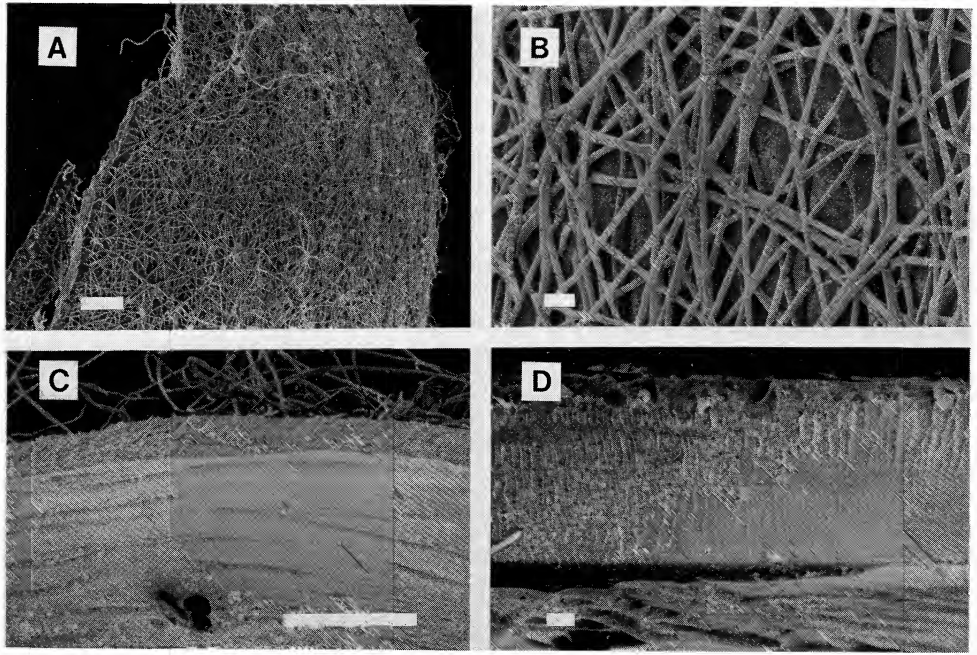

Figure 2. Scanning electron micrographs of fractured *C. comanche* cocoons. (A) Outer cocoon surface (Bar = 100μ). (B) Close-up of (A) (Bar = 10μ) (C) Fractured edge and surface of inner wall with pore (Bar = 100μ). (D) Fractured edge of inner wall; bottom is cocoon interior (Bar = 10μ).

(personal observation), is probably expelled by compression of the entire abdomen. In prepupae, the circular and longitudinal hindgut muscles are enlarged and much more evident (Fig. 1B, 1C), and probably expel the more viscous cocoon precursors by compressing only the hindgut.

Discussion

The hindgut epithelium changes quickly from a very thin layer to a villous tissue that is probably secretory. This inference is supported by two facts. First, the malpighian tubules are the only organs opening proximally into the hindgut; these produce precursors of the fibrous silk, which stain differently than the epithelium-associated substance. Thus, the only tissue apparently responsible for the production of this latter substance would be the villous hindgut epithelium. Second, the appearance of this material coincides with the transformation of the epithelium (presumably to a secretory villous phase). The villous extensions are probably involved in secretion, and could be detaching from the cells and breaking open into the lumen.

Insect hindgut epithelia normally secrete a thin layer of cuticle prior to molting, and the epithelium-associated material may be similar to some cuticle component. This finding supports the placement of chrysopid silk (pertaining to the epithelial substance) with the epithelial-produced cuticulin silks (Rudall and Kenchington 1971). Other insect hindguts with a secretory function are known; in some tephritid flies a pheromone is secreted by a derived hindgut epithelium (Little and Cunningham 1987).

It appears that the fibrous silk of the cocoon is produced by the malpighian tubules; the inner wall may be formed from the epithelium-associated substance. This hypothesis is supported by the temporal changes in the hindgut. The eosinophylic, malpighian tubule-produced silk precursors are found in the lumen during spinning of the fibrous silk. Once the silk layer appears complete, only the epithelium-associated material remains in the hindgut. This stage may coincide with the time when the inner wall is laid down. The gross physical nature of the cocoons also supports this hypothesis. After completion of the fibrous silk layer, the cocoons are very soft; ca. one day later, they become hard, probably as the inner wall is formed.

The fibrous silk probably provides a substrate for the formation of the solid inner wall which is the major cocoon component and has periodic perforations. Aside from mechanical protection, the functions of this wall may include resistance to infection, parasitoid oviposition, and desiccation. It is not known if the inner wall of more mesic species is also the major cocoon component, but *C. comanche* inhabits an arid environment (southern CA), in which desiccation protection can be expected to be vital for the two week metamorphic period. On the other hand, there is need for gas exchange: hence, the pores.

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Summary

The hindgut epithelium in prepupal *C. comanche* becomes unusually villous and may be secreting a substance found in the hindgut lumen. This substance is probably used to form the solid inner cocoon wall; both the inner cocoon wall and the hindgut substance have similar staining properties. Malpighian tubule-produced silk precursors stain similarly to the outer, fibrous cocoon silk. Hence, cocoons appear to be composed of two different substances secreted by different tissues. Cocoon structure is also described.

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THE PHYLOGENETIC SYSTEM OF THE GAYELLINI (HYMENOPTERA: VESPIDAE; MASARINAE)*

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Introduction

The Gayellini is one of the two tribes of Masarinae (Carpenter, 1981). Endemic to the Neotropics, the majority of the species are Patagonian, but one ranges as far north as Mexico. With ten described species, the group is far less speciose than its sister-tribe Masarini, which has over 200 described species (*cf.* Richards, 1962), and most species are rarely collected. These wasps have a very distinctive appearance among Vespidae (Fig. 1), and their taxonomic history has been more turbulent than any other higher vespid taxon. Although the phylogenetic placement of the group as a whole has now evidently been settled (Carpenter, 1981), no study has been made of the species. The current generic classification is fragmented, and there have been no keys to all of the taxa. In this paper, I investigate the phylogenetic relationships of the species, and present a revised generic classification along with keys to all taxa.

Taxonomic History

Saussure (1852–58) placed *Gayella* in the Section "Anomaloptères" of the "Euméniens" because the forewing recurrent veins ($m-cu_{1-2}$) are received in separate cells (Fig. 6), as in the other genera placed in this section (*Raphiglossa,* and *Stenoglossa* = *Psiliglossa*). In other vespids he studied both veins were received by the second submarginal cell. Ashmead (1902a) described the subfamily Raphiglossinae (in his Eumenidae) for this group, but by that time other genera had been described which had the diagnostic character of the recurrent veins. These were *Euparagia* and *Paramasaris,* both considered probable masarines by their authors (Cresson, 1879, and Cameron, 1901, respectively). Ashmead (1902b) proposed the tribe Euparagiini in his Masaridae for these two genera. So the recurrent

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veins were no longer uniquely diagnostic. Bequaert (1918) questioned whether *Gayella* belonged in the Raphiglossinae, since the longitudinal plaiting of the forewings "is very obsolete" in the genus, and Bradley (1922) placed it in its own subfamily in Vespidae *s. l.* Bequaert (1928) transferred *Paramasaris* to this subfamily, based on its possession of the characteristic hindwing venation of *Gayella* (Fig. 3). Richards (1962) included the Gayellinae in his Masaridae, but his dendrogram showed Euparagiinae as more closely related to the subfamily Masarinae. I (Carpenter, 1981) demonstrated that Richards' Masaridae was a paraphyletic group, since Euparagiinae is the sister-group of Vespidae as a whole. Four synapomorphies were adduced which showed a sister-group relationship between gayellines and masarines: presence of hypostomal apodemes, loss of the midfemur basal ring, loss of the scutal lamella and provisioning with nectar and pollen. Gayellines and masarines were treated as tribes in an expanded Masarinae, the system followed here.

Gayella was originally described as monotypic for *G. eumenoides* by Spinola (1851). Saussure (1855 in Vol. 3 of Études), Willink (1956, 1963) and Willink and Ajmat de Toledo (1979) added five species. The latter paper provided a key to the six species, however I believe that the key given here will be easier to use. *Paramasaris* was also originally described as monotypic, for *P. fuscipennis* Cameron. Cameron (1904) later described a new genus *Zethoides* (*non Zethoides* Fox, 1899; *Plesiozethus* Cameron, 1905, and *Metazethoides* Schulz, 1906, are replacement names) for *Z. flavolineatus,* which differed from *Paramasaris* in having only two (Fig. 5), as opposed to three (Fig. 6), submarginal cells. Zavattari (1912) questioned whether Cameron had described this character correctly, and Bradley (1922) suspected that *Plesiozethus* was a synonym of *Paramasaris.* This was confirmed by Bequaert (1928), who showed that the number of submarginal cells was variable, and synonymized *flavolineatus* with *fuscipennis.* Giordani Soika (1974) described two new species in the genus, but provided no key. He also described a new genus, *Paragayella,* monotypic for the new species *Paragayella richardsi.* I consider this genus a synonym of *Paramasaris,* as discussed below. I also give the first key to species of the group.

Materials and Methods

All of the species have been examined. Types of *Paramasaris* have been seen; treatment of *Gayella* follows Willink's concepts. Com-

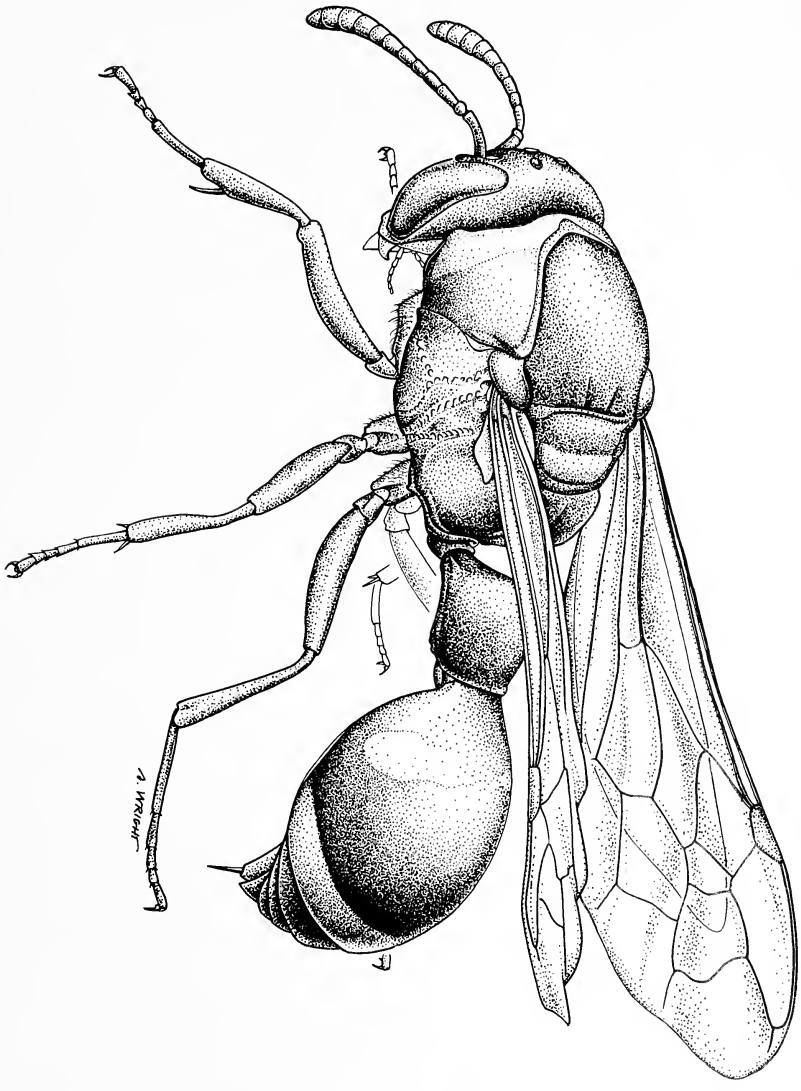


Fig. 1. *Gayella eumenoides*, ♀.

plete label data for all material of *Paramasaris* are listed under taxonomic notes for each species; for the relatively better known *Gayella* only provinces are noted. Acronyms for collections are listed below, along with the name of the individuals who provided the material where this was borrowed.

AMNH	American Museum of Natural History, New York (M. S. Favreau)
BMNH	British Museum of Natural History, London (M. C. Day, C. R. Vardy)
CAS	California Academy of Sciences, San Francisco (W. J. Pulawski)
CP	Charles Porter personal collection
IML	Instituto Miguel Lillo, Tucuman (A. Willink)
IPC	Instituto Pedagógico de Chile
MCZ	Museum of Comparative Zoology, Cambridge
MF	M. A. Fritz personal collection
MNHN	Muséum National d'Histoire Naturelle, Paris
UCD	University of California, Davis (P. S. Ward)
USNM	U.S. National Museum of Natural History, Washington (A. S. Menke)

Morphological terminology follows Carpenter (1981), except that I have adopted Snelling's (1986) more descriptive terms "preoccipital" and "postocular" for the carinae previously termed "dorsal occipital keel" and "ventral occipital keel" (Richards, 1962). Detailed examination of the labiomaxillary complex and male genitalia was made by dissection of these structures, clearing slightly in cold lactophenol, and examination in glycerin. Measurements were made with an ocular micrometer. Illustrations were made with a Wild M-400 photomacroscope employing Kadak TMAX 400 film. Cladistic analysis (Hennig, 1966) was performed for all the features discussed in this paper. Outgroup taxa include Masarini and Euparagiinae, with reference to other Vespidae also occasionally made.

Results

Subfamily characters

First I discuss some morphological features important in higher-level vespid relationships, before turning to consideration of the phylogenetic relationships among the species. Autapomorphies of

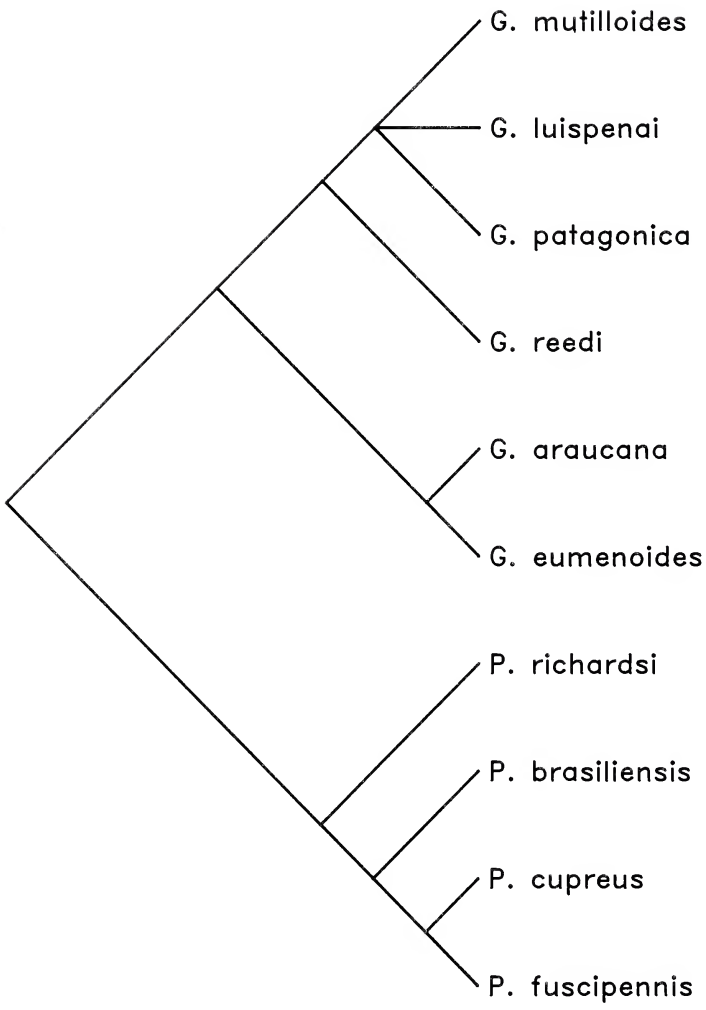


Fig. 2. Cladogram of the species of Gayellini.

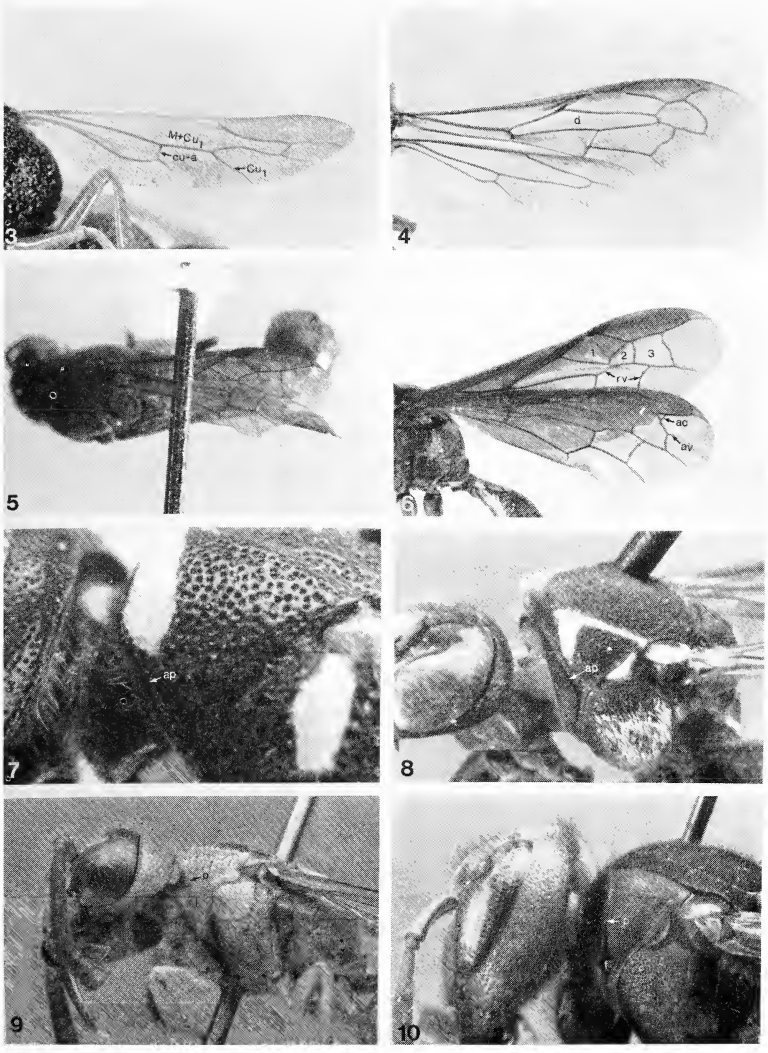
the Gayellini listed by Carpenter (1981) include the hindwing with Cu_1 diverging from $M+Cu_1$ far distad of the insertion of cu-a (Fig. 3), the clypeus with the dorsal margin bisinuate (Fig. 12), the first metasomal tergum and sternum fused and metasomal segments after II retractile (the latter two convergent with other vespids). Some other autapomorphies are mentioned below.

Forewing discal cell. Carpenter (1981:14) noted that the discal cell is shorter than the submedian in *Paramasaris.* This is also the case in *Gayella* (Fig. 1), and this should be considered a reversion from the state of an elongate discal cell in other Vespidae (Fig. 4; *cf.* Carpenter, 1981), and thus an autapomorphy of Gayellini.

Forewing radial region. The variation in the number of submarginal cells in *Paramasaris* was alluded to above. Besides *fuscipennis,* I have seen loss of $r-m_2$ producing two submarginal cells in several specimens of *brasiliensis* (including the allotype and paratype, Fig. 5). The placement of $m-cu_1$ varies as well, sometimes meeting M at the fork where RS diverges. But this is not correlated with number of cells, and most specimens have the usual condition of RS diverging first (Figs. 5–6). In addition, the specimen of *Paragayella richardsi* from Formoso, Brazil, has a very small adventitious cell at the junction of $r-m_3$ and RS on one wing (Fig. 6), and both Goias specimens have an adventitious vein spur arising from the middle of $r-m_3$ (Fig. 6).

Clypeus. The clypeus is narrower than its height in all species, particularly in males (Figs. 11–17). Richards (1962:46) stated that the reverse is true in *Paramasaris,* perhaps a *lapsus.* This is not the usual state in Vespidae, and is perhaps apomorphic, although the degree of narrowing varies in the tribe.

Occipital carinae. Gayellini have both the postocular and preoccipital carinae in the groundplan, contrary to Richards (1962:12). The postocular carina is reduced in length, and may be present only as a trace just ventral to the eye in *Gayella,* but is typically obvious in the *eumenoides* group. The carinae are almost confluent in many specimens of *eumenoides* and *araucana,* separated by only a slight gap (Fig. 18). The "complete" carina in *Paramasaris* (Richards, 1962:46; Fig. 19) is evidently produced by confluence of the postocular with the preoccipital carina, as occurs in some Masarini (Snelling, 1986) and probably other Vespidae (Carpenter, 1988). The postocular carina is effaced in *Paragayella* (Fig. 20).



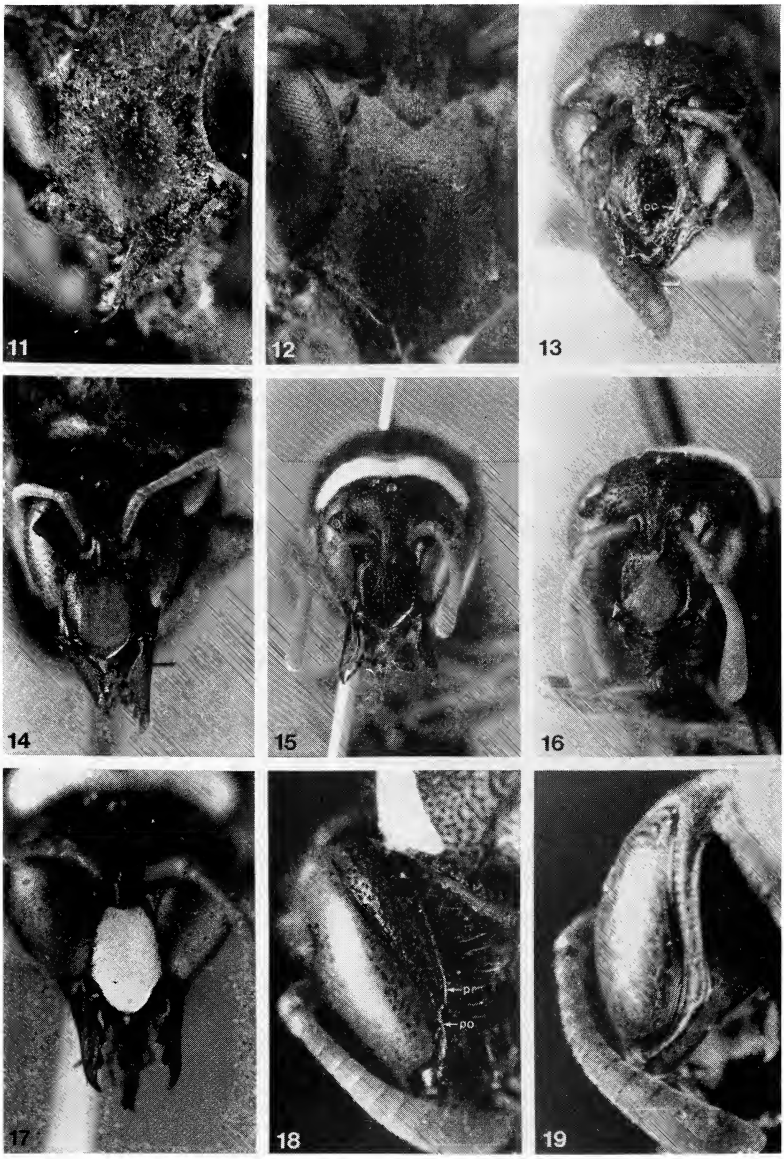
Figs. 3–10. 3. *Gayella araucana,* 7×. Hindwing. 4. *Paragia decipiens aliciae,* 4×. Wings. 5–6. Wings, 6×. 5. *Paramasaris brasiliensis.* 6. *P. richardsi.* Submarginal cells are numbered. 7–10. Lateral view of pronotum. 7. *G. araucana,* 17×. 8. *Euparagia scutellaris,* 10×. 9. *Ischnocoelia robusta,* 6×. 10. *Vespa affinis,* 5×. *ac:* adventitious cell; *ap:* anterior pronotal carina; *av:* adventitious vein; *d:* discal cell; *f:* pronotal fovea; *p:* pronotal carina; *rv:* recurrent veins.

Acroglossal buttons. As noted by Carpenter (1981), Richards (1962) incorrectly stated that acroglossal buttons are lacking from the ligula of Gayellini. The only species in which they are entirely lacking are *Paramasaris fuscipennis* and *cupreus* (Fig. 21). These structures are also absent from the glossa of *Paramasaris brasiliensis,* but are present on the paraglossae. This is a transformation series in reduction. Other gayellines have the buttons on both the glossa and paraglossae (Fig. 22), including *Paragayella richardsi,* the sister-group of *Paramasaris,* and *P. brasiliensis* is the sister-group of *fuscipennis* + *cupreus* (Fig. 2).

Hypostomal apodemes. These are present in all species, which supports the interpretation of synapomorphy with Masarini. They are always very narrow (Fig. 23).

Pronotal carina. Paramasaris and *Paragayella* are notable for having two parallel carinae on the pronotum. One is present at the anteroventral margin of the pronotum; the other is posterior to this and runs towards the humeri and dorsum of the pronotum (Figs. 29–31, 40). The second carina shows a transformation series in development, ranging from short lateral sections only (*Paragayella,* Figs. 24, 29), to extending to the dorsum (*Paramasaris brasiliensis,* Figs. 25, 30), to complete across the dorsum (*P. cupreus* and *fuscipennis,* Fig. 26). This series apparently corresponds to the phylogenetic relationships among these species (Fig. 2). *Gayella* has only the anterior carina (Fig. 7). Euparagiinae also has only the anterior carina (Fig. 8), although the humeri are somewhat raised in *scutellaris.* In Masarini the anterior carina is usually blunt, and a lateral carina on the humeri may be present (Fig. 37). In all these groups, the anterior carina precedes a groove which is frequently crenate (secondarily reduced in various Masarini).

The situation is different in other Vespidae. In Polistinae, the structure termed the "pronotal prominence" (Richards, 1978) is probably homologous with the anterior carina. Although often blunt, it is frequently carinate, and lies at the anteroventral margin of the pronotum (Fig. 38). It precedes the pronotal fovea, which is sometimes set in a deep depression; there is no lateral groove. In the groundplan, there is also a carina on the dorsum (Carpenter, 1989). This second carina is usually quite short laterally, and may closely approach the anterior carina (Fig. 38). In *Polistes* the second carina extends almost to the ventral pronotal margin in many species, and the fovea, which is anterior to this carina, is not preceded by a



Figs. 11–19. 11–12. Clypeus, ♀. 11. *Paramasaris richardsi,* 19×. 12. *P. brasiliensis,* 27×. 13–16. Frontal view of head, ♀. 13. *P. cupreus,* 14×. 14. *Gayella mutilloides,* 5×. 15. *G. eumenoides,* 7× 16. *G. araucana,* 10×. 17. *G. reedi* ♂, 10×. Frontal view of head. 18–19. Lateral view of head. 18. *G. araucana* 15×. 19. *P. brasiliensis,* 21×. *cc:* apical clypeal carinae; *g:* gap between mandibular teeth; *po:* postocular carina; *pr:* preoccipital carina.

"prominence" (Fig. 39). Richards (1973) confused the dorsal carina in *Polistes,* behind the fovea, with the anterior carina in other polistines, in front of the fovea. Eumeninae, which also have a fovea, also have a carina in front of the fovea (Fig. 9), which continues across the *dorsum* in the groundplan (Carpenter and Cumming, 1985). The single carina may be a composite structure, derived from a state resembling certain polistines with two closely approximated carinae (Fig. 38). This is also the case in the groundplan of Vespinae (Carpenter, 1987), where there is a single carina, preceding the pronotal fovea and running across the dorsum (Fig. 10). Stenogastrinae have a highly modified pronotum and lack a posterior carina and fovea (Carpenter, 1988), but have a blunt ridge anteriorly that may correspond to the anterior carina (Fig. 32).

Thus, an anterior carina is clearly an ancestral vespid character, but considering its diverse form, the posterior carina may have evolved multiple times. The alternative interpretation, that it evolved once (in the ancestor of all vespids except Euparagiinae), requires secondary losses within Gayellini (*Paragayella, Paramasaris* and *Gayella* independently) and Stenogastrinae. The interpretation of nonhomology is more parsimonious, and accords with the apparent transformation series in *Paramasaris.* In any case, the separate posterior carina has also been lost on numerous occasions within the Masarini and Polistinae (Carpenter, 1989, and in prep.), and the possibly composite carina has also been lost several times within Eumeninae and Vespinae (Carpenter, 1987; Carpenter and Cumming, 1985). Secondary loss also applies to the pronotal fovea, present in the groundplan of Eumeninae, Polistinae and Vespinae. It has been lost multiple times within Polistinae (Richards, 1978; Carpenter, 1989), and probably also in Stenogastrinae. Presently available morphological and behavioral evidence supports a sister-group relationship between Stenogastrinae and Polistinae + Vespi-

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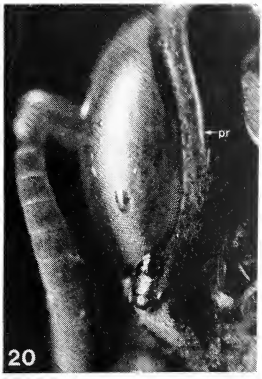
Figs. 20–28. 20. *Paramasaris richardsi,* 17×. Lateral view of head. 21–22. Ventral view of ligula. 21. *P. fuscipennis,* 25×. 22. *Gayella luispenai,* 16×. 23. *G. mutilloides,* 14×. Ventral view of head, mouthparts removed. 24–28. Dorsofrontal view of pronotum. 24. *P. richardsi,* 9×. 25. *P. brasiliensis,* 11×. 26. *P. cupreus,* 13×. 27. *G. eumenoides* ♂, 10×. 28. *G. araucana* ♀, 8×. *ab:* acroglossal buttons; *ap:* anterior pronotal carina; *gl:* glossa; *h:* hypostomal apodeme; *hp:* humeral projection; *pg:* paraglossa; *plp:* posterior lingual plate; *pp:* posterior pronotal carina; *pr:* preoccipital carina.


pr
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gl
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28

nae (Carpenter, 1981, 1988, 1989), thus requiring an inference of loss in Stenogastrinae.

Hind coxal carina. Richards (1962) made contradictory statements concerning the presence of this feature in Gayellini (cf. p. 15 and 44). This was initially followed by Carpenter (1981), but corrected by Carpenter and Cumming (1985:907). All Gayellini lack this carina, a primitive condition.

Claws. Richards (1962:44) erroneously characterized the claws of *Gayella* as simple, and Carpenter (1981:26) initially followed this (corrected in Carpenter and Cumming, 1985:907). In fact, the claws are toothed in all species of Gayellini (variable in *G. mutilloides*). This is the plesiomorphic condition in Vespidae.

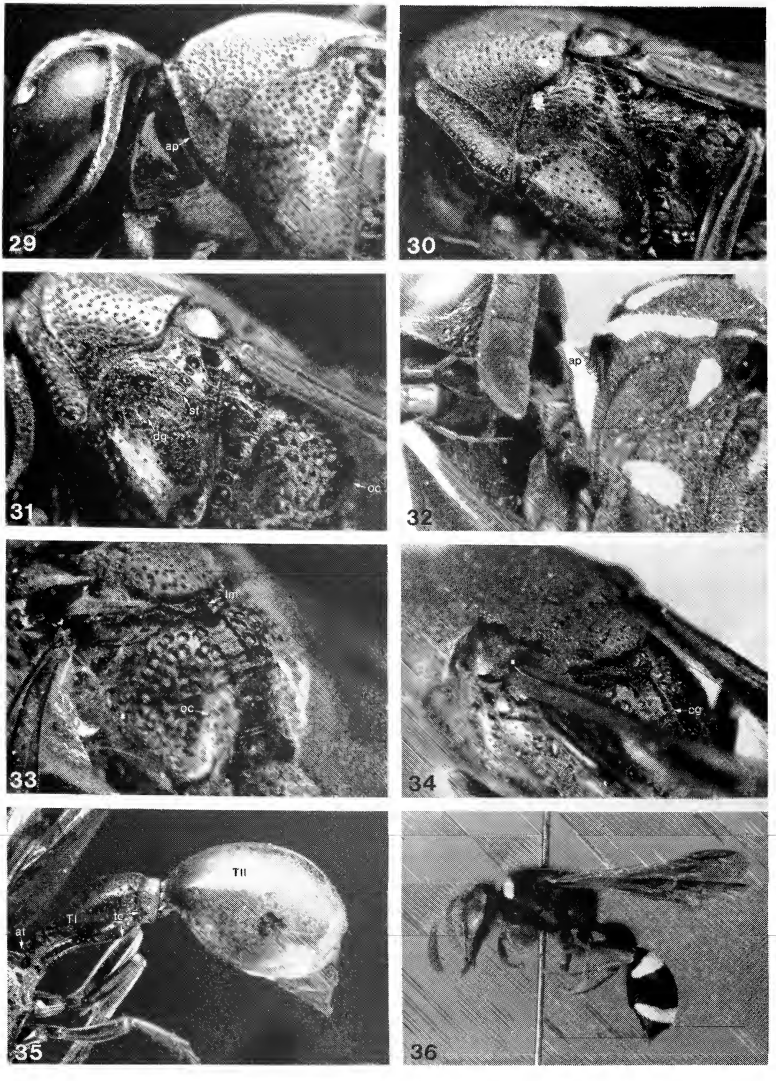
Male genitalia. I have examined the genitalia of all species except *Paramasaris cupreus* and *Paragayella richardsi,* where the males are still unknown. In the groundplan of the tribe, the aedeagus is broadly rounded apically, the digitus is a prominent triangular lobe that is desclerotized ventrally, the cuspis is a small lobe completely fused to the lamina volsellaris, and the parameral spines are long and sharply pointed (Figs. 56–63). Figure 39 of Richards (1962), showing a large, triangular cuspis and rounded digitus in *Gayella araucana,* is incorrectly labelled. What is there termed cuspis is actually the digitus, and the structure labelled as digitus must be the aedeagus (*cf.* Fig. 58). This figure was the reason I previously was unable to characterize the groundplan of the volsella in the tribe (Carpenter, 1981:26), as I had not seen that species at the time. Within genera, the genitalia are relatively uniform, with species differing in details (especially of the volsella); however, there are some consistent differences between the genera. These are discussed below.

Paramasaris

Giordani Soika (1974) characterized *Paragayella* as related to *Gayella,* and stated (my translation): "This genus appears at first sight a *Gayella* by the general aspect and dimensions." The type material I have seen he even labelled as "*Gayella richardsi.*" In fact, *Paragayella* is not really even superficially similar to *Gayella. Paragayella* lacks some of the apomorphies shared by the species of *Paramasaris,* and for some other derived traits which *Paramasaris* and *Paragayella* share the latter has a less developed state. Thus it shares some primitive similarity with *Gayella,* which of course indi-

cates nothing about phylogenetic relationship (Hennig, 1966). On the other hand, *Paragayella* shares several clear synapomorphies with *Paramasaris.* These include the forewing with r–m_3 more or less straight (Figs. 5–6; sinuous in *Gayella* and other Vespidae, Figs. 1, 4), the pronotum with two carinae (Figs. 29–31, 40; one in *Gayella* Fig. 7), the metanotum with a longitudinal median carina (Figs. 33, 46; none in other Masarinae), and the metasoma petiolate (tergum I in dorsal view at least twice as long as wide and half the width of tergum II, Figs. 35, 40–41; it is differently shaped in Euparagiinae, Masarini and *Gayella,* Figs. 1, 43–45). *Paragayella* is the sister-group of *Paramasaris.* Autapomorphies of *Paragayella* include the reduced postocular carina (Fig. 20) and the transversely carinate metanotum (Fig. 46).

The three species of *Paramasaris* share numerous synapomorphies. The postocular and preoccipital carinae are apparently confluent (Fig. 19). These carinae are separated in other Gayellini, and the postocular carina reduced in several species (*Paragayella,* the *Gayella mutilloides* group). The mandibles are tridentate with the proximal teeth separated from the apical one by a gap (Fig. 13). The mandibles are quadridentate in females of *Paragayella* and *Gayella* (Figs. 11, 14–15), and tridentate in males of the latter (Fig. 17; Richards, 1962:44, erroneously characterized the mandibles of *Paramasaris* as quadridentate and those of *Gayella* as simple); there is no gap. Quadridentate mandibles is the groundplan state of most of the Vespidae (Carpenter, 1981), although Euparagiinae has bidentate mandibles. The glossa is shortened and lacks acroglossal buttons, the paraglossae are broadened, and the posterior lingual plate is cordate in shape (Fig. 21). The posterior lingual plate is slightly broadened in other gayellines, but the length of the structure still exceeds its width (Fig. 22). The clypeus is broadly truncate (Fig. 12), which is here treated as derived, convergent with the groundplan of Masarini. *Paragayella* has the clypeus narrowly truncate (Fig. 11), as in Euparagiinae, which is considered the primitive state. A broad truncation seems most simply interpreted as derived from a narrow emargination, as does the pointed clypeus of *Gayella* (Figs. 14–17). The posterior carina of the pronotum extends further dorsad in *Paramasaris* (Figs. 25–26) than *Paragayella* (Fig. 24), a further apomorphic development. The propodeum has oblique carinae more or less developed (Figs. 31, 33), a unique trait in



Figs. 29–36. 29–32. Lateral view of pronotum and mesepisternum. 29. *Paramasaris richardsi,* 13×. 30. *P. brasiliensis,* 14×. 31. *P. fuscipennis,* 17×. 32. *Parischnogaster mellyi,* 16×. 33–34. Oblique lateral view of propodeum. 33. *P. fuscipennis,* 17×. 34. *P. cupreus,* 15×. 35. *P. brasiliensis* holotype, 9×. Lateral view of metasoma. 36. *Gayella reedi* ♂, 3×. Lateral view. *ap:* anterior pronotal carina; *at:* anterior truncation of metasomal tergum I; *cg:* carina delimiting

Masarinae. The first metasomal tergum has a blunt posterior ridge that is continued anterolaterally and drawn out into projections posterolaterally (Figs. 35, 40), a feature unique in Vespidae. The tergum is also strongly truncate anteriorly (Fig. 35). The second tergum has a median longitudinal ridge (Figs. 40, 42), which however is variably developed in *brasiliensis* (strong in the male and not developed in the female, Fig. 35). A longitudinal ridge is found elsewhere in Vespidae only within Eumeninae (*Cyphomenes,* where it is anterior). Finally, the parameral spines of the male genitalia are extremely elongate in *brasiliensis* and *fuscipennis,* being longer than the parameres and extending far beyond the apex of the aedeagus (Fig. 56). This is apparently a derived condition; in *Gayella,* Eupagiinae and Masarini the spines are shorter than the parameres and extend little beyond the aedeagus (Figs. 57–63). Males of *cupreus* are predicted to share this synapomorphy, and possibly also *Paragayella.*

Within *Paramasaris, cupreus* and *fuscipennis* are sister-groups. This is shown by the paraglossae also lacking acroglossal buttons (Fig. 21), the female clypeus with a pair of short apical carinae (Fig. 13), the second carina of the pronotum more complete dorsally (Fig. 26), and the longitudinal carina on tergum II well developed in females (Figs. 40, 42). Autapomorphies of the species are: for *cupreus* the propodeal median groove delimited by more lamellate carinae (Fig. 34); for *fuscipennis* the oblique propodeal carina better defined (Fig. 33), and the dorsal groove and scrobal furrow of the mesepisternum broader and deeper (Fig. 31, *cf.* with 29–30, 40). I have not discovered any autapomorphies of *brasiliensis.*

Since *Paragayella* is the sister-group of *Paramasaris,* recognition of both genera is consistent with monophyly. However, it serves little useful purpose. *Paragayella* itself has few apomorphies—it mostly lacks those of *Paramasaris.* Recognition of *Paragayella* thus contributes little to the process of efficient diagnosis. Since *Paragayella* is monotypic, and *Paramasaris* consists of but three

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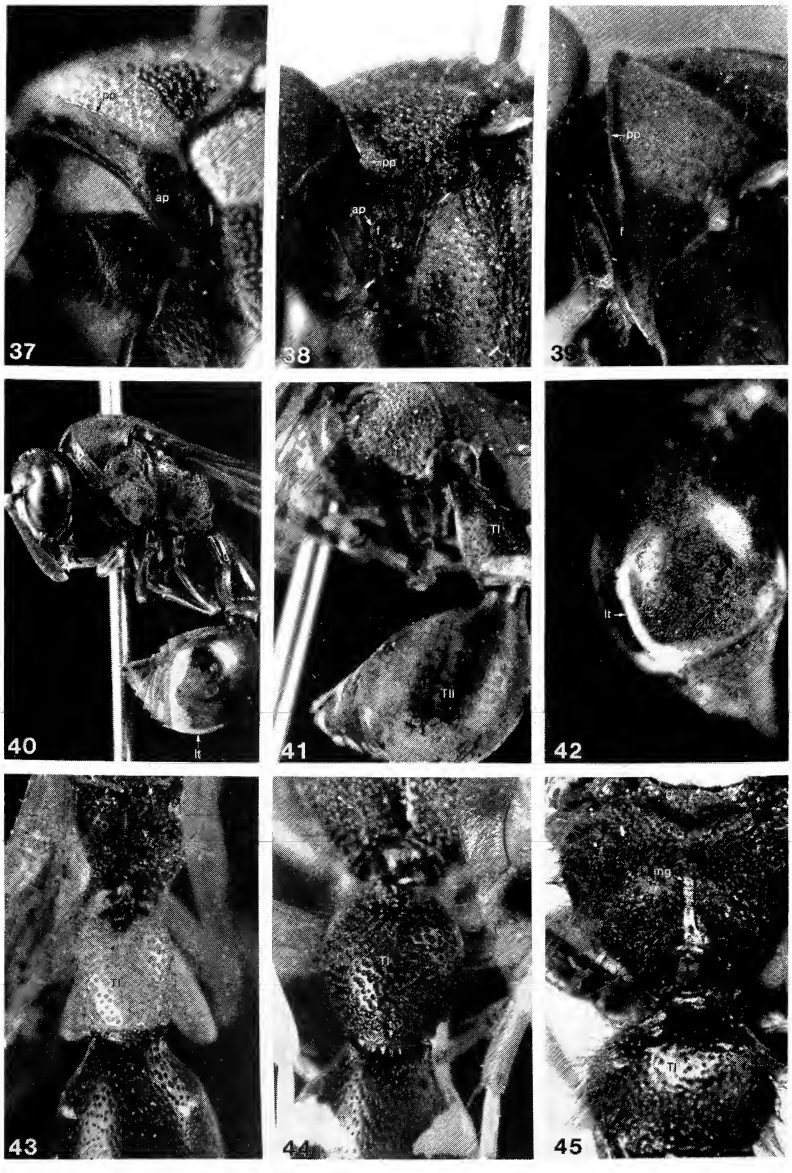
propodeal median groove; *dg:* dorsal groove; *lm:* longitudinal metanotal carina; *oc:* oblique propodeal carinae; *pp:* posterior pronotal carina; *sf:* scrobal furrow; *TI:* metasomal tergum I; *TII:* metasomal tergum II; *tc:* posterolateral tergal projection.



Figs. 37–45. 37–39. Lateral view of pronotum. 37. *Metaparagia doddi* holotype, 13×. 38. *Parachartergus apicaloides,* 13×. 39. *Polistes anduzei,* 10×. 40. *Paramasaris cupreus* 6×. Lateral view. 41. *P. richardsi,* 8×. Oblique dorsal

species, recognition of *Paragayella* is but another example of the current needless fragmentation of vespid generic classification, which I have decried elsewhere (Carpenter and Cumming, 1985; Carpenter, 1987, 1988). A fully sequenced cladistic classification (Wiley, 1979) is possible with a single genus. I am therefore synonymizing *Paragayella* with *Paramasaris.*

Gayella

The monophyly of the genus is shown by the pointed clypeus (Figs. 14–17; not similar to that of Stenogastrinae and Polistinae), the temples projecting somewhat and the emarginate and bispinose last metasomal tergum (Figs. 50–52). In other Masarinae and Euparagiinae the clypeus is truncate or emarginate, the temples do not project and the last visible metasomal tergum is neither emarginate nor spined. Several characters of the male genitalia are also synapomorphies. The digitus is enlarged relative to *Paramasaris* (*cf.* Figs. 56 and 57–63), the cuspis is tuberculate basally (Figs. 57–61, 63), and the paramere has an enlarged lobe (*dorsal* to the spine, Fig. 62). The combination of features of the male genitalia is unique in Vespidae. Finally, the globose shape of the first metasomal tergum may be apomorphic, but this is variable within the genus (Figs. 43–45).

Within the genus, two monophyletic species groups may be recognized, which allows a classification that is phyletically sequenced (Wiley, 1979). These are the *eumenoides* group, for *eumenoides* and *araucana,* and the *mutilloides* group, inlcuding *reedi, patagonica, luispenai* and *mutilloides.*

Eumenoides group

The monophyly of the *eumenoides* group is established by the tegula, which lacks the short posterior lobe found in *Paramasaris* and the *mutilloides* group (*cf.* Figs. 47 and 48). This feature is approached in *reedi* (Fig. 49), diminishing its strength. The projection from the cuspis is tuberculate and apical relative to that

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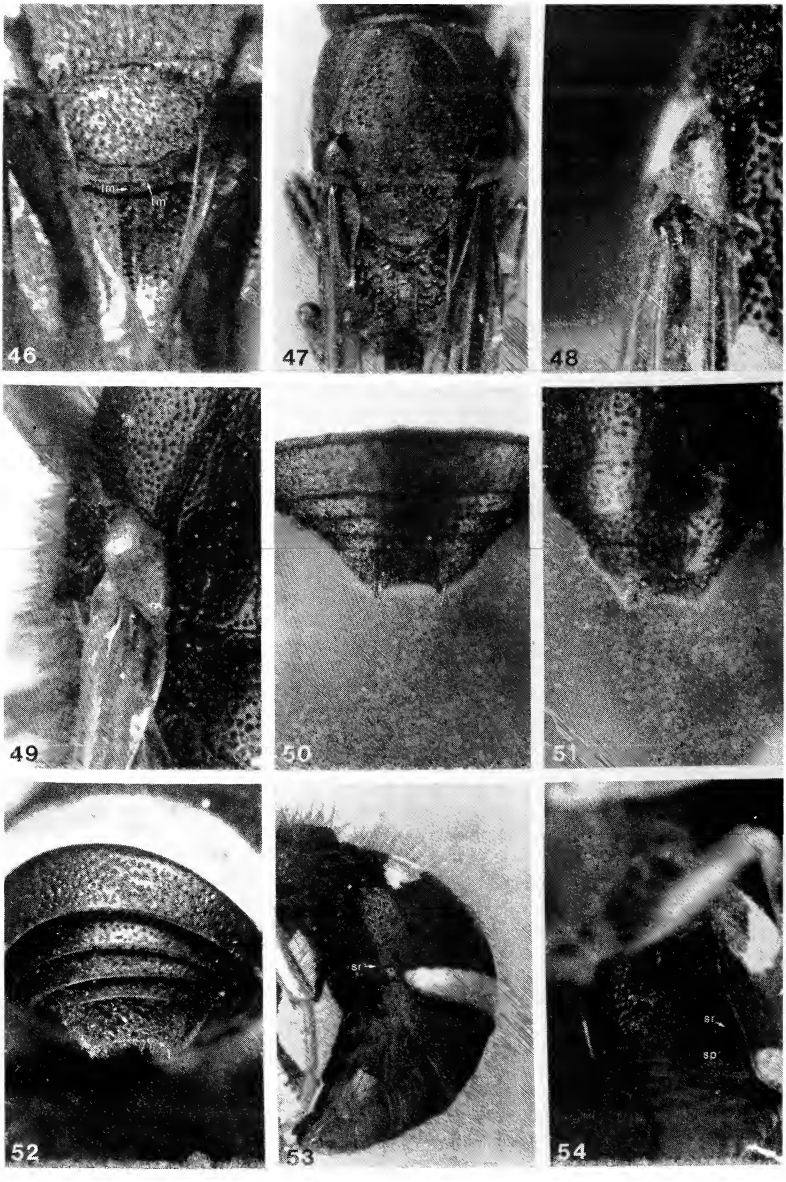
view of metasomal terga I and II. 42. *P. fuscipennis,* 13×. Lateral view of metasomal tergum II. 43–44. Dorsal view of ♂ metasomal tergum I, 10×. 43. *Gayella araucana.* 44. *G. eumenoides.* 45. *G. luispenai* ♀, 10×. Posterodorsal view of propodeum and metasomal tergum I. *ap:* anterior pronotal carina; *f:* pronotal fovea; *lt:* longitudinal carina of metasomal tergum II; *mg:* propodeal median groove; *pp:* posterior pronotal carina; *TI:* metasomal tergum I; *TII:* metasomal tergum II.



Figs. 46–54. 46. *Paramasaris richardsi*, 14×. Dorsal view of scutellum and metanotum. 47. *P. cupreus*, 13×. Dorsal view of mesosoma. 48–49. Tegula. 48. *Gayella araucana*, 21×. 49. *G. reedi*, 15×. 50–52. Dorsal view of ♂ metasomal

in the *mutilloides* group (*cf.* Figs. 57–58 and 59–61, 63), and is here inferred as an elaboration. A sister-group relationship therefore obtains between *eumenoides* and *araucana.* The first has the autapomorphy of the humeri projecting above the anterior pronotal carina (Fig. 27). A very weak angle is also found in *reedi,* and *Paramasaris* has an angle of a different form (Fig. 24), but the projection is much stronger in *eumenoides.* Willink and Ajmat de Toledo (1979: fig. 3) depict *eumenoides* as having an apically bilobed aedeagus; however the shape varies among specimens in my dissections, and most have a broadly rounded apex as in other *Gayella* (Fig. 57). The sister-species of *eumenoides, araucana,* also has some autapomorphies. The acroglossal buttons are very reduced in size in the male, whereas they are elongate in the female and other *Gayella.* The pronotal punctation in *araucana* is relatively coarser than in the rest of the tribe, so this may also be a derived feature. The margins of the pronotum are more or less subparallel in *araucana* and more convex in other *Gayella* (*cf.* Figs. 27 and 28), but the difference from *eumenoides* is slight. The first metasomal tergum is narrower than in other species of the genus (*cf.* Figs. 43 and 44–45), but this is approached in some specimens of *eumenoides.* The male genitalia has the cuspis with the basal tubercle sharply pointed (Fig. 58). The tubercle is usually less pointed in *eumenoides* (Fig. 57), but some specimens approach *araucana.* Willink and Ajmat de Toledo (1979: fig. 5) depict a rather different digitus in *araucana.* However, their figures were evidently drawn from specimens flattened on slides, and do not accurately portray the relative uniformity in this structure (or the aedeagus) among the species (Figs. 57–63).

Mutilloides group

The most obvious feature supporting the monophyly of the *mutilloides* group is the coat of elongate black hairs (Figs. 36, 45, 53). This trait can be an ecological correlate in other vespids, being found for example in species of *Hypodynerus* (Eumeninae) sympatric with *Gayella.* Members of the *mutilloides* group share other

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tergum VII. 50. *G. reedi,* 17×. 51. *G. araucana,* 20×. 52. *G. eumenoides,* 17×. 53. *G. patagonica* ♂, 7×. Lateral view of metasoma. 54. *G. luispenai* ♂, 8×. Oblique ventral view of metasomal sternum II. *lm:* longitudinal metanotal carina; *sp:* sternal ridge projection; *sr:* posterolateral ridge of metasomal sternum II; *tm:* transverse metanotal carina.

derived features, however. The preoccipital carina is evanescent and separated from the postocular carina by more than an ocellar diameter in species of this group, whereas both are well developed and closely approximated in the *eumenoides* group and Euparagiinae. The femur is punctate in the *mutilloides* group; it is smooth in other gayellines. The spines defining the emargination of the last visible metasomal tergum are narrow and elongate in the *mutilloides* group (Fig. 50), whereas they are broader and shorter in the *eumenoides* group (Figs. 51–52). Since both states uniquely characterize monophyletic groups, the polarity cannot be clearly inferred. However, the state of the metasomal spines in the *mutilloides* group is a more extreme development, and is here suggested as relatively apomorphic.

Within the group, *reedi* is the sister-group to the remaining three species. I have not discovered any clear autapomorphies of this species. Synapomorphies uniting *patagonica, mutilloides* and *luispenai* include greater development of the long black hairs on the metasoma (extending over the disc of tergum II, Fig. 53), and an elongate malar space (length 1/2 to greater than the width of the interantennal distance, Fig. 14; shorter than this in other gayellines, Figs. 15–17). The postocular carina tends to be more effaced (as in Fig. 20), but traces appear to be present in some specimens. Metasomal sternum II in the male and to some extent also the female is bordered posterolaterally with blunt ridges (Figs. 53–54), however these are variably developed in *patagonica,* and *reedi* approaches this condition. Among these three species, the features I have polarized are autapomorphies. Hence, the relationships are at present unresolved (Fig. 2). Autapomorphies of the species are: for *mutilloides* the very long malar space (Fig. 14), the acroglossal buttons more elongate and the glossa more deeply bifid than other *Gayella,* and the cuspis tubercle quite blunt (Fig. 61); for *luispenai* the male metasomal sternum II projections elongate (Fig. 54); and for *patagonica* the female propodeal median groove narrowed before broadening dorsally (Fig. 55; smoothly narrowed in other *Gayella,* Fig. 45).

Identification Keys

Genera

1. Pronotum with two transverse carinae (Figs. 29–31); clypeus emarginate to truncate (Figs. 11–13); last tergum neither

emarginate nor bispinose apically ... *Paramasaris* Cameron
- Pronotum with one carina (Fig. 7); clypeus pointed or rounded (Figs. 14–17); last tergum widely emarginate and bispinose apically (Figs. 50–52) ..... *Gayella* Spinola

Paramasaris

1. Pronotum with posterior carina extending no further dorsad than anterior carina (Fig. 24); head with carina not extending from vertex to mandibular base (Fig. 20); propodeum without oblique carinae (Fig. 41) (Brazil) .... *richardsi* (Giordani Soika)
- Pronotum with posterior carina extending much further dorsad than anterior carina (Figs. 25–26); head with carina extending from vertex to mandibular base (Fig. 19); propodeum with oblique carinae (Fig. 33) 2
2. Pronotum with posterior carina incomplete dorsally (Fig. 25); female clypeus without lateral carinae (Fig. 12) (Argentina, Brazil) ..... *brasiliensis* Giordani Soika
- Pronotum with posterior carina continuous dorsally (Fig. 26); female clypeus with lateral carinae (Fig. 13) 3
3. Propodeum with median groove delimited by carinae which are higher than the adjacent areolae (Fig. 34); mesepisternum with dorsal groove narrower, shallow (Fig. 40) (Colombia, Peru) ..... *cupreus* Giordani Soika
- Propodeum with median groove not delimited by carinae which are higher than adjacent areolae (Fig. 33); mesepisternum with dorsal groove broad, deep (Fig. 31); (Colombia to Mexico) ..... *fuscipennis* Cameron

Gayella

1. Thorax and metasoma with short, sparse whitish pubescence (Fig. 1) 2
- Thorax and at least TI, TII basally and sterna with long, thick black hairs (Fig. 36) 3
2. Pronotum rounded laterally (Fig. 28)..... *araucana* Willink
- Pronotum angled laterally (Fig. 27) .... *eumenoides* Spinola
3. Malar space as long as width of interantennal distance (♀, Fig. 14) or longer (♂) ..... *mutilloides* Saussure
- Malar space less than the width of the interantennal distance 4
4. TII with long hairs only anteriorly, posterior terga without long hairs (Fig. 36) ..... *reedi* Willink

– TII with long hairs extending to apex, posterior terga densely haired (Fig. 53) 5

5. Male SII with blunt posterior projections (Fig. 54); female with propodeal median groove narrowing dorsally (fig. 45) ..... *luispenai* Willink & Toledo

– Male SII without projections (Fig. 53); female with propodeal median groove narrowed ventrally before broadening dorsally (Fig. 55) ..... *patagonica* Willink

Taxonomic Notes

Tribe Gayellini Bradley, 1922

Genus *Paramasaris* Cameron, 1901:311. Type species *Paramasaris fuscipennis* Cameron, 1901. Monotypic.

Zethoides Cameron, 1904: 93. Type species *Zethoides flavolineatus* Cameron, 1904. Monotypic. *Non Zethoides* Fox, 1899.

Plesiozethus Cameron, 1905:269. Replacement name for *Zethoides* Cameron.

Metazethoides Schulz, 1906:213. Unnecessary replacement name for *Zethoides* Cameron.

Paragayella Giordani Soika, 1974:87, 89, 99. Type species *Paragayella richardsi* Giordani Soika, 1974. Original designation. NEW SYNONYMY.

Paramasaris richardsi (Giordani Soika), NEW COMBINATION

Paragayella richardsi Giordani Soika, 1974:101, fig. 2, pl. II, ♀ (BMNH)—"Brasile: Mato Grosso, Serra Roncados, R. S. Base Camp."

In his description, Giordani Soika referred to 13 specimens; however I have seen only four specimens in the British Museum. The holotype is on a pin with a paratype, which is not mentioned in the description. The holotype label is above the paratype label, and so the upper specimen is presumably to be treated as the holotype.

In addition to the material in the British Museum, I have seen female specimens from the following localities in Goias in Brazil: "24 kil. E. Formoso, June 6, 1956 (F. S. Truxal)" UCD; "S. Isabel do Morro, Ilha do Bananal, June 1961 (M. Alvarenga)" MCZ.

Paramasaris brasiliensis Giordani Soika

P. brasiliensis Giordani Soika, 1974: 105, ♀♂ (type ♀ MCZ) —"Brasile: Nova Teutonia, Santa Catarina."

Giordani Soika cited the holotype and allotype as deposited in the USNM, but both are in fact in the MCZ, along with the paratype collected on I-1967. I have seen additional specimens, both in the collection of UCD, from "Brazil: Nova Teutonia, Santa Catarina, I 1965 (F. Plaumann)"; and "Argentina: Haut Parana, Thu-Cuare prés San Ignacio, 1911 (E. R. Wagner)".

Paramasaris cupreus Giordani Soika

P. cupreus Giordani Soika, 1974: 106, ♀ (BMNH)—"Columbia: Caqueta, Florencia, 480 m."

Besides the holotype one of the paratypes mentioned by Giordani Soika is in the British Museum. New localities in Colombia include: "Putumayo, Mocoa, 30.X.1974 (M. Cooper)" now in the MCZ; "Dept. Magdalena, Socorpa Mission, Sierra de Perija, VIII.5-25.1968 (Borys Malkin)" 3 ♀ AMNH and MCZ. One of the Magdalena specimens is labelled "1500m." The specimen from Mocoa has a label reading "collecting mud in forest." I have also seen a specimen from "Peru: Loreto, Pucallpa 10.iv.1965 (J. M. Schunke)" BMNH.

Giordani Soika (1974) alluded to various differences in sculpture between *cupreus* and *fuscipennis* in his description, but several of these do not hold up in the additional material I have seen. The pronotal carina and tergal punctation are similar in most specimens, and the clypeus is not more narrowly emarginate in *cupreus*. The finer and sparser punctation on the dorsum of the mesosoma in *cupreus* is usually consistent, particularly the pronotum, but one of the Magdalena specimens has the punctures on the scutum and scutellum about as in *fuscipennis*.

Paramasaris fuscipennis Cameron

P. fuscipennis Cameron, 1901: 312, ♀ (BMNH)—"Santa Fé Mountains, New Mexico."

Zethoides flavolineatus Cameron, 1904: 94, ♂ (BMNH)—"Panama (Pacific side)."

The statement of the type locality as being in New Mexico is perhaps an error. As Bradley (1922:387) put it: "I have not been able to learn of any mountains bearing this name." There is a Santa Fé mountain in Jalisco in Mexico (20°30'N, 103°02'W), and this species has been later collected in other parts of Mexico, but never in the United States. Krombein (1979) did not include this species in the revised Catalog of Hymenoptera north of Mexico. Besides the types, I have seen specimens from Guatemala: S. Geronimo (Champion) (BMNH and one now in MCZ); "Mexico: Jalisco, Chamela, IX-26-1985, ex. *Nissolia* (R. J. McGinley)" USNM; "Sinaloa, 5 mi. NW Choix, VIII-27 and 31, and IX-5-1968 (T. A. Sears, R. C. Gardner & C. S. Glaser)" UCD and MCZ. It has also been recorded from Colombia: Bogotà by Zavattari (1912; confirmed by Giordani Soika, 1974).

Genus *Gayella* Spinola, 1851: 328. Type species *Gayella eumenoides* Spinola, 1851. Monotypic.

Eumenoides group

Gayella eumenoides Spinola

G. eumenoides Spinola, 1851:333, pl. II, fig. 2, ♂♀ (lectotype ♂ MNHN, designated by Giordani Soika, 1974:98)—Chile, "provincias del norte y sobretodo en Santa Rosa."

G. sicheliana Schulthess, 1910: 189. As a synonym of *eumenoides,* attributed to Saussure.

Common in central Chile, this species has also been recorded from Argentina: Mendoza by Brèthes (1903) and following him various authors; however, Willink (1956) considered this record dubious. I have seen specimens from Aconcagua, Atacama, Coquimbo, Curicó, Maule, O'Higgins, Santiago and Valparaíso.

Bequaert and Ruiz (1942) summarized early literature on this species. Reed (1893) pointed out that Spinola had confused the sexes in the original description, and Willink (1956) observed that Spinola and Saussure confused *eumenoides* and *araucana.* This is the only gayelline for which any behavioral information has been published, by Claude-Joseph (1930). It provisions clusters of free mud cells with nectar.

Gayella araucana Willink

G. araucana Willink, 1956:341, 342, 346, figs. 3, 4, ♀♂ (type ♀ IPC)—"Chile, Prov. Santiago: Renca."

I have seen specimens from Aconcagua, Atacama, Coquimbo, O'Higgins, Santiago (including paratypes from BMNH and IML) and Talca. Willink and Ajmat de Toledo (1979) recorded this species from Bío-Bío.

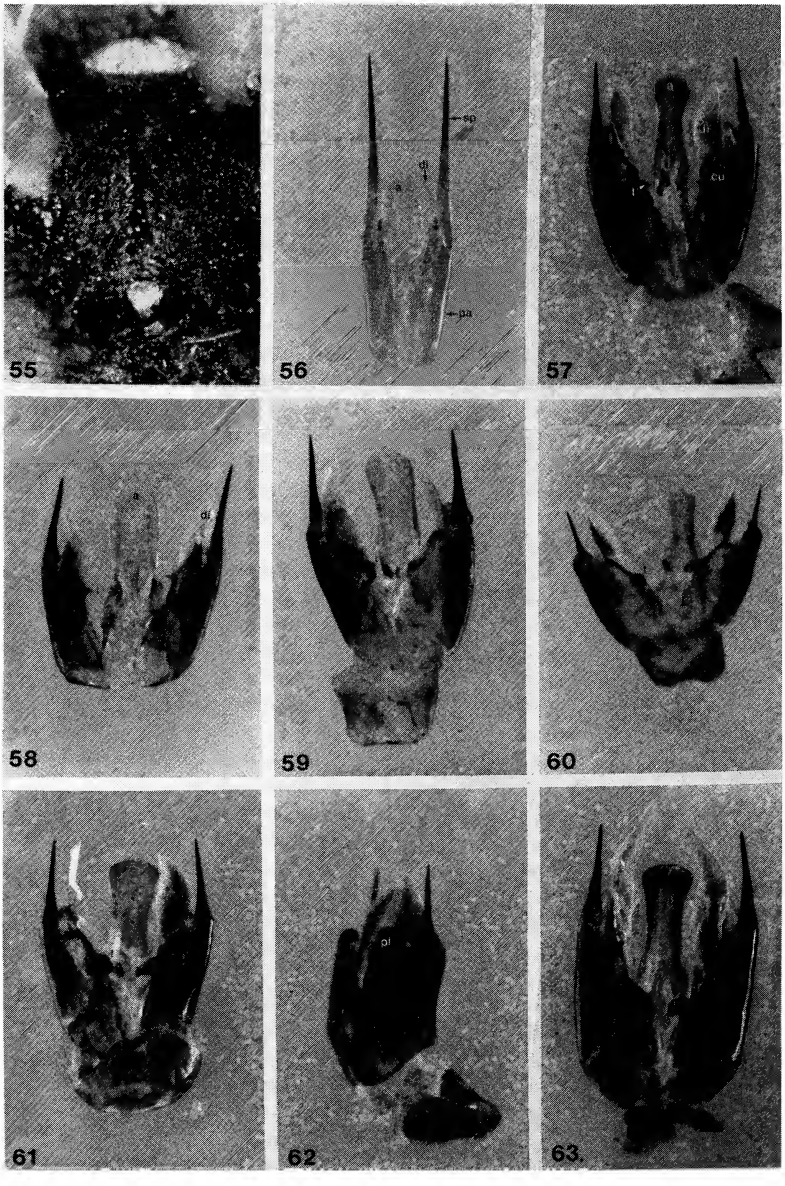
Willink and Ajmat de Toledo (1979) recognized the same species groups as the present paper, but stated that *araucana* is the most distinct and should possibly be treated as a different genus. They even stated that morphologically it approaches eumenines of the genera *Ancistrocerus* and *Stenodynerus,* but it does not possess any of the synapomorphies of that subfamily (Carpenter, 1981). The characters cited as distinguishing *araucana* are only trivially different from other *Gayella.* These characters comprise the mesosoma with lateral margins subparallel, the malar space nearly obliterated, the form of the emargination of male metasomal tergum VII and the form of the male genitalia. The condition of the malar space is primitive, and similar to *eumenoides* (*cf.* Figs. 15 and 16); the emargination of male tergum VII is little different from that of *eumenoides* (*cf.* Figs. 51 and 52). As noted above, their figures of the male genitalia are misleading; *araucana* is no more different in the digitus or aedeagus than the other species are from each other (Figs. 57–61, 63). The cuspis is autapomorphic in having a sharp tubercle, but this again is not properly illustrated in the other species, all of which have some projection. The subparallel mesosoma is also autapomorphic, but this is a minor difference compared to the outstanding similarities shared by all species of *Gayella.* Placement of *araucana* in a separate genus would render *Gayella* paraphyletic, which is reason enough to reject doing so.

Mutilloides group

Gayella reedi Willink

G. reedi Willink, 1963:385, 1 fig., ♀ (CAS)—"Casa Blanca, Valparaíso, Chile."

I have seen material from Atacama, Coquimbo (including a USNM paratype) and Valparaíso (including CAS and IML paratypes). The male has not previously been described. One specimen labelled "Chile, Coquimbo: Llano de la Higuera, N. of La Serena, Sept. 29, 1980 Luis E. Peña" AMNH, and two from "Chile: Atacama 20 km. E on Ruta 31 nr. Puquios, 9-X-1984 (C. Porter & T. O'Neill)" CP and MCZ, evidently belong to this species. The pilosity is the same as in the female (Fig. 36). The color markings are also



Figs. 55–63. 55. *Gayella patagonica* ♀, 11×. Posterodorsal view of propodeum. 56–63. Male genitalia. 56–61. Ventral view. 56. *Paramasaris fuscipennis,* 26×. 57. *G. eumenoides,* 17×. 58. *G. araucana,* 21×. 59. *G. reedi,* 18×. 60. *G. pata-*

identical, except that the clypeus is whitish (Fig. 17); the scutellum is completely black (often with some white in females). The clypeus is longer than wide and weakly pointed, the mandibles are tridentate, the postocular carina is very short, the malar space is about 1/2 the width of the interantennal distance, the pronotum projects very slightly, the first metasomal tergum is about 1 1/3 as long as wide, and sternum II has traces of posterolateral ridges. The genitalia are illustrated in Fig. 59.

Gayella mutilloides Saussure

G. mutilloides Saussure, 1855: 114, ♀ (BMNH)—"Le Chili."
G. odyneroides Schulthess, 1910: 189. *Lapsus* for *mutilloides.*
G. mutilloides nigerrima Giordani Soika, 1960 (1958): 80, ♀ (Giordani Soika coll.)—"Cile."

The synonymy was established by Bequaert and Ruiz (1942) and Willink (1963). Willink (1956) described the male, and recorded the species from Argentina: Chubut and Neuquén. In addition to the holotype of *mutilloides,* I have seen material from Chile: Ñuble, ?Valdivia (CAS), and "El Manzano" (MCZ); and Argentina: Rio Negro. It has also been recorded from Aconcagua and Malleco by Willink and Ajmat de Toledo (1979).

Gayella patagonica Willink

G. patagonica Willink, 1956:341, 342, 350, figs. 9, 10, 11, ♀♂ (type ♀ IML)—"Esquel, Chubut, Argentina."
G. cerceroides Giordani Soika, 1960 (1958):82, ♀ (BMNH)—"N. W. Patagonia, 1000–3000 piedi."

The synonymy was established by Willink (1963), who also recorded this species from Chile: Lo Valdés, Cordillera de Santiago 2500 m (stated to be in the MCZ but not there; Willink and Ajmat de Toledo, 1979, cite what is evidently this specimen as in IML). In addition to the holotype of *cerceroides,* I have seen specimens from Argentina: Chubut (including a paratype from MF) and Rio Negro,

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gonica, 11×. 61. *G. mutilloides,* 13×. 62. *G. mutilloides,* 13×. Lateral view. 63. *G. luispenai,* 15×. Ventral view. *a:* aedeagus; *di:* digitus; *cu:* cuspis; *ng:* narrowing of propodeal median groove; *pa:* paramere; *pl:* dorsal parameral lobe; *sp:* parameral spine; *t:* tubercle of cuspis.

as well as the BMNH paratypes from "N. W. Patagonia." Willink and Ajmat de Toledo (1979) also mention a Mendoza record.

Gayella luispenai Willink and Ajmat de Toledo

G. luispenai Willink and Ajmat de Toledo, 1979: 427, 428, 429, figs. 1, 6, 7, ♂♀ (type ♂ IML)—"Riconada, Jujuy, Argentina."

I have seen two specimens, a male from Jujuy, Est. Iturbe 17-I-1979 (L. Fidalgo) and a female from Mendoza, Uspallata 5.XII.1979 (A. Roig). This species was also recorded from Bolivia: Potosí by Willink and Ajmat de Toledo (1979).

This species is very similar to *patagonica,* as noted by Willink and Ajmat de Toledo (1979:430). Most of the characters they cite will not distinguish females. The series of *patagonica* I have seen from Rio Negro (MF) overlaps in size, length of the malar space and development of protuberances on female metasomal sternum II. The punctation tends to be less coarse on the scutellum of *patagonica,* but this varies among the specimens. The propodeal median groove will separate them (Figs. 45, 55), but as I have seen only one female of *luispenai,* I cannot be certain that this feature does not vary. Males are readily distinguished by the sternal projections in *luispenai* (Fig. 54).

Biogeography

It is clear from the few records for some species that their distributions are very poorly known, and further collecting, particularly of *Paramasaris,* will doubtless extend the ranges of some of these. Nevertheless, a few remarks about biogeography may be made. *Paramasaris* and *Gayella* occupy completely different regions, Tropical American *versus* Patagonia, which corresponds to a well-known vicariant break. Within *Gayella,* most of the species overlap broadly in distribution. The clade *mutilloides* + *patagonica* + *luispenai* is the only group which occurs on the eastern side of the Cordillera, but the first two species are also found in Chile. By contrast, *Paramasaris* shows a pattern of endemism. Within the genus, the distribution of the sister-species *fuscipennis* and *cupreus* is basically trans-Andean: Central America *versus* western Amazonia. There is a record of *cupreus* from the *western* side of the Sierra de Perijá, but this was elevated in the late Oligocene (Kellogg, 1984). In turn, the sister-group of this clade, *brasiliensis,* is southeastern Brazil, and the sister-group of all three species, *richardsi,* is southern Amazon

basin. This pattern does not correspond to that shown by the avifauna, for example Cracraft and Prum (1988), where southeastern Brazil is not closely related to a western Amazon/trans-Andean clade. However, that study showed southeastern Brazil as a composite area, implying either dispersal or differing ages for components of the regional biota. The latter factor may well explain the incongruence; Gayellini is an ancient group, since the Masarinae as a whole is gondwanian (Carpenter, 1981).

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Summary

The phylogenetic relationships of the gayelline wasps are investigated using cladistic methods. *Paragayella* is the sister-group of *Paramasaris,* and is synonymized with that genus. This taxon is the sister-group of *Gayella.* Cladograms are presented for the species in each genus, along with keys and distributional notes.

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NOTES ON THE BEHAVIOR OF *THALASSIUS SPINOSISSIMUS* (ARACHNIDA: ARANEAE: PISAURIDAE)

By Petra Sierwald

Delaware Museum of Natural History, Wilmington, DE 19807

Introduction

The present paper reports predatory, copulatory and parental behavior as observed in *Thalassius spinosissimus* (Karsch, 1879) in its natural habitat and in the laboratory. Spiders of this species have been reported to hunt on the surface of freshwater and to catch fish (Abraham 1923, Lawrence 1970). *Thalassius spinosissimus* is the most widespread and commonly collected species in the genus. It is distributed over Africa south of the Sahara.

Observations

Habitat

Thalassius spinosissimus inhabits banks with lush vegetation close to freshwater. A population of a small freshwater pond in an indigenous forest five miles north of Pietermaritzburg (Natal, South Africa) was observed for one year (1980). The abundance of *T. spinosissimus* was high (2.8–6.4 spiders per m^2 in the study area; recorded at 20 visits at the study side during the summer season). The distances between individuals hunting on the water surface varied between 5 and 20 cm (distances were measured between the tips of extended legs of individuals; recorded 11 times).

Life cycle

At the study site, *T. spinosissiumus* overwintered from May to September; specimens were found immobile hiding under rocks and logs near the pond. The active season is the summer between October and May. Adults were found during November through March; in April and May only juveniles were observed.

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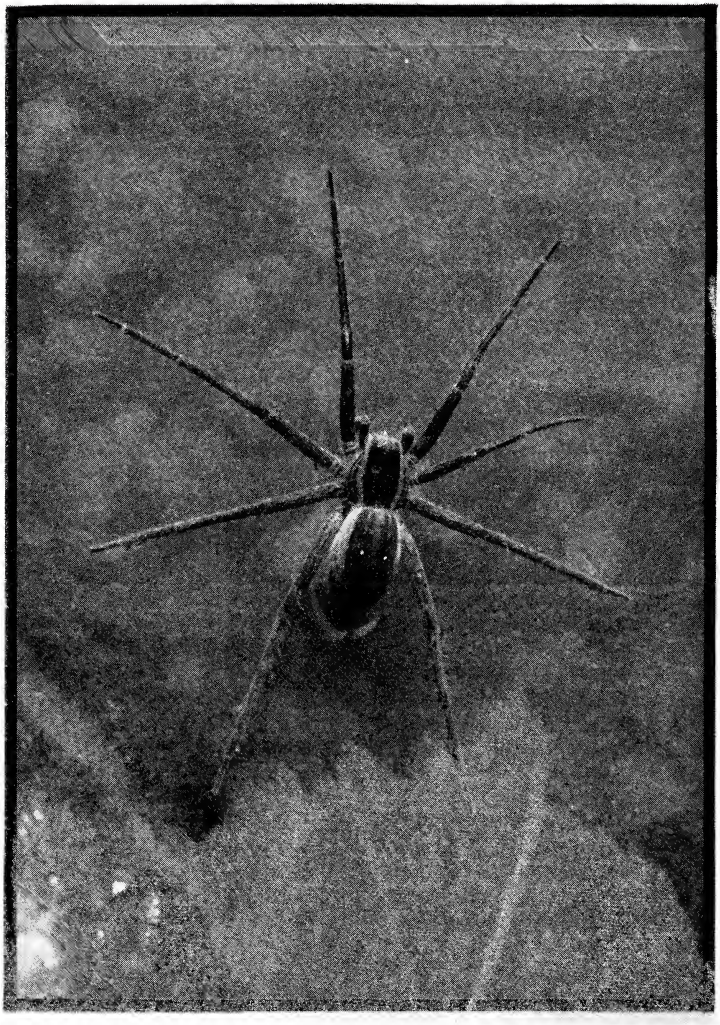

Fig. 1. Hunting position of *Thalassius spinosissimus*.

Daily activity pattern

During the summer season, spiders of all instars spend apparently most of the day on the water surface, unless hindered by heavy rain and storm (observations at study site between 9 am and 11 pm). Spiders kept in aquaria under a tent, exposed to daily temperature fluctuations demonstrated similar activity patterns. They were found in the hunting position nearly 24 hours a day and accepted prey at any hour (fed with tadpoles of *Bufo rangeri* and fruit flies).

Hunting position

In the hunting position, the spider anchors itself by one or two hind legs to a stone, log or vegetation. The other legs are extended, with metatarsi and tarsi touching the water surface (Fig. 1). During observation periods of up to two hours at the study site, the observed spiders did not change their location significantly unless they attacked prey or were disturbed. Single legs were frequently groomed with the chelicerae.

Animals "resting" on the vegetation near the water often moved to the surface and assumed the hunting position in response to minor disturbances, a behavior observed frequently both in the habitat and in the laboratory, presumably serving camouflage. The white lateral stripes of the body blend well with the vegetation, disrupting the visual body profile.

Diving

If disturbed by touch or strong, close movement, *T. spinosissimus* submerges by climbing along the substrate. They are not able to break freely through the water tension nor can they swim under water. The spiders remained submerged for an average of five to ten minutes, although longer periods of up to 35 minutes were recorded.

Prey capture

T. spinosissimus hunts for appropriately sized prey (insects, crustaceans, fish, tadpoles, and toads) exclusively on the water surface. In the laboratory and in the field, prey was put on the water surface in different distances and positions from the spider. To capture mobile prey, e.g., swimming water insects or tadpoles, the spiders waited until the prey had come close enough to be grasped with the front legs. A few spiders continuously orientated the spread front legs towards the moving prey.

Prey struggling on the water surface such as terrestrial insects

which have fallen on the water surface elicited a different prey catching behavior. Capture attempts were made after reorientation of the spread front legs towards the source of waves and motionless periods of varying length. The spiders responded to close stimuli (within 6 cm) by jumping on the prey. More distant prey (6–25 cm away) was reached by "rowing": the front legs remain spread out on the water surface at a fixed angle, while legs II and III perform rowing motions, pushing the spider forward. The IV pair remains extended on the water.

Since the spiders did catch ants (but dropped them quickly) and hunted regularly at night, chemical and visual stimuli are probably not involved in prey detection.

T. spinosissimus chewed its prey with the chelicerae, turning it with the aid of its pedipalps. While feeding, the spiders frequently discharged clear drops of liquid from their anus.

Mating behavior (twelve matings observed)

Two to four weeks following the final molt, the females stopped hunting and spun a loosely woven three-dimensional mesh (mating-web). While resting in the web, the females hung upside down and assumed a distinct posture: all femora were held upright, the patellae nearly touching each other above the prosoma; tibiae and metatarsi were bent downwards.

Males did not hunt after the final molt but built small triangular sperm webs during the night. Charging of the palps was not observed. Males responded to threads from mating-webs placed in their aquaria with courtship behavior by touching and hitting the threads with their front legs. Threads of subadult females did not elicit courtship behavior.

Males reaching a mating-web initiated courtship by pulling at the threads with their pedipalps and beating them with their front legs. Intense trembling of the male opisthosoma was observed. The female's response consisted of pulling at the threads with her palps and front legs and enforcing her "resting" posture. Once the female responded, the male entered her web and continued his courtship. After each female response, the male moved closer to the female until he reached her. Courtship lasted 3 to 75 minutes.

The male touched the female's prosoma first with his front legs, then beat rapidly at the female's opisthosoma. The male climbed onto the female from the side and positioned his prosoma over her

opisthosoma. The male then spun broad threads around the female's patellae (Fig. 2). To insert the embolus, the male reached under the female's opisthosoma with the right or left palp along the female's right or left side, respectively (Fig. 3).

The males expanded the bulb in front of the epigynum (Fig. 4); insertions lasted five to twenty seconds for each bulb. In ten out of twelve copulations both bulbs were used alternately, three to five insertions occured during copulations. After copulation, the male left the fastened, inactive female. Females began to remove the threads around the patellae two to seven minutes after copulation.

Males and females of *spinosissimus* were able to mate more than once either with the same or with other mates (three males and two females were used twice for matings).

Parental care

Egg laying and cocoon building were not observed. The cocoons are round and whitish and carried by the female in the chelicerae under the prosoma. Between 150 and 200 spiderlings hatched after 19–21 days (at 20° to 25° C) from each of 7 cocoons observed in the laboratory. Shortly before hatching, the females spun an irregular nursery-web and fastened the cocoon in its center. The spiderlings remained in the nursery-web for up to six days; they tended to stay in a central cluster, spinning additional threads. The females remained almost inactive at the edge of the web (Fig. 5). Without molting, the spiderlings began to disperse and moved to the upper corners of the laboratory windows.

Discussion

The copulatory position of *T. spinosissimus* agrees with that of other hunting spiders (Gerhardt & Kästner 1937/38: 547; type three in Foelix 1982: 194). The same position is described for *Dolomedes fimbriatus* (Clerck, 1758) by Gerhardt (1926: 7). Spinning threads around the females legs by the males prior to copulation has been observed in *Pisaurina mira* (Bruce & Carico 1986).

The parental care as displayed by *T. spinosissimus* occurs in other Pisauridae as well: *Pisaura* and *Dolomedes* (Gerhardt & Kästner 1937), *Afropisauria* (Blandin 1979: 82), *Pisaurina* (Carico 1972: 303), *Tinus* (Carico 1976: 301), *Megadolomedes* (Davies & Raven 1980: 139) and *Architis* (Nentwig 1985: 301). The results obtained

Fig. 2. Copulation of *T. spinosissimus*. Male spins threads (arrow) around female's legs.

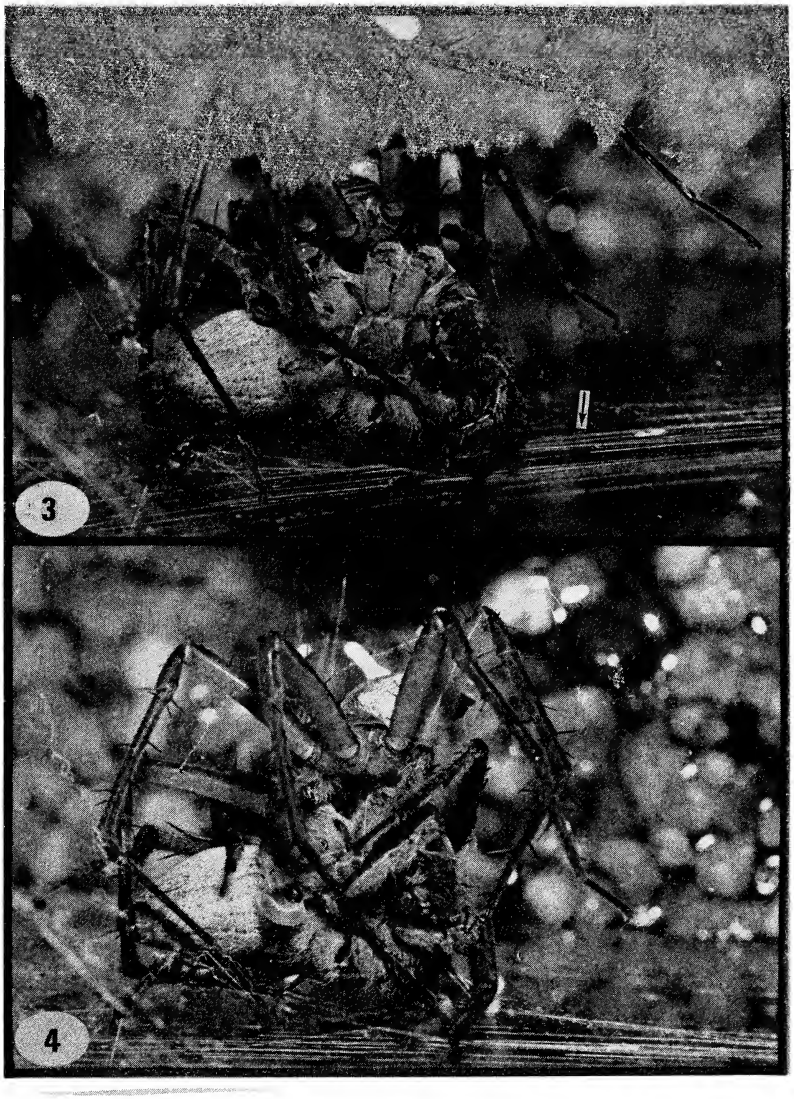

Fig. 3–4. Copulation of *T. spinosissimus.* (3) Male positions his palp in front of the female epigynum. Arrow indicates threads of the mating-web. (4) Expansion of the male bulb in front the epigynum. Body length of spiders approximately 15 mm.

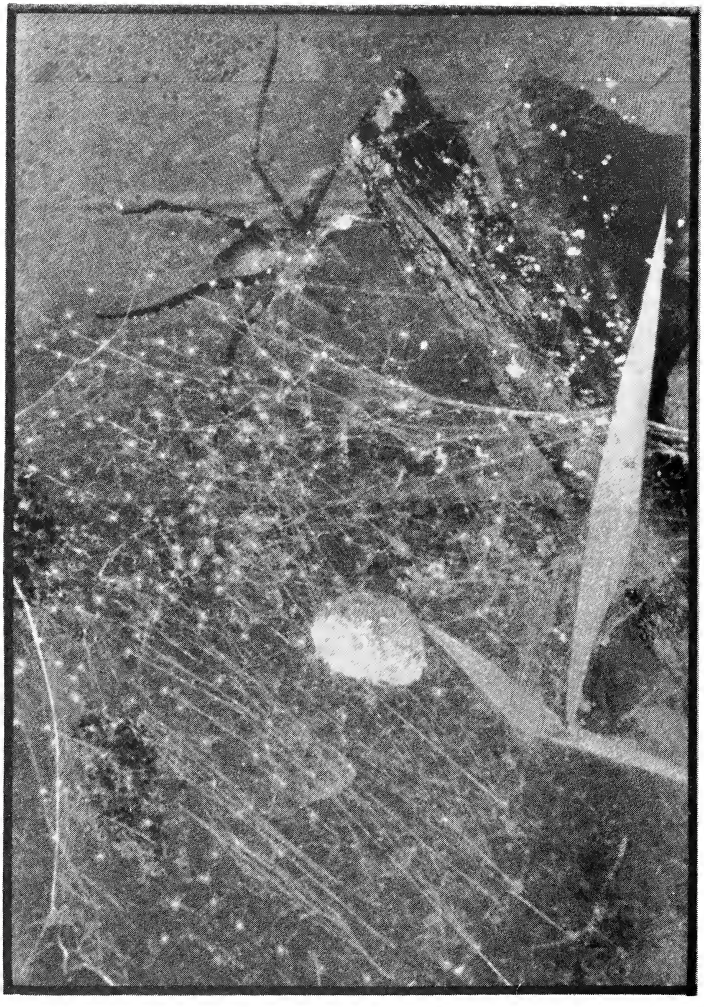

Fig. 5. Female *T. spinosissimus* with nursery-web.

from the present study indicate that *Thalassius* is related to *Dolomedes, Pisaura* and *Pisaurina.* Lehtinen's placement (1967) of *Thalassius* in the Ctenidae appears to be unjustified (see Sierwald 1987).

The prey catching behavior of *T. spinosissimus* is similar to that of some species of *Dolomedes* which hunt on the water surface as well (*Dolomedes triton:* Bleckmann 1982, Bleckmann & Barth 1984, Bleckmann & Rovner 1984; *D. aquaticus* and other New Zealand species: Williams 1979). Rowing movements over the water surface have been described in *D. fimbriatus* by Ehlers (1939: 485); diving behavior is known from *Dolomedes* species as well (McAlister 1959: 109).

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CHALEPOXENUS BRUNNEUS, A WORKERLESS "DEGENERATE SLAVE-MAKER" ANT (HYMENOPTERA, FORMICIDAE)

By Alfred Buschinger[1], Henri Cagniant[2], Werner Ehrhardt[1], and Jürgen Heinze[1]

Chalepoxenus is a genus of parasitic ants with several closely related species mainly occurring around the Mediterranean (Buschinger et al., 1988). *C. kutteri* and *C. muellerianus* as well as *C. insubricus* and *C. siciliensis* (the latter two presumably synonymous to *C.m.*) are actively dulotic species having a considerable worker-force and enslaving several *Leptothorax* species (Ehrhardt 1982, 1987). Their sexuals engage in essentially normal mating flights, and new colonies are founded through single queens who penetrate a host nest, kill all adults by stinging them, or drive them off, and take over the broods from which the first slaves emerge.

Little has been known on the life history of *C. brunneus,* however. The species was described (Cagniant 1985) after a number of males and females which emerged in laboratory culture from a colony of *Leptothorax* cf. *marocanus* Santschi. This colony had been collected near the pass road to Tizi-n'-Test, 2000 m, in the Great Atlas of Morocco.

During a second visit to the type locality by A.B., H.C., J.H. and X. Espadaler on 6 May 1987, a total of 11 colonies with queens and/or sexual pupae of *C. brunneus* was collected. Subsequent laboratory observations revealed that this species is in fact workerless, and that the young queens are accepted by most of the adult host colony workers. Apparently *C. brunneus* has reached the stage of a "degenerate slavemaker", convergently to some species of the genus *Epimyrma* (Buschinger, in press).

Materials and Methods

The colonies of *C. brunneus* and its host species were found beneath flat rocks in the soil and debris. The fairly complete societies were aspirated into vials, and carried back to Germany in PVC

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tube-nests as described by Buschinger and Heinze (in press). In the lab, the colonies were kept in formicaries according to Buschinger (1974), and fed three times a week with diluted honey and insect pieces (*Tenebrio molitor* pupae, cockroaches). Artificial daily and annual temperature cycles were applied in analogy to that which had proved to be effective in rearing other leptothoracines from high elevations in the Alps.

Thus, "summer" conditions with 10h/17°C and 14h/28°C daily (dim light during the warm hours) were provided from the arrival in the lab on 28 May 1987 for 6 weeks, until most sexuals had left the nests for mating, and pupation had ceased. "Fall" conditions were simulated with 12h/15°C and 12h/25°C for another 6 weeks, followed by 12h/10°C and 12h/20°C for 3 weeks until the larger larvae had somewhat shrivelled. The colonies then were placed in hibernation conditions at a constant 10°C for five months. After 2 weeks at 10/20°C and 6 weeks at 15/25°C the first new prepupae appeared in the nests, and in 17/28°C a week later sexual pupae were observed. The whole "annual cycle" thus was shortened to about 10 months. No different temperature regimes were tested, but might as well be suitable.

Sexual behavior was observed either spontaneously in the formicaries, or sexuals who had left the nest chambers and were crawling and fluttering around were placed into a transparent flight-cage (15 × 20 × 30 cm) exposed to natural or artificial light. Females were dissected for control of insemination as was described by Buschinger and Alloway (1978). For colony foundation experiments single newly inseminated females, or dealate ones found in the formicaries, were placed into a formicary containing a queenright or queenless host-species colony.

Results

Sexual behavior:

As in most leptothoracine ants the young sexuals of *C. brunneus,* when ready to mate, leave the nest and, in our formicaries, crawl or flutter around. When transferred into the flight-cage, they move towards the light and assemble in a loose "swarm" like sexuals of other *Chalepoxenus* species. The *C.b.* sexuals, however, are generally quite sluggish with respect to flying.

Mating was directly observed four times in a flight-cage, on 11, 12 and 15 June, 1987, hence about 2 weeks after the sexuals had hatched. The colonies were kept in a daily temperature rhythm of 17/28°C with the temperature increase at 3 a.m. Sexual behavior was observed at 3 to 6 p.m., thus about 12 to 15 hours after the morning rise in temperature.

The females did not exhibit any conspicuous behavior indicating a sexual calling or other stimulating actions. Males often made mating attempts already in the chambers of the formicaries, and one copulation was also seen there. Dealate females found in the formicaries often proved inseminated when dissected. In one colony 11 out of 12 dealate females were inseminated, only one had an empty receptacle. Such females, thus, could be used for colony foundation experiments.

A sexual pheromone is present in the poison glands of *C. muellerianus* and *C. kutteri.* Pieces of filter paper soaked with the content of such a gland attract males and stimulate homosexual mounting attempts. The secretion is interspecifically active, and even cross-breeding of *C.m.* and *C.k.* was possible (Ehrhardt 1987). In order to check for a sexual pheromone in the poison glands of *C. brunneus* a few preliminary experiments were made. However, their number was restricted due to the small number of sexuals available, and the somewhat unexpected results certainly would deserve confirmation with more material.

In repeated experiments the *C. brunneus* males failed to show any reaction to the poison gland content of their own females, and *C. muellerianus* males also were not stimulated by *C.b.* glandular secretion. Immediately after the test the same *C.m.* males showed the usual reaction to the sexual pheromone of conspecific females. When *C. muellerianus* poison gland secretion was presented to *C. brunneus* males, however, they were also attracted and stimulated and eventually engaged in homosexual contacts. Thus, *C. brunneus* has perhaps lost the ability to produce (much of) a sexual pheromone, but the males have retained the capability to perceive the (similar or identical) pheromone of congeneric females.

Colony foundation:

When collected in the field, six out of 12 colonies (including the first one of Cagniant, 1985) contained one *C. brunneus* queen each,

in one colony we found two queens, and five colonies were queenless. The latter were orphaned already in the field, or we had lost the queens during collecting. None of the 12 colonies contained a host-species queen, but most had a *C. brunneus* brood, the small pupae being easily identifiable. A variable number of about 15 to 80 *L. marocanus* workers was present.

These field records suggest that the host species queens might be eliminated by the *C. brunneus* queens, as in the related dulotic *Chalepoxenus* species. With a total of 24 dealate *C.b.* females, colony foundation experiments were set up, using 6 queenright and 4 queenless *L. marocanus* colonies (Tab. I). Since many *C.b.* females died soon or were killed by the host-colony workers, up to four *C.b.* females were introduced subsequently into one nest. In a few instances (col. no. 5 and 8) where the *C.b.* females died during or after their first hibernation, newly reared females were introduced in the following "summer". Out of 20 females which died during the experiments, nine could be dissected; 6 of them were inseminated and 3 were not. Thus, lack of insemination cannot explain the failure of so many females.

In the four queenless host-colonies a total of 9 *C.b.* females were introduced. Only one (col. no. 1) was successful in that male and female offspring were reared in the year after the colony foundation. In another colony (no. 4) only one *C.b.* male was produced.

Fifteen *C.b.* females were placed into the six queenright host colonies. In two colonies both male and female offspring were reared; in two others only one and seven males, respectively, were reared.

Most interesting is the behavior of the *C.b.* females toward the host colony queens. Unfortunately, the results are somewhat ambiguous. Clearly, in colonies no. 6 and 9, the *C.b.* females killed the host colony queens. In col. 6 this happened 27 days after the *C.b.* female had been introduced into the nest. The *L.m.* queen was presumably stung; she was paralyzed, lying on her side or back, and a week later she was dead and carried out of the nest. Nevertheless, the *C.b.* female in this nest did not reproduce. In col. 9 a total of three *C.b.* females were killed first by the host workers (two were not inseminated, the third one could not be dissected), until the fourth *C.b.* female finally succeeded in paralyzing the *L.m.* queen, 9 days after the introduction. During this time the *C.b.* female had been staying within the nest, among the workers and brood; she had

Tab. 1. Colony foundation experiments with dealate *Chalepoxenus brunneus* females and queenright or queenless *Leptothorax marocanus* colonies.

L. marocanus col. no.	*L.m.* queen	*C. brunneus* queens introduced (dead after n days) (i = inseminated[1])	*C.b.* brood produced		Remarks
1	absent	1. (surviving)[2]	9♂	15♀	2 *L.m.* ♀♀ also produced
2	"	1. (33,i) 2. (35,i) 3. (17,i?)	—	—	*L.m.* ♂♂ produced
3	"	1. (1,i?) 2. (37,i) 3. (3,i?)	—	—	♀♀ and ♀♀ *L.m.* produced
4	"	1. (13,i) 2. (60,i)	1♂		1♂ *L.m.* produced
5	present	1. (247,i?) 2. (7,i?)	7♂		♀♀ and ♀♀ *L.m.* produced, *C.b.* ♀♀ *coexisted* with surviving *L.m.* queen
6	"	1. (254,i?)	—	—	♀♀ and ♀♀ *L.m.* produced, *L.m.* ♀ *killed*
7	"	1. (22,i?) 2. (surviving)	5♂	10♀	1st *C.b.* ♀ paralyzed *L.m.* ♀ which recovered, 2nd *C.b.* ♀ *coexists* with surviving[2] *L.m.* queen. ♀♀ and ♀♀ *L.m.* produced.
8	"	1. (10,i) 2.(235,i?) 3. (surviving)	1♂		♀♀ and ♀♀ *L.m.* produced, *L.m.* ♀ surviving, *coexistence*
9	"	1. (1,ni) 2. (1,i?) 3. (2,ni) 4. (surviving)	3♂	15♀	4th *C.b.* ♀ *killed L.m.* ♀; *L.m.* ♀♀ ♀♀ produced together with *C.b.* sexuals
10	"	1. (13,ni) 2. (26,i?) 3. (28,i?)	—	—	many ♀♀ and ♀♀ *L.m.* produced *L.m.* ♀ surviving

1) i = inseminated; ni = not inseminated; i? = organs too decayed to permit determination whether or not inseminated.
2) surviving until second hibernation (August 1988).

paralyzed at least 12 *L.m.* workers (see below), and her gaster became visibly swollen. The *L.m.* female remained paralyzed, in the nest, for 40 days until she had died. This colony produced a considerable number of *C.b.* offspring (3 males, 15 females), but also some *L.m.* females and workers after the hibernation.

In colony no. 7, the first *C.b.* female introduced was seriously attacked by the host workers. She paralyzed 18 out of the 30 workers present, and on day 7 the *L.m.* female also was paralyzed. Five days later the host queen had recovered, however, and another 10 days later the *C.b.* female was dead. A second *C.b.* female was introduced, and after short aggressions through the *L.m.* workers she was accepted and survived for more than a year. Both the host and the parasite queen coexisted, and the colony produced 5 males and 10 females of *C. brunneus.*

Colony no. 5 and no. 8 represent two other instances where coexistence of the host and parasite queens occurred for a long time. In col. 5 the first *C.b.* female, after a short aggression, was accepted by the host workers, stung and paralyzed a total of 7 among them, and remained in the nest together with the host queen until she died 247 days later, after the hibernation. A second *C.b.* female, introduced in the next "summer" period, survived less than a week. The colony produced *L.m.* offspring and 7 *C.b.* males. Col. 8 had a similar fate, with the second *C.b.* female coexisting with the *L.m.* queen for 235 days, and a third *C.b.* female living in the colony for 2 months. The production of this colony, however, was only 1 *C.b.* male and a number of host workers and females.

As was mentioned above, the *C.b.* females, having penetrated the host nest, are usually attacked by the host workers, and sometimes quickly killed through biting and pulling off their appendages. When the *C.b.* female escapes these attacks, and sometimes very soon (within one hour after first having entered the nest), she stings several host workers, which are then paralyzed, lying inside or outside the nest for as long as a week, with slightly trembling appendages. Most of them eventually die; only a few may recover. Paralyzation of host workers also occurred in orphaned *L.m.* colonies; thus in col. no. 1 seven out of 19 workers were stung to death, and in col. no. 3, nineteen out of 30. The stinging of host workers may continue for more than 2 weeks.

Tab. 2. Production of five *Chalepoxenus brunneus* colonies collected in the field (1st brood May/June, 1987; 2nd brood in April, 1988) and three founded in the laboratory (1st brood in April, 1988).

	Production of sexuals					
	1st brood		2nd brood		total	
Field col. no.	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1	15	56	5	8	20	64
2	4	8	2	2	6	10
3	1	1	4	4	5	5
4	—	—	6	16	6	16
5	3	9	8	6	11	15
Sex ratio ♂/♀ = 0.44					48	110
	1st brood					
Lab col. no.	♂♂	♀♀				
1	9	15				
7	5	10				
9	3	15				
	17	40	♂/♀ = 0.42			
All colonies	65	150	♂/♀ = 0.43			

Brood production and sex ratio

In laboratory-founded colonies the *C.b.* females usually develop a somewhat swollen gaster even during the second week after having penetrated a host colony. Egg-laying apparently begins soon after, since higher egg numbers were recorded about 2–3 weeks after the colony founding, when the *C.b.* female survived that long. Egg-laying continues until the fall; the female of col. no. 1 was seen to lay an egg on day 73 after colony founding.

Evidently there is no "rapid brood" production since in all colonies the first *C.b.* sexual pupae appeared in the "summer" after colony founding and hibernation, having developed from hibernated larvae.

No *C.b.* workers were ever produced, neither in the field-collected colonies nor in the laboratory-founded ones. Only in one field colony a worker pupa with ocelli, perhaps an intermorph, was recorded; however, a week later it was destroyed.

The number of *C.b.* sexuals produced was highly variable, certainly in part dependent upon the numbers of host workers in the

colonies. Tab. II reveals the records from field and laboratory colonies. The sex ratio (male/female) is close to 0.43 both in the field and laboratory colonies, thus markedly female-biased. This is not substantially changed when the three laboratory-founded colonies, which only produced males (Tab. I, no. 4, 5, 8), are included; the sex ratio then would be 0.49, still more than 2 females per male.

Discussion

Our field and laboratory data clearly reveal that *Chalepoxenus brunneus* is a workerless parasitic ant, in contrast to the other species of this genus. Except for *C. spinosus,* of which only alate sexuals are known (Buschinger 1987), all other species have a worker caste, and *C. muellerianus* (including *C. insubricus* and *C. siciliensis*) as well as *C. kutteri* have been shown to conduct slave raids. For *C. tramieri* (Cagniant 1983) dulotic life habits are also assumed. *C. brunneus* thus represents a "degenerate slavemaker" like several species in the genus *Epimyrma,* which are parasites of *Leptothorax* species (s.g. *Myrafant* and *Temnothorax*) as is *Chalepoxenus* (Buschinger and Winter 1985, Buschinger et al. 1987, Buschinger in press).

As in the workerless *Epimyrma corsica* and *E. adlerzi,* the *C. brunneus* females apparently are able to eliminate the host colony queens during parasitic colony founding, using the genus-specific technique of stinging them, while *Epimyrma* females throttle the host queens to death. Different from the dulotic *Chalepoxenus* species, however, where the host queen soon dies when stung, the *L. marocanus* queens are only paralyzed by the *C.b.* female, and may even recover, as was shown in one experiment, or die only after several days. Another difference refers to the behavior towards the host colony workers: In *C. muellerianus* and *C. kutteri* the parasitic queen stings most of the workers to death (some workers and the queen often escape), and takes over only their broods. *C. brunneus,* on the other hand, stings only part of the host workers, which also do not die immediately (only after several days), and she is accepted by the remainder of the adult host colony workers. This parallels our observations in *Epimyrma,* again, in that during colony foundation the *Epimyrma* queens also sting a small number of host workers (Buschinger and Winter 1985, Buschinger et al. 1987, Douwes et al. 1988), and are accepted by the others. Adoption of the

parasitic queen by adult host workers, however, occurs in all *Epimyrma* species, not only in the degenerate slave-makers. This acceptance in *Epimyrma* thus is a preadaptive feature already present in the slave-making species; it is certainly favorable for a degenerate slave-maker who, when workerless, cannot replenish its slave stock through raiding. In *Chalepoxenus brunneus,* on the contrary, the queens had to evolve *de novo* the capability of being accepted by adult host workers.

It remains an open question of whether or not *C. brunneus* is on the way to an even more specialized type of coexistence with the host queens, a true inquilinism. Some of our experiments seemingly support such an assumption. However, the observed instances of coexistence between the *C.b.* and the host queens might well be artifacts due to inappropriate laboratory conditions. In the field such a coexistence has not been observed. And also in *C. muellerianus* and *C. kutteri*, in a total of now close to 500 field colonies checked, a coexistence of host and parasite queens has never been found. In laboratory colony founding experiments, however, it has been recorded in a couple of instances, also in these species (Ehrhardt unpubl.).

As was demonstrated in our laboratory cultures of *C. brunneus,* the production of sexuals is markedly queen-biased, with a numerical sex-ratio close to 0.43 (male/female). This might indicate a certain degree of inbreeding, with sexuals mating close to the maternal nests; in fact we saw mating behavior within our narrow formicaries. The apparent absence of a female sexual pheromone would fit to this assumption. Queen bias is usually found in such parasitic (and also free-living) species, where inbreeding occurs, most evidently in *Epimyrma* species with mating inside their nests (Buschinger and Winter 1985, Douwes et al. 1988). For a discussion of this feature see Buschinger (in press).

The *C. brunneus* population of Tizi-n'-Test, according to our observations, is very small, covering an area of not more than 50 × 100 m, and is certainly isolated. The species has not been found in close vicinity nor in farther distant sites of similar elevation, exposition, etc., despite our spending several days in search of additional localities. With an estimated population of less then 100 nests at any time a high degree of inbreeding is inevitable, even if sexuals do not mate exclusively with those of the same, or closely neighboring, nests.

In conclusion, we may state that *C. brunneus* is a workerless species, derived from actively dulotic congeners. The queens have evolved the capability to coexist with adult host workers of the colonies, which they invade for colony foundation. The higher initial number of host workers makes slave-raiding less necessary. The *C.b.* queens have retained (always?) the feature of killing the host colony queens through stinging, as their dulotic congeners.

Due to overgrazing and deforestation of the Great Atlas, as in other parts of Morocco, suitable habitats of *C. brunneus* have been largely destroyed. The population we studied is certainly but a tiny relic of a once much more widespread species, and it appears close to extinction. We do not know whether or not such relics exist elsewhere. It remains also questionable how much of the peculiar features of *C. brunneus* is due to the secondarily very small population size and isolation, and what was characteristic of the species as a whole.

Summary

Chalepoxenus brunneus, found in only one very small site in the Great Atlas of Morocco, represents a workerless parasitic species which is derived from actively dulotic congeners ("degenerate slave-maker"). The host species is *Leptothorax* cf. *marocanus.* The *C.b.* queen apparently eliminates the host colony queen by stinging her. She also stings to death a considerable part of the host colony workers, but, different from the dulotic congeners, the *C.b.* queen then is accepted by the remaining adult host workers. The sexual production is queen-biased (sex ratio 0.43 male/female); mating presumably takes place close to the nest. We found no evidence for a female sexual pheromone, but the *C.b.* males react on the pheromone from poison glands of other *Chalepoxenus* species. The life history of *C.b.* parallels that of other "degenerate slave-makers" in the genus *Epimyrma.*

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ALLOCHARES AZUREUS: AN UNUSUAL WASP EXPLOITS UNUSUAL PREY (HYMENOPTERA: POMPILIDAE; ARACHNIDA: FILISTATIDAE)

By Mark Deyrup[1], James T. Cronin[1], and Frank E. Kurczewski[2]

The spider wasp genus *Allochares* includes a single species, *A. azureus* (Cresson), occurring across the extreme southern U.S. from Florida to California, and southward to the Mexican states of Vera Cruz and Jalisco (Evans 1951). This species shows, for a pompilid, unusual morphological simplicity and nudity. The legs are almost spineless, the body is devoid of erect hairs, and the mandibles lack setae. The tarsal claws, unlike those of other pompilids, are almost straight, widened dorsoventrally, and flattened below (Fig. 1A). The head is strongly convex in front and somewhat concave behind, and the pronotum is rather long (Evans 1951, 1966a) (Fig. 1C). Adults have been collected on flowers of *Baccharis* and *Solidago* (Evans 1951); otherwise, nothing is known of the biology of *A. azureus.*

At the Archbold Biological Station (Highlands Co., Florida), *A. azureus* was first seen around buildings. A recent 3-year Malaise trap study of scrub insects at the Station produced no specimens of *A. azureus,* indicating that this wasp might be associated with domestic spiders. This suspicion was confirmed in the summer of 1987, when we observed *A. azureus* hunting a species of hackled band spider, *Filistata hibernalis* Hentz, found in dark, confined places, such as the inside of open sheds. We realized then that *A. azureus* was probably amenable to laboratory and field study.

Materials and Methods

Filistata hibernalis, collected from the buildings of the Archbold Biological Station, were established in 30 × 30 × 30 cm screened cages. From one to four spiders eventually occupied each cage

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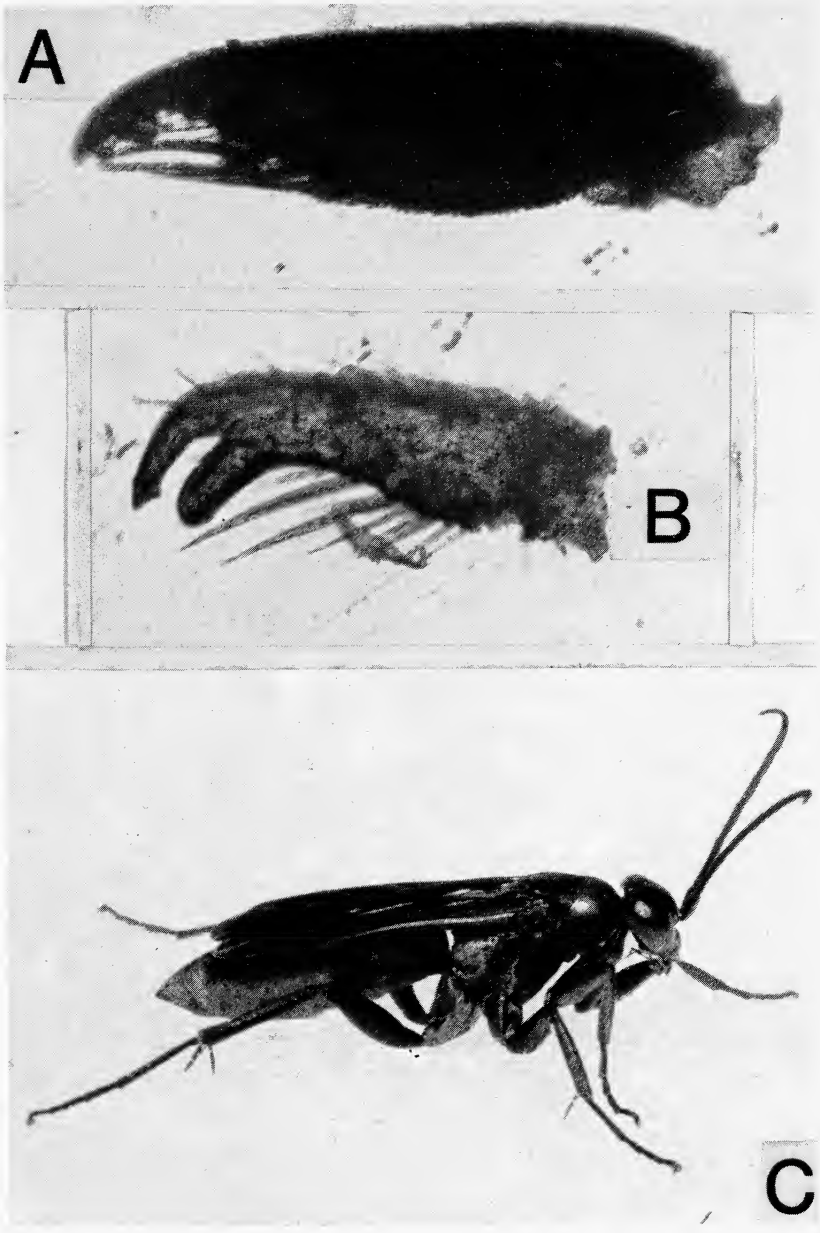

Fig. 1. A, Claw of *Allochares azureus;* B, claw of *Episyron conterminus;* C, *A. azureus,* female.

before we introduced the wasps. Vertical cardboard strips, 4 cm wide, were placed in each of four corners of the cages, extending from top to bottom of the cages. The placement of the strips produced artificial crevices about 1 cm deep between the cardboard and the screening. Most of the spiders spun webs with retreats between the screening and the cardboard, so the behavior of the spider and the hunting wasp could be observed easily. Additional spiders were introduced into cages to replace those taken by the wasps, and these spiders readily occupied vacated webs. Spiders were provided various insect prey, chiefly tabanids. Five female *A. azureus* were collected as they hunted *F. hibernalis* around buildings and introduced singly into the cages. Additional wasps were reared in the laboratory. We observed more than 50 hunting sequences, both in the field and in the laboratory. Once parasitized, most spiders were removed from their cages and placed in vials, although a few were left in the cages. Male wasps were collected outdoors as they were attracted to cages containing virgin females. When wasps emerged from their cocoons in the laboratory, they were usually placed in a cage with a member of the opposite sex. Females were later admitted into cages containing spiders. Spiders and wasps were kept at 24°C. A honey-water solution was provided *ad libitum* as nourishment for the caged wasps.

Hunting Behavior

F. hibernalis builds its web (Fig. 2A) in cracks and recesses in sheltered sites, and it is in such places that we observed *A. azureus* hunting outdoors. Because *A. azureus* normally attacks spiders in dark, restricted places, the confines of our laboratory setup did not appear to impose too unnatural a situation on the hunting wasp. Wasp behavior in the laboratory appeared very similar to the behavior observed in the field. *A. azureus* hunts primarily on foot, running rapidly with the short rushes and wing-flicking typical of many pompilids. Occasional flights of a meter or less are made to new hunting spots. The wasps were sometimes tolerant of human approach, and occasionally continued hunting when we approached for close observation. Any attempt to capture a wasp was likely to cause it to fly out of sight.

When a wasp encounters a *Filistata* web, she pauses, orients toward the center of the web, and quickly walks into the central

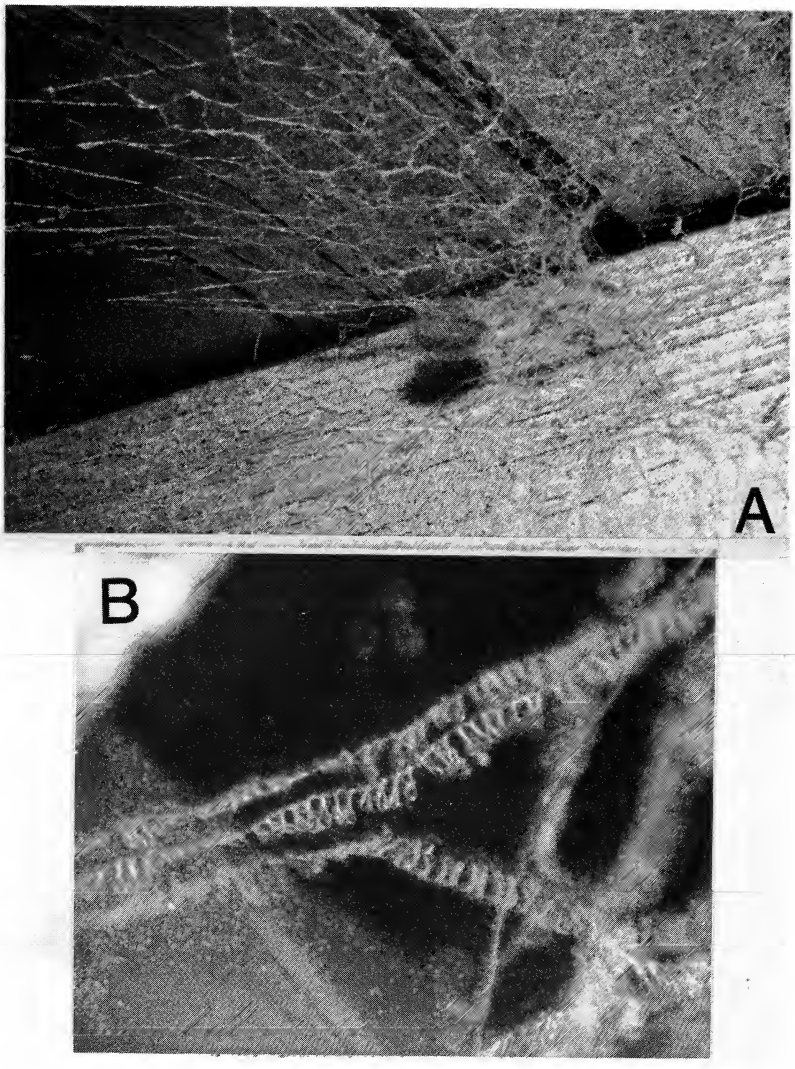

Fig. 2. A, web of *F. hibernalis* with cocoon of *A. azureus,* site is open shed; B, web of *F. hibernalis,* showing loops of Hackled bands.

tube-like retreat (Fig. 2A). As soon as the wasp moves into the main area of the web, the spider runs rapidly out of the back of the retreat, usually leaving the web completely. If a narrow crack is available, the spider may wedge itself in, and may be able to escape from the hunting wasp. The spacing of the cardboard in the laboratory cages provided cracks wide enough to allow even the largest wasps complete access to the spiders. Spiders in these cages, when approached, leave their webs and hide in one of the cardboard cracks or in the web of another spider. Once the spider has taken up a position outside its own web, it remains completely motionless, even when closely approached by a wasp. The wasps are apparently unable to recognize a motionless spider, and on many occasions a wasp repeatedly searched the abandoned web, passing within 1–2 mm of its intended prey lying motionless outside the web. If the wasp actually touches a spider, the latter normally rushes away, closely pursued by the wasp. Contact with a *Filistata* appears to elicit in the wasp an attack response. If a wasp is captured and imprisoned in a vial, it dashes about attempting to escape, but if a *Filistata* has been included in the vial, the wasp stings it on first contact, and begins to drag it about the vial while seeking an exit.

Once a wasp contacts a spider, she attempts to sting it in the sternum. The movements of both wasp and spider are so rapid that we have not established an exact sequence of events. The wasp usually attacks from behind, standing on top of the spider and curving her gaster around to the venter of the spider. In some cases the spider either turns itself over or is actually flipped over by the wasp. We have never seen a frontal confrontation with the spider attempting to use its chelicerae to ward off the wasp, though the largest *Filistata,* when cornered, appear to stab with the front legs at the approaching wasp. The entire conflict lasts no longer than 2 or 3 seconds, and terminates abruptly when the wasp succeeds in delivering a thrust to the sternum, causing instant paralysis of the spider.

Unlike most pompilids, *A. azureus* does not bury or otherwise conceal her prey, but rather places it in the spider's own web. The web is strongly built, and its tangling hackled bands of microscopic loops remain functional for a long time without maintenance. After initial inspection of the prey, during which she may apply her mouthparts to the site of the sting, the wasp attempts to relocate the web. She may begin at once hauling the spider about by the base of

a leg or pedipalp as she searches for the web, or she may leave the spider and make small forays. Once she has found the spider's web or the vacant web of another spider, she inspects it thoroughly, then returns to the spider. Because the spider usually drops to the ground after it has been paralyzed, it is often necessary for the wasp to drag the spider, which may be much larger than she, up vertical surfaces. Although this species of wasp lacks strongly curved tarsal claws, she seems to have no difficulty finding purchase, probably because she is supported by large tarsal pads, not only on the last tarsal segment, but on all the others as well.

The wasp may spend many minutes entangling the spider in the web, sometimes removing the spider from the web after a prolonged effort, only to begin over again. The spider is dragged into the densest part of the web, tangled extensively, and, with rapid pawing movements of one foreleg, the wasp attempts to draw loose strands over the spider. In the laboratory the wasp larva develops normally on a spider removed from the web and placed on a flat surface, but in a natural situation a spider that fell from the web would quickly be attacked by ants and other scavengers.

Before ovipisition *A. azureus* straddles the spider and makes rapid thrusting movements with the tip of her gaster along the abdomen of the spider where the egg is to be laid. The effect of these movements is to shave all the hairs from an oblong area, usually about 2 mm long. An egg about 1.5 mm long is attached to the bare spot (Fig. 3A). This bare spot allows secure attachment for the egg and provides the newly hatched larva with an initial feeding site. In many species of Pompilidae the tip of the gaster is used for such tasks as tamping soil on the burrow entrance or trowelling mud (Evans 1963); depilation of prey can now be added to the list. Depilation of a spot on the spider's abdomen may not be unique to *A. azureus;* such behavior in most other pompilids would occur in the concealment of a cell.

Morphological Adaptations Associated with Hunting

A. azureus has apparent morphological adaptations that suggest it has a long evolutionary association with *Filistata.* Compared to most other members of the Pompilini, such as species of *Anoplius* and *Poecilopompilus,* the body of *Allochares* is elongate and

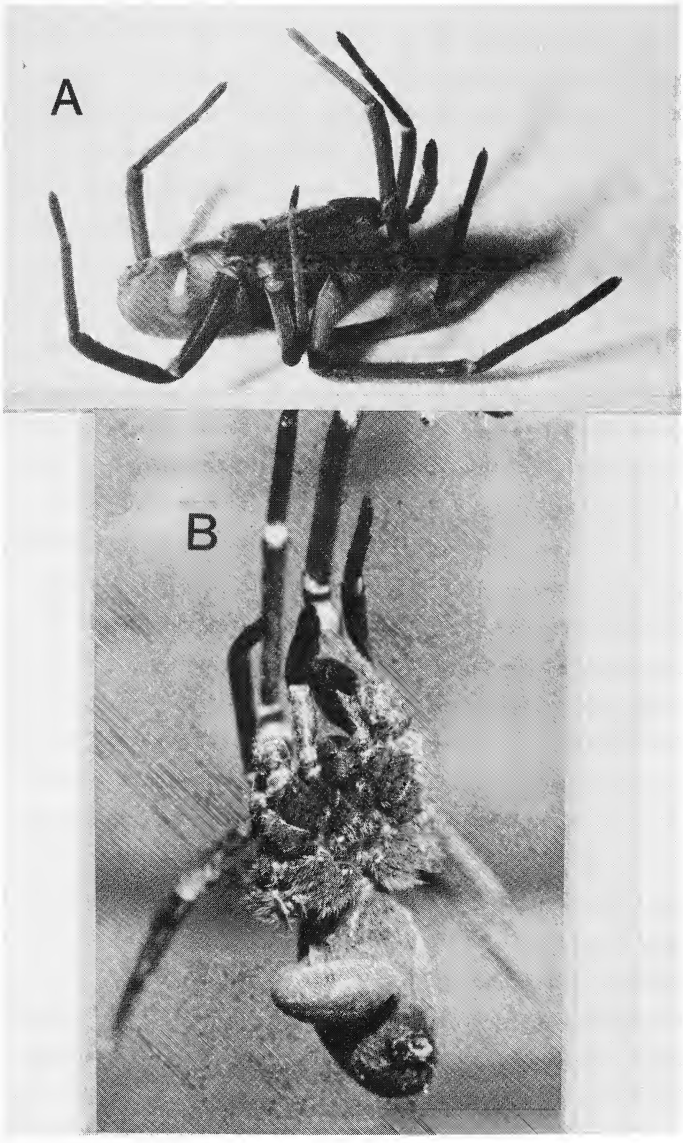

Fig. 3. A, *F. hibernalis* with egg of *A. azureus;* B, larva of *A. azureus* at 3 days.

slightly flattened, with short, thick legs (Fig. 1C). This allows it to move about freely in narrow spaces.

The web of *Filistata* has strong threads of smooth silk along which are festooned masses of minute sticky loops (Fig. 2B), forming the hackled band. These loops easily entangle the appendages of most insects by becoming engaged in the hairs and tarsal claws of their legs. The hairless and spineless nature of the body and appendages of *A. azureus* may assist its progress through the hackled bands. It would seem that the absence of digging spines on the legs of *Allochares,* and the replacement of the prey in its own web are both dependent on the hackled band and its operation both as a trapping device for the spider and a protective barrier for the wasp larva.

The thick straight claws of *Allochares* (Fig. 1A) also assist in smooth movement through the hackled bands. When we placed specimens of the pompilid *Episyron conterminus posterus* (Fox) in the cages, their progress through the webs was slow, with frequent stops to untangle the tarsal claws. *E. conterminus,* which attacks orb-weaving spiders (Evans and Yoshimoto 1962), has curved and toothed claws (Fig. 1B) typical of many pompilids. *F. hibernalis* clearly recognizes the threat implied by the easy and rapid passage of *A. azureus* through its web, and vacates the web before the wasp has approached closely. No such escape response was evoked by *E. conterminus.*

Larval Development and Morphology

The development of *A. azureus* is rapid. The egg hatches in about 3 days and the larva completes its development in 10–12 days at 24°C. Figures 3B, 5A, and 5B show larvae at 3, 5, and 8 days,

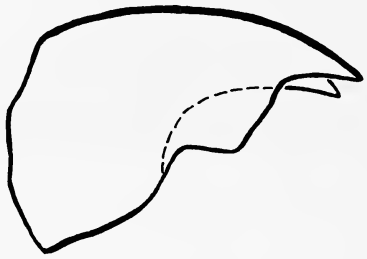

Fig. 4. Mandible of mature larva of *A. azureus.*

respectively. The larva is attached to the spider while consuming the abdomen, but transfers its hold to the web or to nearby objects while consuming the remainder of the spider.

While the larva is small its host remains able to move and even run rapidly if seized by an appendage. Normally the spider does not move, but remains in the position in which it was left by the wasp. By the time the larva is half grown, the spider can no longer move and appears to be dead. A number of spiders were stung and left in the bottom of the cages; these spiders never resumed activity, though they could be stimulated to move.

The larva is able to consume the entire spider, though it does not always do so, as part of the spider may fall out of the web. The abdomen is consumed first, then the cephalothorax and legs. The older larva can be seen gnawing off bits of the spider, using well-developed mandibles. Parts of the spider appear to be deposited in a liquescent mass held in the ventral curve of the body (Fig. 5B), as is typical of many larval Pompilidae and Sphecidae. It is possible that some external digestion occurs within this glob of food.

A superficial examination of the larva shows some morphological divergence from the larvae of other pompilid species described by Evans (1959). The body is unusually smooth, lacking the prominent lobes and tubercles often found in other pompilids. The apex of the body is tapered and slightly flattened dorsoventrally, unlike any pompilid larvae described by Evans (1959), and may be a feature associated with hanging upside down by the tip of the abdomen. The mandibles are somewhat unusual in having a conspicuous dorsal medial angle (Fig. 4), but no ventral angle. They are totally unlike the edentate mandibles of *Homonotus* (illustrated by Evans 1959), a non-fossorial Old World genus that parasitized free-living spiders (Richards and Hamm 1939).

Cocoon Construction and Emergence

The cocoon of *A. azureus* (Fig. 4C) may be unique in the Order Hymenoptera. The entire surface of the cocoon is beset with long, erect hairs of uniform length. The larva begins by spinning a small net of silk at the posterior end of its body, using threads to attach this net to the surrounding web or substrate. The outer cocoon is then constructed as a loose net composed of loops. Each loop is a double strand of silk attached to the rim of the previously con-

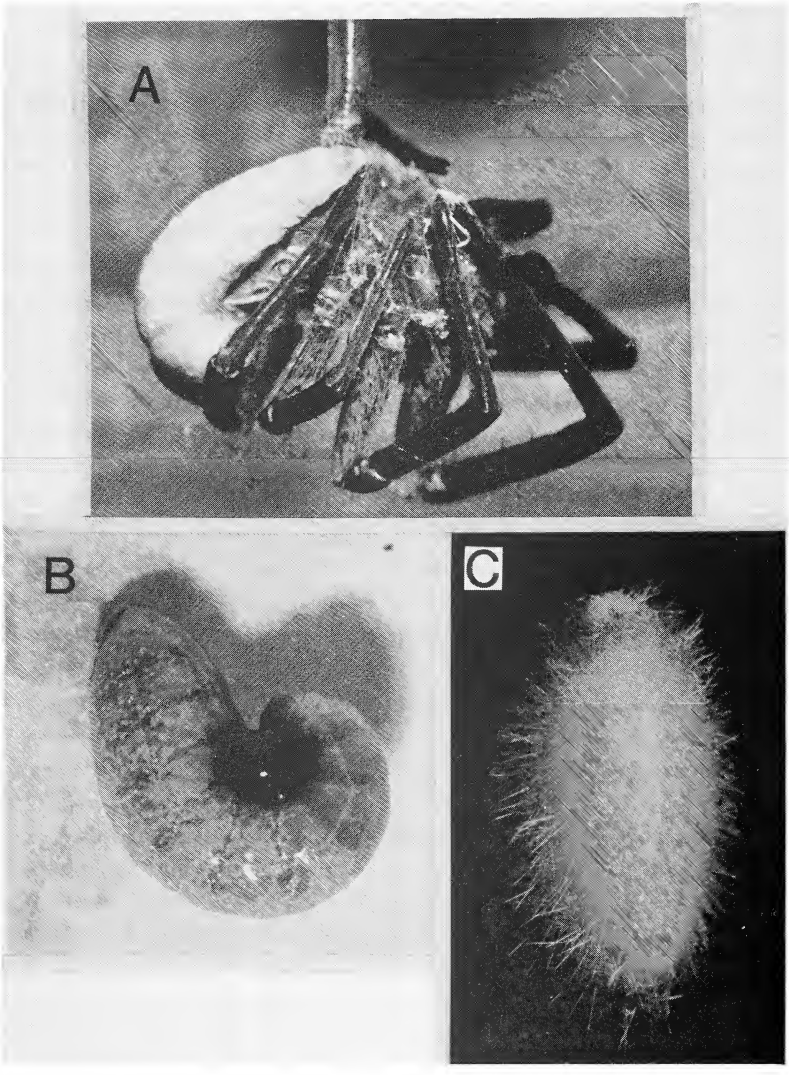

Fig. 5. Larva of *A. azureus* at 5 days (A) and 8 days (B); C, cocoon of *A. azureus*.

structed section of cocoon. After completing a loop, the larva rears back its head drawing out two threads, then attenuates the threads, and breaks them with a movement of the head. The head is lowered and another loop initiated at the base of the hairs (Figs. 6A & B). The larva works steadily with stereotypic motions. If disturbed, the larva draws its head into the finished part of the cocoon; when no longer alarmed, it raises its head, repeatedly touching the side of the cocoon until it reaches the rim, whereupon it begins to make loops and hairs as before. The shape of the outer cocoon is determined by the reach of the larva, and is larger and rounder than the finished cocoon. When the opaque inner cocoon is constructed, it draws together the outer cocoon to make it narrower and more compact. The larva requires about 48 hours to complete its cocoon.

The function of the hairs is unclear. They might lodge the cocoon even more securely in the web, but the numerous threads holding the posterior end of the cocoon in place appear adequate for this purpose. It seems likely that the hairs have a defensive function. It might be easier to guess the function of the hairs if we knew what potential enemies were present in natural habitats such as deep bark fissures and piles of rocks. *Zatypota nigriceps* (Walsh) is an ichneumonid with habits similar to those of *A. azureus:* it lives as an external parasitoid on spiders in their webs, and the cocoon is suspended in the web. The cocoon of this species is covered with erect loops (Townes and Townes 1960). We reared a larva of *Z. crassipes* Townes at the Archbold Biological Station; this specimen produced a cocoon covered with loops that were more or less appressed, but still provided a loose covering over the entire cocoon. The cocoons of both *Allochares* and *Zatypotus* are completely exposed to small parasitoids that could evade the strands of the spider web. It seems likely that the hairs and loops on these cocoons may offer some protection from small generalist parasitoids that attack exposed cocoons, such as the widespread pteromalid *Dibrachys cavus* (Walker). Studies of crop plants show that a dense pile of erect hairs is a general defense against sap sucking insects (Levin 1973) as well as some parasitoids and predators of these insects (Schuster and Calderon 1986). The same physical principles should apply to the cocoon of *Allochares.*

The color of *A. azureus* cocoons collected outdoors is medium to dark brown. The cocoons produced in the laboratory were white

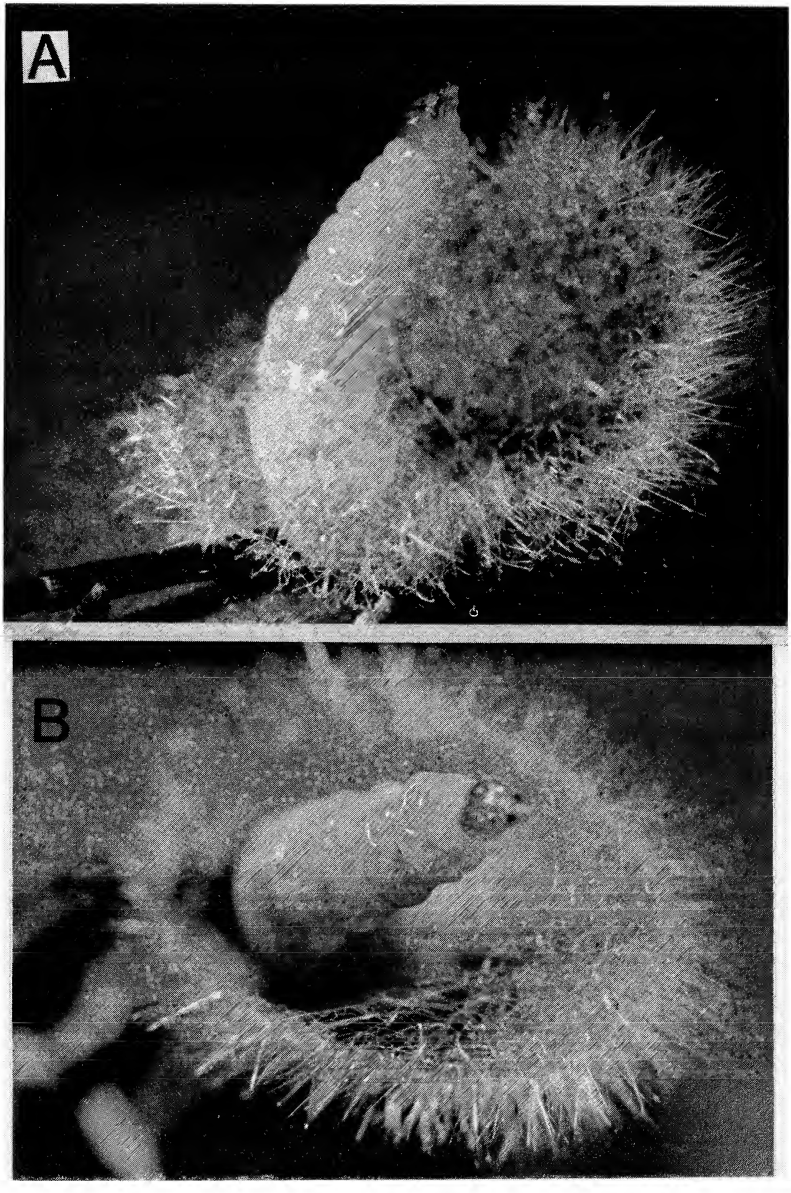

Fig. 6. A & B, larva of *A. azureus* spinning outer cocoon.

and remained that color. We eventually discovered that the white cocoons turned brown rapidly when placed in a saturated atmosphere. In natural situations the cocoons are likely to be exposed to high humidity, and we do not consider this color change to have any adaptive significance.

The adult emerges 35 to 60 days after cocoon formation, cutting a narrow slit almost encircling the anterior end of the cocoon. The cap usually remains attached to the cocoon after emergence.

Mating

Virgin females are willing to hunt and paralyze spiders, though they do not always oviposit. Eggs of virgin females appear to produce normal larvae, which develop into adult males. It appears that unmated females pass on their genes through production of at least a few male offspring, though it is not known whether unmated females are likely to occur in nature.

Virgin females placed outdoors attracted males; a total of 9 males were attracted to caged females. We have not seen males on the outside of the building where we placed the females, and it seems clear that the males are attracted by pheromones. When a male is caged with a virgin female, he runs rapidly about the cage. Upon encountering the female, he buzzes his wings a few times and attempts to climb on her back, without any noticeable courtship behavior. The male immediately extrudes his genitalia and attempts to mate. In our laboratory setup females seem reluctant to mate though the male may persist in his attempts for 15 minutes or more. If a spider is present in the cage, the female continues to hunt while the male is on her back. One female carried a paralyzed spider up the side of the cage, while apparently ignoring a male perched on her back attempting to mate. There were at least two successful matings in the laboratory, as shown by production of female offspring by lab-raised wasps.

A. azureus males are significantly smaller than females (males: $\bar{X} = 7.57$ mm, SE = .93, n = 7; females: $\bar{X} = 11.62$ mm, SE = 1.78, n = 10; $t = 4.16$, $P < .005$). In addition, *Allochares* size (cocoon length), irrespective of sex, is positively associated with spider weight ($r^2 = .917$, n = 14, $P < .0001$). It seems probable that females tend to lay female eggs on larger spiders and male eggs on smaller spiders. Since spiders of all sizes are constantly available, sex ratios would

not be excessively skewed by a tendency to lay male eggs on small hosts and female eggs on large hosts. Host size appears to be associated with sex of parasitoids in a number of families of wasps (Clausen 1939, Charnov 1982, Deyrup and Manley 1986).

Seasonal Occurrence

Specimens of *A. azureus* have been collected at the Archbold Biological Station from May to November, and Evans (1951) listed collections in the southeastern U.S. from April to December. There are probably several generations of wasps per year. The host spider may live several years, and all sizes of hosts are available through the year. There is no reason to suppose *A. azureus* shows any seasonality other than protracted or arrested development during cool weather.

Discussion

Allochares azureus differs structurally, ecologically, and behaviorally from all other pompilids that have been studied. The structural pecularities of the adult suggest two other genera of non-fossorial pompilids, the Old World *Homonotus* and the New World *Notocyphus*. Members of these genera paralyze and oviposit on free-living spiders, which recover from the effects of the sting and resume their normal activities. After the larva has fed for about a week, the spider dies (Williams 1928, Richards and Hamm 1942, Iwata 1942). The genus *Minagenia* may have similar habits, but has not been studied except for casual rearings (Kaston 1959). Numerous pompilids, including species of the tribe Aporini and some species of *Pepsis,* use the burrows of spiders as ready-made nests for the larvae (Evans 1953). *A. azureus* is apparently unique among pompilids in its use of the web for deposition of the spider and in having a larva that feeds and constructs its cocoon in the web. This is not to say that *A. azureus* occupies a previously unexploited adaptive zone, as members of the entire ichneumonid tribe Polysphinctini are very similar to *A. azureus* in larval habits (Townes and Townes 1960).

In its ecology *A. azureus* may resemble polysphinctine ichneumonids more than it does any pompilid, but *A. azureus* is not a particularly primitive species, nor even a specialized representative of a primitive offshoot of the Pompilidae. Evans (1953) points out

that the other non-nesting pompilids are a phylogenetically diverse group of specialists that apparently have lost components of the typical pompilid behavioral repertoire. *A. azureus* would seem to fit this pattern perfectly. Although *A. azureus* may be ecologically similar to a polysphinctine ichneumonid, it is behaviorally much more complex in that it searches for the spider's abandoned web, transports prey, arranges the spider in the web in a special way, and prepares the prey for oviposition by removing a patch of hair.

The only other species of pompilid known to attack filistatid spiders is *Pompilus (Perissopompilus) phoenix* Evans (Evans 1966b). Members of the subgenus *Perissopompilus* are distinguished in part by unusually weakly spinose legs and absence of erect hairs on the body (Evans 1951). We suspect the loss of hairs and spines in *Perissopompilus* is convergent with *Allochares* and associated with the structure of the filistatid web.

Conclusions

Allochares azureus is a highly specialized parasitoid of *Filistata hibernalis,* and we would not expect it to attack unrelated spiders. The straight, thickened tarsal claws, the use of the web as a protected site for prey placement and oviposition, and the densely hairy cocoon all seem to be unique adaptations among the Pompilidae. *A. azureus* appears to be a convenient pompilid for laboratory study. We hope our work will stimulate more intensive behavioral and ecological work on this highly unusual spider wasp.

Summary

The mating, hunting, provisioning, ovipositional, and developmental behavior of the spider wasp *Allochares azureus* (Cresson) were studied under laboratory conditions at the Archbold Biological Station, Lake Placid, FL during 1987. The species preyed upon the domestic hackled band spider, *Filistata hibernalis* Hentz, during the warmer months of the year. The wasps flushed spiders from their silken retreats, stung them in the underside of the cephalothorax, causing instant paralysis, transported the spider into its web or another nearby, and entangled the prey in the web, using the forelegs. The wasp laid an egg on the spider's abdomen after depiling the hairs from the ovipositional area with the end of her abdomen. The larval wasp fed upon the spider while suspended in the

web and then constructed a unique cocoon beset with long, erect hairs of uniform length. Morphological adaptations that may assist the wasp in hunting and prey entanglement are discussed. Key words: *Allochares azureus, Filistata hibernalis,* Pompilidae, Filistatidae, Parasitoid, Host-parasitoid interaction, Behavior, Adaptations

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CASTE AND REPRODUCTION IN ANTS: NOT ALL MATED EGG-LAYERS ARE "QUEENS"*

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The existence of two classes of adult females is characteristic of the *highly-eusocial* insects, which comprise termites, ants, various bees (*Bombus, Apis,* Meliponini) and vespine wasps. Queen and worker castes differ phenotypically as a result of morphological adaptations for efficient reproduction (dispersal, egg-laying) and maintenance activities respectively. Reproductive role partitioning in highly-eusocial species is specified by caste membership, but exceptions exist (for example, ponerine ants without queens). By contrast, in *primitively-eusocial* insects, adult females are all similar in form. Individual differences in size often occur as a result of environmental variations during larval growth (such as nutrition) and, together with age and insemination, are the basis for reproductive differentiation (reviewed by Wheeler 1986). Thus, although reproductive division of labor is a feature of both primitively- and highly-eusocial insects, it is achieved in two distinct ways: role differentiation among monomorphic adults, or production of alternative adult phenotypes. This dichotomy is not reflected by the current use of "queen," "worker" and "caste." Each of these terms has alternative meanings, and this, we suggest, obscures various evolutionary processes associated with eusociality.

The two meanings of caste

Dimorphic adult females are produced by divergent developmental pathways coordinated by endocrine signals, and this involves the expression of different sets of genes (see Wheeler 1986, Craig and Crozier 1978, West-Eberhard 1986). "Caste" has been used (as early as Latreille 1802) to distinguish these distinct female phenotypes. However, "caste" has also become a synonym for the separation of reproductive and sterile roles (e.g. Michener 1985: 303; Wilson 1985: 308; Fletcher and Ross 1985), or it sometimes serves to describe the

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partitioning of non-reproductive activities among workers (e.g. brood care, foraging). In his major contribution (outlined in Wilson 1985) to the study of the ergonomic design of colony organization in ants, E. O. Wilson has adhered to a functional concept of caste: "a set of colony members... that specialize on particular tasks for prolonged periods of time." This definition stems from the need, for the purposes of optimization studies, to define age groups (= "temporal castes") as equivalent to morphological castes (Wilson 1968). Thus "caste," which originally denoted alternative female phenotypes, is now also used solely to describe role. This leads to ambiguity in the literature, because to some authors "caste differentiation" refers simply to reproductive division of labor, while to others it refers to morphological dimorphism. We suggest that it is useful to restrict "caste" to denote groups of female adults which have distinct phenotypes following pre-adult differentiation. This usage will give proper emphasis to the significance of morphological specialization, which is characteristic of the highly-eusocial insects. "Caste" should not be used to describe groups of workers whose behavior is age-correlated, or fertile as opposed to sterile females. Age-correlated behavior occurs throughout the animal world (Caro and Bateson 1986), and should not be equated with dimorphism in morphology.

A terminology based on form or function?

The equivocal use of "caste" is paralleled by that of "queen" and "worker". In highly-eusocial insects, "queen" denotes the existence of a developmentally-distinct reproductive caste with specialized morphological traits, except that in various bumblebees queen-worker dimorphism is limited to a set of physiological changes (Röseler 1977). In contrast, Michener (1974: 373), Fletcher and Ross (1985) and others use "queen" to describe role ("colony member that is primarily active in egg-laying and relatively or totally inactive in foraging"). The use of this operational criterion is common in primitively-eusocial bees and wasps, and thus authors studying different taxonomic groups differ in their use of "queen". This needs not be ambiguous to non-specialist readers provided that the absence of (phenotypic) castes is made explicit. We are concerned however that "queen" is also used in a functional sense in various highly-eusocial species in which secondary modifications have resulted in caste and reproductive role being no longer concurrent.

Workers also can reproduce

The queen caste has been lost in several ponerine ants, and mated workers lay all the eggs (Peeters 1987). Reproductive differentiation in queenless ants is analogous to that in primitively-eusocial wasps and bees since it occurs in the adult stage. A major difference however is that queenless ponerine colonies consist exclusively of members of the worker caste, while primitively-eusocial colonies consist of undifferentiated females.

Problems in terminology arise when describing individuals from the same morphological caste that perform different roles. Mated ponerine workers are the functional reproductives in a colony, but if they are designated as "queens" (e.g. Hölldobler and Bartz 1985) their developmental origin is disguised. They clearly differ from members of the queen caste, because they cannot start new colonies independently, and they have a lower egg-laying rate as a result of simpler ovaries (Peeters and Crewe 1985). Furthermore, in *Rhytidoponera confusa,* colonies can have either one queen or several gamergates, which is a major biological difference (Ward 1983). A description specifying both phenotype and role is thus sometimes necessary, for example "unmated workers laying diploid eggs" (in the myrmicine *Pristomyrmex pungens;* Itow et al. 1984), or "mated laying workers". The latter have been termed "gamergates" partly for convenience, and partly to highlight this eusocial alternative and distinguish them from wingless queens with an external worker appearance (= ergatoid) (Peeters and Crewe 1985).

Buschinger's proposed nomenclature

Buschinger (1987 and earlier publications) also recognized that there is a need for a combination of structural and functional terms to describe the members of non-orthodox ant societies. Buschinger has suggested that "queen" and "worker" take on a strictly functional meaning (reproductive or not), and that new terms be adopted to describe morphology in all Hymenoptera. For example, mated egg-laying workers ("gamergates") would be called "ergatomorphic queens", and infertile queens would be "gynomorphic workers". It is crucial to note that Buschinger (pers. comm.) understands these new terms to refer to *external* morphology only; this stems from the very precise meaning of the German word "Morphologie". Since characters such as ovariole number or presence of

spermatheca are excluded, there is not always a precise correspondence between Buschinger's new terms and the phenotypes of adult females. A case in point might be a species with ergatoid queens where queen-worker dimorphism is most obvious with respect to internal differences such as reproductive organs. Buschinger's nomenclature has a clear taxonomic aim: visual appearance and role are combined in order to identify colony members. In contrast, we advocate that the terms "queen" and "worker" be used consistently in a structural sense across all highly-eusocial species, so as to gain an evolutionary perspective of the developmental origin of reproductive individuals. It is only in a minority of ant species that there will be a need for appropriate modifiers to describe roles (or appearance, e.g. "ergatoid").

Conclusions

"Queen", "worker", and "caste" are deeply embedded in the literature on eusociality, yet they are currently ambiguous. Reproductive division of labor, and the occurrence of (phenotypic) castes, are two completely distinct phenomena associated with eusociality—the former can occur without the latter. A more rigorous use of these terms, with the emphasis on morphology rather than on function, is likely to produce a better insight into various evolutionary modifications associated with eusocial organization, for example reproduction by mated workers in some ponerine ants. Wheeler (1986) emphasized that increased complexity of social organization has required changes in the underlying developmental programs that produce the members of a society. The evolutionary divergence of queen and worker morphology in some groups is thus fundamental, and this must be appreciated through a discriminating use of the terminology.

Summary

The term "caste" has an equivocal meaning in writings on eusocial Hymenoptera. It is used in a morphological sense to describe the different female phenotypes which result from separate patterns of larval development, or it is used in a functional sense to describe reproductive role (or the individuals who perform that role). Similarly, "queen" and "worker" have alternative definitions. Various authors use "queen" to describe the phenotype which is a result of morphological adaptations for more efficient reproduction. Others

use "queen" simply to describe individuals which are mated and fertile. This confused practice obscures the fact that morphological castes do not exist in many eusocial hymenopterans. Thus, in *primitively-eusocial* species, reproductive division of labour occurs among morphologically-undifferentiated female adults. In contrast, in *highly-eusocial* species, female adults have one of two different phenotypes, and normally only members of the queen caste reproduce. However, in several ponerine ants, the queen caste has been lost, and some of the workers mate and lay eggs. The latter have sometimes been called "queens", which conceals their developmental history.

We advocate that "caste", "queen" and "worker" be used only in a strict morphological sense (including both internal and external characters), with an additional mention of role when this does not correspond with caste membership.

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A NEW MEXICAN GENUS AND SPECIES OF DINOCAMPINI WITH SERRATE ANTENNAE (HYMENOPTERA: BRACONIDAE: EUPHORINAE)*

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The cosmopolitan braconid subfamily Euphorinae (*sensu* Shaw 1985, 1987, 1988) comprises 36 genera of koinobiont endoparasitoids, which parasitize the adult stages of holometabolous insects or nymphs and adults of hemimetabolous insects (Muesebeck 1936, 1963; Shenefelt 1980; Loan 1983; Shaw 1985, 1988). Occasionally the parasitoids of holometabolous insects will oviposit into larvae as well as adults (Smith, 1960; David & Wilde, 1973; Semyanov, 1979), but this only occurs where larvae are ecologically coincident with adults, living and feeding on the same plants (Tobias, 1966). Obrycki *et al.* (1985) found that *Dinocampus coccinellae* (Schrank) will oviposit into all larval instars, and pupae, as well as adults; however, the highest percentage of successful parasitization occurred when adults were attacked. Only a few papers have discussed euphorines of Mexico in particular (Muesebeck 1955; Shaw 1987).

The euphorine tribe Dinocampini was defined by Shaw (1985, 1987, 1988) to comprise three genera with ocular setae, antennal scape three times longer than wide, and labial palpus reduced to two segments. As far as is known, members of the tribe Dinocampini parasitize adult beetles; *Dinocampus* Foerster parasitizes Coccinellidae (Shenefelt 1980) and *Ropalophorus* Curtis parasitizes Scolytidae (Shenefelt 1960, Shaw 1988). The hosts of the third included genus, *Centistina* Enderlein, are not known. Because these genera are known only from females (Balduf 1926; Shenefelt 1960), it seems possible that females of the entire tribe are thelyotokous, reproducing parthenogenetically and producing only female progeny. The purpose of this paper is to describe a fourth genus of Dinocampini from Mexico. This new genus and species is remarkable because it has serrate antennae, unlike any other known braconid.

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The morphological terminology used in this paper is mostly that of Shaw (1985, 1987) and van Achterberg (1974). Microsculpture terminology is that of Harris (1979). Flagellomeres, from base to apex, are abbreviated as F1 through F13.

Genus **Betelgeuse** Shaw, NEW GENUS
(Figs. 1–3)

Type species: *Betelgeuse aztecus* Shaw, n. sp.

Etymology: Following greek mythology, the constellation of Orion is depicted on astronomical charts as a sword-bearing hunter. Because females have a conspicuous sword-like ovipositor, this genus is named for the star Betelgeuse (pronounced "beetle-juice"), which is part of the constellation of Orion. The name is masculine.

Description: Head (Fig. 2) transverse, in dorsal view 2.3× broader than long; surface sculpture coarsely and evenly rugose; eyes elongate oval, not bulging anteriorly beyond frons; eyes in anterior view distinctly converging ventrally; shortest inter-ocular distance 2× clypeus width; minute ocular setae present; median frontal carina weakly present, extending from midpoint of face to between antennal insertions; inter-antennal distance 3.25× socket width; scrobes not protuberant; scape elongate, gradually curved, gradually wider apically; scape length 4× width at apex; pedicel somewhat globose; flagellum 13-segmented, considerably shorter than body length; F1–F5 longer than wide, gradually wider apically, somewhat flattened, forming serrations antero-laterally, each serration terminating apically in a sharp point and a single long seta; F1 3× wider than apical width, F2–F5 each relatively shorter than preceding flagellomere; F6–F12 each compact, about as long as wide, segments gradually slightly thicker apically, each with a single long seta projecting dorso-apically; apical flagellomere 2× as long as wide, apically pointed; ocellar triangle small, distance between lateral ocellus and eye 4× distance between lateral ocelli; occipital carina complete; malar space short, slightly less than 1/4 eye height; malar suture indistinct; facial setae minute, not obscuring face; lower clypeal margin truncate; mandibles when closed overlapping for slightly less than half mandible length; maxillary palpus 5-segmented; labial palpus 2-segmented.

Mesosoma with surface sculpture entirely coarsely rugose to rugo-punctate; notaulus and sternaulus indistinct from general

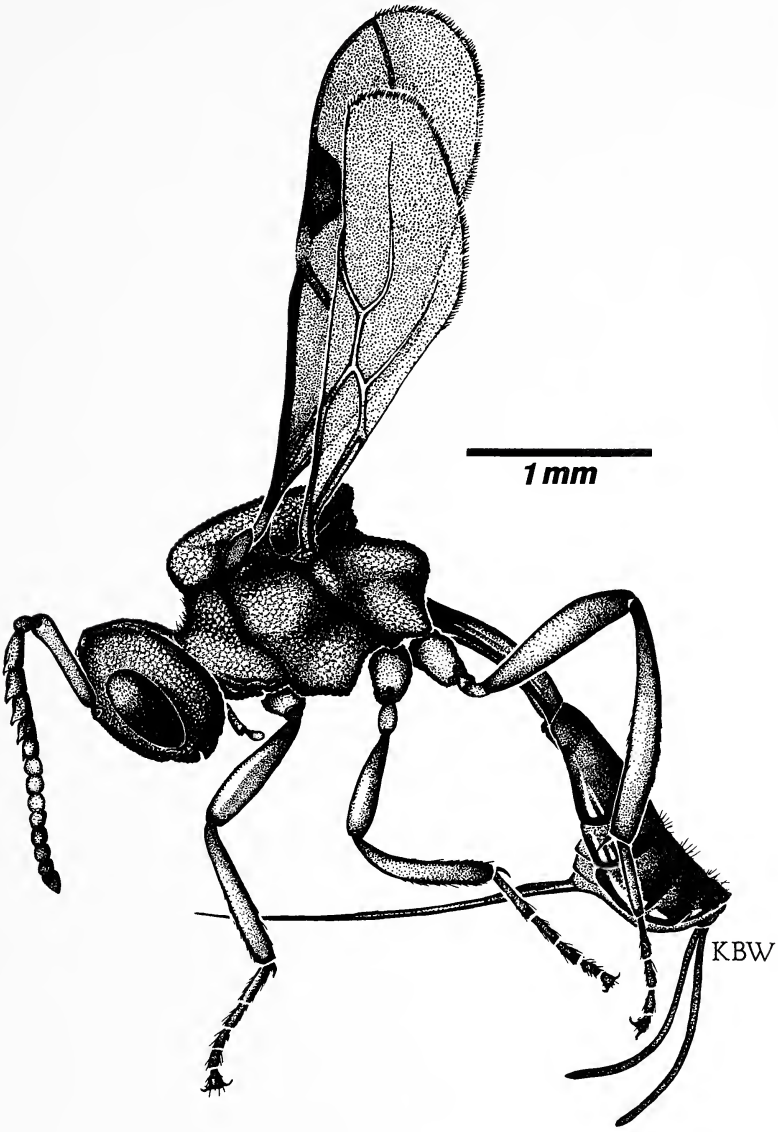


Fig. 1. *Betelgeuse aztecus,* lateral habitus.

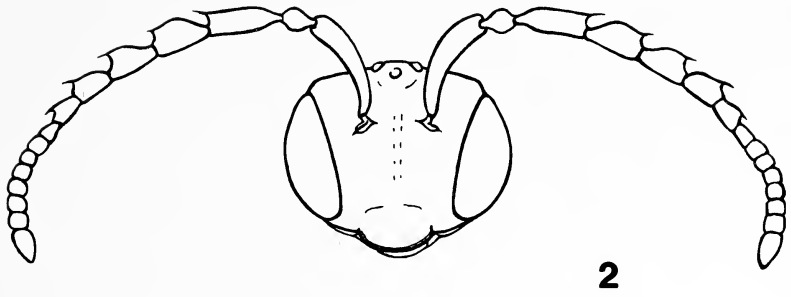
rugose sculpture; scutellar furrow 10-foveate, cross-carinae present; anterior margin of scutellar furrow carinate; propodeum rugo-areolate; propodeal impression present, as deep as basal width of petiole; postero-lateral corners of propodeum developed as prominent tubercles; petiolar notch short, not extending past metacoxal cavity; hind leg except tarsus coarsely granular; metafemur length 4.25× maximum width; tarsal claw simple.

Wings as in Fig. 3; stigma large, nearly semi-circular; basal vein gradually curved; second intercubitus absent; second cubital abscissa present; discoideus present; brachius present; first intercubitus present; radius reaching wing margin slightly before wing apex, radial cell longer than stigma; radius complete to wing margin, but more weakly sclerotized apically; metacarpus present, but very weakly sclerotized; recurrent vein present; subdiscoideus present; first cubital abscissa absent; nervulus postfurcal, bisecting discocubital cell; medius present; submediella present; nervellus present; costella present; radiella and cubitella present as weak infumation.

Metasoma with petiole not fused ventrally, smooth dorsally, rugose laterally, apex 4× broader than base, about 3/4 as long as metasoma beyond petiole excluding ovipositor; glymma absent; dorsope absent; petiolar spiracles near middle of petiole, moderately prominent; syntergum 2+3 shorter than 3/4 length of metasoma beyond petiole excluding ovipositor, several following segments exposed; sides of syntergum 2+3 not overlapping ventrally; lateral fold of syntergum 2+3 present; suture between terga 2+3 present laterally; ovipositor 0.94× as long as metasoma; sheaths shorter, about 0.56× as long as metasoma.

Diagnosis: In the key to genera of Euphorinae of the world by Shaw (1985) *Betelgeuse* will run to couplet 29, but will not key further because the scape configuration does not match either of the two alternatives at that point. In the identification manual for North American genera of Braconidae (Marsh *et. al* 1987) *Betelgeuse* will run to couplet 212, where it keys out near *Ecclitura* Kokujev from which *Betelgeuse* can be distinguished by its distinctive serrate antenna. Indeed, it can be distinguished from any other braconid genus by this character alone.

Phylogeny: The phylogeny of euphorine genera was reviewed by Shaw (1985, 1987). Because the fore wing lacks the first segment of



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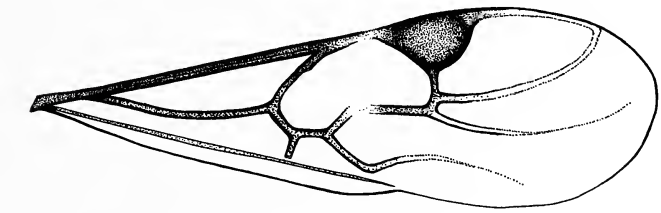

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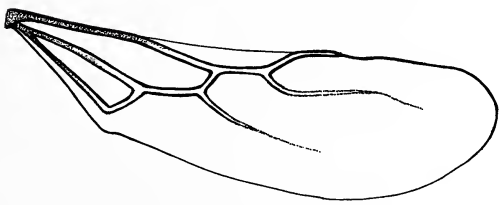

Fig. 2. *Betelgeuse aztecus,* head in anterior view.

Fig. 3. *Betelgeuse aztecus,* wings.

the cubitus, the phylogenetic position of *Betelgeuse* is not immediately obvious. The loss of this vein is synapomorphy defining the euphorine Section 3 (*sensu* Shaw 1985) cluster of tribes; however, *Betelgeuse* lacks the other three synapomorphies that define that

group: smooth mesopleuron, smooth scutellar disc, and carinate-rugulose propodeum. Furthermore, *Betelgeuse* does have a suite of synapomorphies which place it in the Section 2 tribe Dinocampini (*sensu* Shaw 1985): deep propodeal impression, coarse frontal sculpture, minute ocular setae, elongate scape, and 2-segmented labial palpus. In view of this, I regard *Betelgeuse* as a member of the Dinocampini, which has lost the first segment of the cubitus (a convergence with Section 3 genera). Within the Dinocampini, *Betelgeuse* has two synapomorphies of the lineage comprising *Dinocampus* + *Ropalophorus:* wide face, and areolate propodeum. At least two putative synapomorphies suggest a sister-group relationship with *Ropalophorus:* flagellum reduced to 13 segments or less (8 in *Ropalophorus*), and propodeum produced dorso-laterally as distinct tubercles. The latter is particularly convincing as a synapomorphy since it does not occur elsewhere in the Euphorinae, and was previously known only in *Ropalophorus.* The monophyly of *Ropalophorus* remains indicated by its 8-segmented clavate flagellum (Shaw, 1985). These relationships are expressed as a cladogram (Fig. 4) modified from Shaw (1985, 1987).

Betelgeuse aztecus, NEW SPECIES
(Figs. 1–3)

Holotype. Female, Mexico: Durango, 9000′, El Salto, 10 mi. W., 8 June 1964, (W.R.M. Mason). [Canadian National Collection, Ottawa]

Diagnosis of holotype female: Body length 3.83 mm; forewing length 2.92 mm; flagellomere length ratios (F1–F13) 19:14:12:11:9:6:5:5:5:5:5:5:8; malar space 0.16 eye height; ovipositor length 2.2 mm.

Body predominantly reddish brown except apex of antenna (F10–F13) and metasomal terga 2–7 infused with black; F6–F8 yellowish brown; wing venation dark brown; wing membrane hyaline except amorphous infused patch along basal vein and another below stigma; ovipositor sheaths dark brown; ovipositor yellowish brown.

Paratype female: Essentially as in holotype except F9 apically infused with black; F6–F8 more yellow.

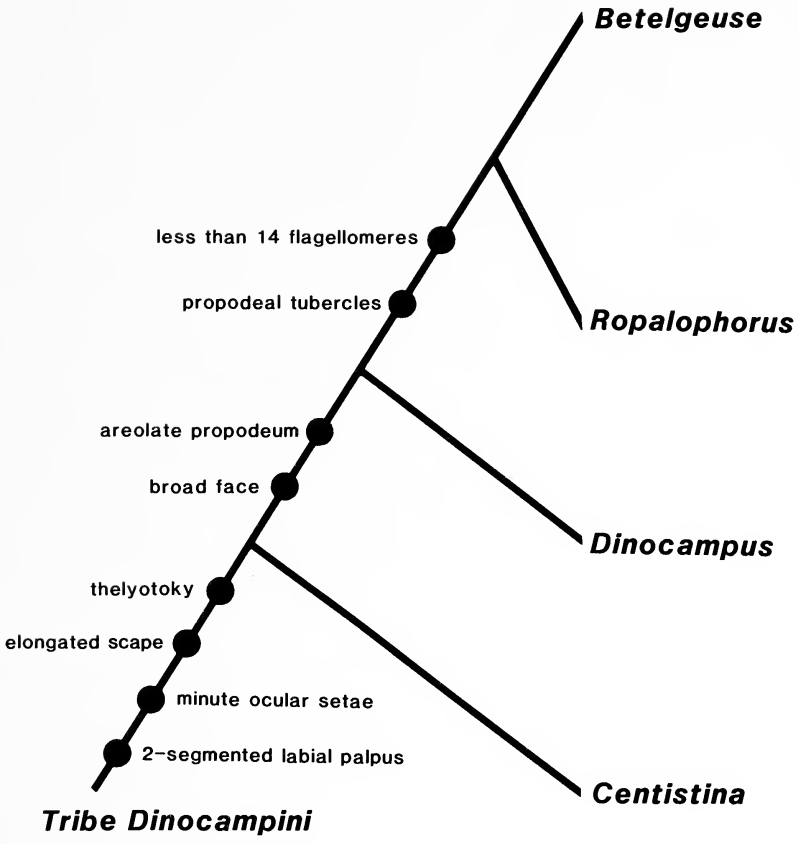

Fig. 4. Hypothesis of relationships among genera of the tribe Dinocampini. See text for discussion.

Male: Unknown.

Paratype data: 1 female, same data as holotype [Museum of Comparative Zoology, Cambridge].

Host: Unknown; however, the host is probably an adult beetle since other dinocampine species (*sensu* Shaw 1985) parasitize adult beetles (Shaw 1985, 1988).

Distribution: Known only from the type locality in Durango, Mexico.

Etymology: The specific epithet refers to the Aztec indian tribe in Mexico.

Acknowledgments

Figures 1–3 were prepared by Ms. Kathy Brown-Wing, who deserves much credit, especially for the care and meticulous detail applied to the habitus illustration. Thanks are due to Dr. M. Sharkey, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, for arranging the loan of these remarkable specimens and also for critiquing the manuscript. Additional thanks to Dr. P. M. Marsh, Systematic Entomology Laboratory, U.S. Department of Agriculture, c/o National Museum of Natural History, Washington D.C., who reviewed the manuscript as well, and provided many helpful comments. Special thanks are due to Dr. W. R. M. Mason, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, for collecting the specimens, recognizing their significance as a new euphorine genus, and calling them to my attention in the first place.

Summary

Betelgeuse aztecus Shaw, a new euphorine braconid genus and species from Mexico is described and illustrated. Reasons for placing it in the tribe Dinocampini are given, and its phylogenetic position relative to other genera in that tribe is discussed.

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A NEW METHOD FOR MARKING ANT LARVAE

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In most ethological studies, an observer must recognize individual animals or at least certain classes of animals in order to acquire meaningful information. Individual animals are distinguished either by morphological differences or through the application of a distinguishing mark by the investigator.

In recent studies conducted by Hare (1987) and Alloway & Hare (under editorial review) where brood of a slave-making ant species (*Harpagoxenus americanus*) and host species (*Leptothorax longispinosus*) were offered simultaneously to host species workers, an observer was required to identify the species of any given larva quickly and reliably. Species identification of ant larvae has traditionally relied upon one or more of the following morphological characteristics: general body shape, mandible shape, pattern, structure and abundance of hairs, location and abundance of integumentary spinules, head shape, dentition of the mandibles and physical characteristics of other mouthparts (see Wheeler & Wheeler, 1960). None of these characteristics are useful in distinguishing *Harpagoxenus* from *Leptothorax* larvae (Wheeler & Wheeler, 1960; Hare, personal observation). Thus for our research, we required a technique whereby larvae could be given a visible mark that would not bias the acceptance of marked versus unmarked larvae.

Several techniques have been developed for marking adult ants (see Stuart 1986 for a review). Techniques reported for marking brood either damage the brood (e.g. filling eviscerated larval skins with coloured gelatine; Brian 1975), or the marks do not persist because of grooming by adult workers [e.g. spots of of coloured wax applied to larval cuticle (Brian 1975), bits of coloured plastic glued

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to the larval cuticle (Isingrini et al. 1985) or coloured spots of paint applied to cocoons (R. J. Stuart, personal communication)]. Other techniques, although effective, are not efficient in terms of the time required to obtain marked larvae. For example, Brian & Rigby (1978) and Cole (1981) report that Sudan black, an oil soluble dye, fed to a queen results in the production of coloured eggs. Apparently, this mark is retained through all life stages including adulthood (R. J. Stuart, personal communication). For the purposes of our experiments, waiting for dye to be ingested by the queen and for the marked eggs to develop into larvae was inefficient.

Adult ants are known to devour even slightly damaged brood rapidly and to regurgitate this material to healthy larvae (Wilson, 1971). Thus it seems plausible that if a coloured substance is applied externally to brood that causes workers to perceive marked brood as damaged, the coloured substance will end up inside healthy larvae in the colony. Such a mark would be visible to a human observer through the translucent larval cuticle, and if effective would provide a rapid and inexpensive means of marking large numbers of larvae. Here I describe a technique for obtaining marked larvae, present data on the persistence of the mark, and demonstrate that marking does not bias larva acceptance by *Leptothorax ambiguus* or *L. longispinosus* workers.

Methods and Materials

Nests of both *L. ambiguus* and *L. longispinosus* were collected during September, October and November 1985 and from April through July 1986 at various sites within the regional municipalities of Halton and Peel, Ontario, Canada. Ant colonies were cultured in the laboratory employing techniques described by Alloway (1979) and Hare (1987).

In a pilot study, 10 larvae smeared with Testor's red enamel paint (#1150, commonly used to paint plastic models and available at local hobby retailers) were placed inside the nest of each of 17 *L. longispinosus* colonies. Within 24 h, 5 to 10 (8.5 ± 1.87 [mean $\pm$ SE]) of those larvae were cannibalized by adult workers. During this 24 h period, trophallactic exchange of food from workers to previously unmarked larvae resulted in a large proportion (0.63 ± 0.17 [mean $\pm$ SE]) of each colony's larvae becoming marked internally

with the paint. Between 31.5% and 85.7% of the previously unmarked larvae became marked internally, thus providing a minimum of 6 and a maximum of 34 marked larvae in the test colonies. The colour red was selected for use in all experiments because ants are not sensitive to light of this wavelength (Wilson, 1971), thus reducing the possibility of any visually mediated bias in larva acceptance.

To test for any influence of the mark on larva acceptance, an experiment was performed. Internally marked larvae were obtained by covering the mouthparts and at least 50% of the cuticle of several *L. ambiguus* larvae with Testor's red enamel and placing these larvae inside an *L. longispinosus* nest. Adults of the recipient colony cannibalized these larvae and in most cases fed this material to their own larvae. Allospecific larvae were used to 'transmit' the mark since they are less likely to be accepted for tending (see Hare and Alloway, 1987) and are thus more likely to be cannibalized.

On the next day, worker groups were established by choosing three *L. longispinosus* workers arbitrarily from each of 13 colonies and placing each group in a new culture dish with a nest, water vial and food (see Hare and Alloway 1987). Groups were allowed 24 hours to explore their new environment prior to testing.

Since Plateaux (1960) found that *Leptothorax nylanderi* workers could only distinguish between conspecific larvae and *Solenopsis fugax* larvae when conspecific larvae were present, larvae of the two 'types' were offered simultaneously to the workers. Under this protocol, a single larva of each 'type' (marked and unmarked) were placed on a clean glass coverslip and positioned immediately in front of the nest entrance. Within each pair, larvae were matched visually for size and placed as close together as possible, (but not in physical contact) in the centre of the coverslip. Workers were allowed to retrieve one larva into their nest, their choice was recorded, and a new pair of larvae was presented. Paired presentations of this sort continued until the supply of either marked or unmarked larvae for a given donor colony was exhausted. For the 13 worker groups (replicates) the number of initial paired presentations ranged from one to 12 (8.2 ± 0.8 presentations [mean $\pm$ SE], mode = 10 presentations). Since each worker group was derived from a separate maternal colony, replicates were independent and the difference in the number of the two types of larvae accepted in

paired presentations across groups can be analysed using the Wilcoxon paired sample test (Zar 1974). Occasionally more than one ant was involved in the retrieval of larvae, and in some instances both larvae were judged to be taken simultaneously. For the purpose of analysis those ties were omitted and the number of presentations for that group consequently reduced.

Following the series of paired presentations, marked and unmarked larvae which had not been taken were re-introduced in one large pile on a glass coverslip outside the nest entrance. The amount of time taken to retrieve the remaining larvae was recorded (if time allowed on the day of the trial) and the number of each type of larva remaining in the nest was recorded daily until the internal mark could no longer be distinguished (6 to 16 days). For each day, data were analysed using a heterogeneity Chi-Square test (Zar 1974) that compared the observed number of each type of larva in the nest tc an expected null difference within each group (i.e. if no preference were exhibited then we would expect equal numbers of the two types inside the nest) and for the pooled difference across groups.

The experiment was replicated using 16 *L. ambiguus* worker groups and larvae from their own maternal colonies. For *L. ambiguus,* the number of initial paired presentations ranged between five and 17 (9.0 ± 1.1 days [mean $\pm$ SE]). Data from these presentations are included and analysed as outlined above. However, the marked larvae used in these trials were marked seven to 10 days (7.7 ± 0.9 [mean $\pm$ SE]) in advance of the trials (i.e. these were marked for a pilot study addressing the feasibility of obtaining marked larvae). Consequently the record of the number of marked and unmarked larvae remaining in the nest became increasingly confounded over time as the internal mark faded or disappeared. This trend became noticeable on the third day of observations and thus for *L. ambiguus* data are only presented on acceptance over time for the first two days.

Results

Reliable data on the persistence of the internal mark are available only for the larvae offered to *L. longispinosus* workers in the "mark bias" experiment. In those trials, the mark duration ranged from six to 16 days (11.1 ± 1.0 days [mean $\pm$ SE], mode = 12 days) across groups.

In the series of simultaneous presentations neither *L. ambiguus* nor *L. longispinosus* worker groups showed a significant preference for retrieving marked or unmarked larvae ($T=32.5$, $P>0.50$ and $T=37$, $P>0.50$ for *L. ambiguus* and *L. longispinosus* respectively). An average of 4.7 ± 0.77 (mean$\pm$1 SE) marked and 4.3 ± 0.52 unmarked larvae were retrieved first by the 16 *L. ambiguus* groups while 4.3 ± 0.49 marked and 3.6 ± 0.51 unmarked larvae were retrieved first by the 13 *L. longispinosus* worker groups (Fig. 1, day 0). Furthermore, the number of groups accepting a greater number of marked larvae; unmarked larvae, or equivalent numbers of both types in paired presentations (Table I) was similar across the two species (3×2 contingency table analysis (Zar 1974), $x^2=1.1659$, $P>0.25$).

For both *L. ambiguus* and *L. longispinosus,* the data from individual worker groups were homogeneous on each day of observation and no significant preference for either marked or unmarked larvae was shown by any single group over the course of the study (all $P>.25$, see Appendix B-1 in Hare, 1987). Similarly, no significant differences in the number of marked and unmarked larvae remaining in the nests of either species were detected when data were pooled by day (all $P>.50$, see Appendix B-1 in Hare, 1987). The mean numbers of marked and unmarked larvae accepted by worker groups on any given day were similar, although at almost all time intervals the average number of marked larvae per nest was slightly higher than that for unmarked larvae (Fig. 1).

The large increase in the mean number of marked and unmarked larvae accepted for groups of both species between day 0 and day 1 reflects the fact that the day 0 data include only those larvae retrieved first in the series of paired presentations. Following this series of presentations, 'non-preferred' larvae were re-introduced and overall, 99.3% of the marked larvae and 97.2% of the unmarked larvae available to the *L. ambiguus* worker groups were accepted by day 1 while 98.3% of the marked larvae and 100% of the unmarked larvae available were accepted by *L. longispinosus* worker groups during the same period. Thus, even those larvae that were 'non-preferred' in a simultaneous choice situation were acceptable to *Leptothorax* workers.

The increase in the mean number of marked larvae in the *L. longispinosus* nests between days 14 and 15 (Fig. 1) is a result of the

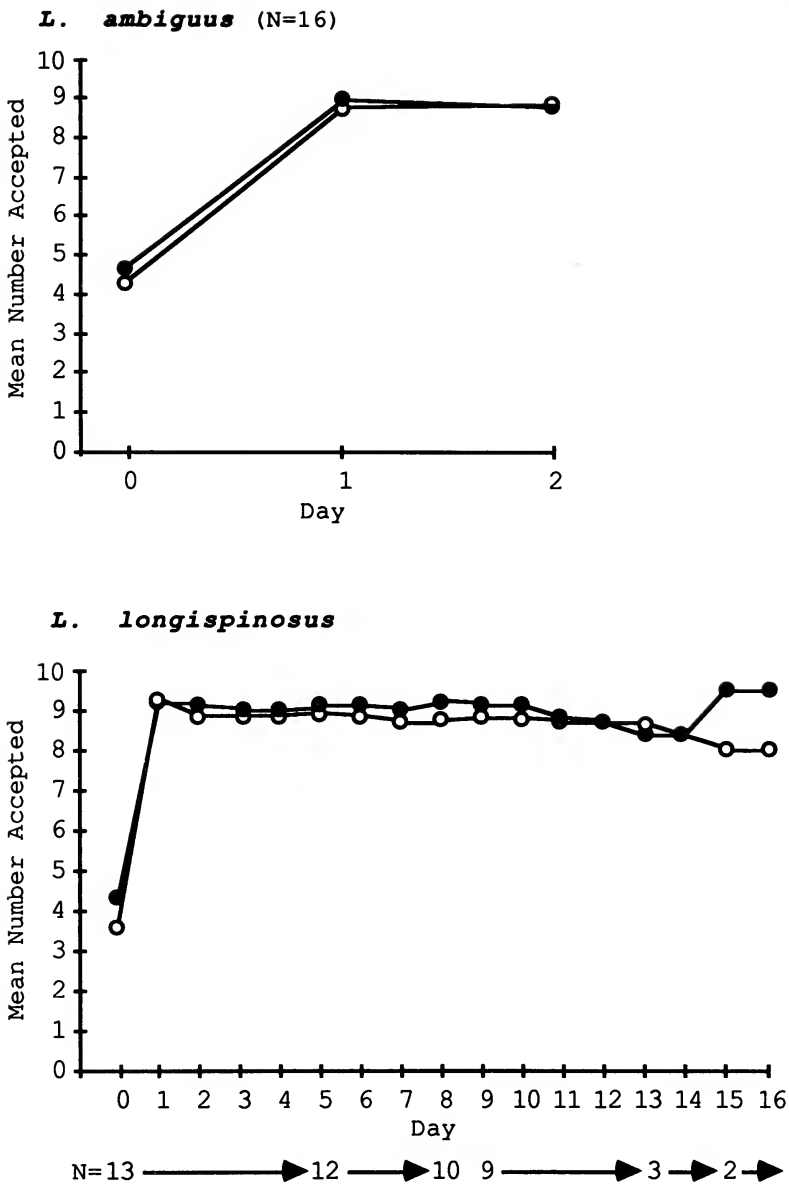

Figure 1: Mean number of marked larvae (solid circles) and unmarked larvae (open circles) accepted by *Leptothorax* worker groups over time. [Note Day 0 = number accepted upon termination of paired presentations].

Table 1. Initial preference profiles of *Leptothorax* worker groups.

	Worker Species	
	L. ambiguus	*L. longispinosus*
Groups accepting more marked larvae	7	8
Groups accepting more unmarked larvae	6	4
Groups accepting equal numbers of both types of larvae	3	1

reduced sample size and does not reflect a change in the number of larvae in the nests of the remaining groups (see Appendix B-1 in Hare, 1987). For the two *L. longispinosus* groups that were observed on the sixteenth day, 95% of the marked larvae and 80% of the unmarked larvae that were initially available remained intact within the nest. Without exception, marked and unmarked larvae were placed in a common brood pile within the nests of both species throughout the experiment.

Discussion

The introduction of larvae marked externally with Testor's paint provides an inexpensive and reliable technique through which large numbers of internally marked larvae can be obtained rapidly (<24h). Fading of the mark was perceivable in some groups as early as six days after marking, but remained visible in others to a maximum of sixteen days. Thus, this technique would not be useful in situations requiring an extended mark duration, but its utility would ultimately depend on the specific rate of trophallactic food exchange of the ants in question. The technique should also be limited to use with small worker groups since high rates of trophallaxis between larvae and workers in full colonies can lead to contamination of unmarked larvae with the mark (Hare, unpublished data). However, this would not present a problem over the short term since "contaminated" larvae possess a very faint mark relative to those introduced as "marked" larvae in the first place (Hare, personal observation). For the purposes of our experiments with *Leptothorax,* the mark duration was more than adequate and there were no instances of contamination in any trial using groups of three workers.

No significant preference for marked or unmarked larvae occurred at any time interval and overall neither *L. ambiguus* nor *L.*

longispinosus showed a preference on any day for marked or unmarked larvae. Furthermore, ants placed marked and unmarked larvae in a common brood pile within the nest. Thus the presence or absence of the mark itself did not influence larva-acceptance by *Leptothorax*.

Throughout the course of the experiment, deviations from equivalent numbers of marked and unmarked larvae accepted typically were in the direction of a greater number of marked larvae within both species. However, those deviations were quite small. The explanation for this pattern lies in the observed tendency of *Leptothorax* workers to prefer large larvae (Hare 1987). Whenever larvae were marked, it appeared that large larvae became marked more readily than small larvae. This in itself suggests that large larvae receive preferential treatment (in terms of regurgitation from adults) in their maternal colonies and results in uneven size distributions of marked and unmarked larvae. In spite of efforts to match larvae as closely as possible on the basis of size, marked larvae were often slightly larger than the unmarked larvae used, thus explaining any apparent trend towards preferential acceptance of marked larvae.

Summary

A technique is described whereby a visually observable mark can be transmitted to the gut contents of ant larvae. The technique is inexpensive, provides large numbers of marked larvae on demand, and is useful in situations requiring a mark duration of less than 10 days. Results of a choice experiment demonstrate that the mark itself does not bias larva acceptance by *Leptothorax* workers.

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POLYGYNY AND FUNCTIONAL MONOGYNY IN *LEPTOTHORAX* ANTS (HYMENOPTERA: FORMICIDAE)

By J. Heinze[1] and A. Buschinger[2]

The number of queens present in colonies of social insects may affect several features of colony structure, such as the relationship between workers within the nest. The high degree of relatedness of nestmates, which is thought to be one of the fundamental traits in the evolution of altruistic behavior in Hymenoptera, can be sustained only if all the female brood is produced by one single queen (monogyny) that has been inseminated by only one male (monoandry).

During the last two decades numerous studies on queen number and colony structure of ants have shown, however, that in about 50 percent of all species colonies may contain several fully fertile queens (Buschinger, 1974a). Some species (e.g., *Leptothorax acervorum* or *Myrmica ruginodis*) are facultatively polygynous; in other species (e.g., *Plagiolepis pygmaea* or *Formica exsecta*) virtually all colonies are polygynous. Colonies of some highly polygynous species, such as *Formica polyctena,* may contain thousands of queens. Polygyny may arise by the cooperative foundation of new colonies by several inseminated young females (pleometrosis), by the fusion of colonies, or by the adoption of young, inseminated females into a colony.

In some taxonomic groups, polygyny appears to be associated with ecological factors, such as patchy distribution of habitats or high instability of nesting sites (Hölldobler and Wilson, 1977), and recently queen number has been interpreted as an ecologically responsive trait, explainable by a combination of kin selection and ecological elements (Nonacs, 1988). An obvious advantage of polygyny on the colony level is that the presence of multiple fertile

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queens ensures the colony's continuation in the event of one or more queen deaths. In many monogynous species the death of the queen results in the dissolution of the colony (e.g., *Oecophylla* spec., Vanderplank, 1960). Polygyny, however, is not the only mechanism for queen replacement observed in ants. In some species, several dealate females may be present in a colony but only one lays eggs. Occasionally some of the extra females are sterile, uninseminated females that somehow missed the mating flight. Others are inseminated females, which do not lay eggs in the presence of the fully fertile queen. Tschinkel and Howard (1978) demonstrated the presence of these sterile, inseminated females in colonies of *Solenopsis invicta* by removing the single fertile queen. In 27 percent of the test colonies a previously sterile female began to lay fertilized eggs.

The presence of sterile, though inseminated females, in addition to a fertile queen has been termed "functional monogyny." Originally described by Pardi with the paper wasp, *Polistes gallicus* (1940; 1946), functional monogyny appears to be very rare in ants. In addition to *Solenopsis invicta,* in which it occurs along with polygyny and monogyny, functional monogyny has so far been proven to exist only in some species of the well-studied ant tribe Leptothoracini: in *Leptothorax gredleri* (Buschinger, 1968a), *Leptothorax sphagnicolus* (Francoeur, 1986), and in some, if not all species of the xenobiotic genus *Formicoxenus* (Buschinger, 1979a; Buschinger and Winter, 1976; Buschinger et al., 1980; Francoeur et al., 1985).

With the exception of *L. gredleri,* which is fairly common in some populations in Bavaria (Buschinger, 1966), functionally monogynous leptothoracines are quite rare. Thus, more detailed studies on colony and population structure are difficult. During the past few years, however, we have collected numerous colonies of a new, functionally monogynous species of *Leptothorax* closely related to the palaearctic species *L. muscorum.* The taxon is to be described by A. Francoeur (Univ. of Quebec, Chicoutimi); here we again refer to it as *Leptothorax* spec. A (Heinze and Buschinger, 1987). This ant is common in suitable habitats throughout Quebec and the northern part of New England, and it is abundant especially on the rocky shore of St. Lawrence River near Tadoussac, Quebec. A most important trait of *Leptothorax* spec. A is that it has a genetically mediated queen-polymorphism, with primarily winged, gynomor-

phic females and more or less workerlike, wingless queens, called intermorphs. Intermorphic queens most probably are of the genotype Ee and EE, whereas gynomorphs are always ee (Heinze and Buschinger, in prep.).

The small size of colonies and the ease of rearing them in the laboratory make *Leptothorax* spec. A an ideal ant for studies on colony and population structure and colony foundation behavior related to functional monogyny.

During our studies on *L.* spec. A we have gathered much data on the occurrence of polygyny in additional North American species of the subgenus *Leptothorax* s. str. M. R. Smith (= *Mychothorax* Ruzsky). In this paper we present field data and results of laboratory experiments concerning the colony structure of *Leptothorax* spec. A as well as field data on related species. In addition we summarize information on mono- and polygyny in some palaearctic *Leptothorax.*

Methods and Material

A total of 272 complete colonies of *Leptothorax* spec. A were collected in June 1983, 1985, and 1988 in Quebec (Tadoussac, La Baie, Laurentides). More than 250 additional colonies were gathered since 1979 in Quebec and adjacent areas of Ontario and Northern New England (Me.: Bar Harbor, Baxter State Park; N.H.: Mt. Monadnock). Some dozen colonies were kept alive for several breeding cycles under artificially shortened annual rhythms (Buschinger, 1974b), in the laboratory at TH Darmstadt, and for several months at room temperature in the MCZ labs in Cambridge.

Other *Leptothorax,* most living sympatrically with *L.* spec. A, were collected: *L. retractus* (Que.: Rouyn-Noranda; Alta.: Jasper, Banff), the presently undescribed *L.* spec. B (Que.: Tadoussac, La Baie, Laurentides; N.H.: Mt. Monadnock), *L.* spec. C (Alta.: Jasper, Banff, Kananaskis; B.C.: Yoho N.P.), and a *Leptothorax* species similar to *L.* spec. B (B.C.: Sutton Pass, Mt. Seymour, Manning Provincial Park).

Dissections of females and workers were carried out as described by Buschinger and Alloway (1978). Instead of killing the females by using acetic acid ethyl ether or ethanol, water with a drop of detergent was used in most cases, because it kills small ants faster than

ethanol and does not affect the condition of the ovaries by dehydration. The ovaries were prepared by removing the subgenital plate with a pair of tweezers under a binocular microscope at 30× magnification. Ovariole development, contents of the receptacle and presence of corpora lutea were studied at 30× to 70× magnification. The condition of the ovaries was rated using the following classification, based on a system by Buschinger (1968a) and Buschinger and Alloway (1978).

A-females	Inseminated, fertile queens. Ovarioles are elongated, corpora lutea are present. In the reproductive season they contain numerous eggs with white yolk deposits.
a-females	Old, inseminated females, sterile. No corpora lutea present, ovarioles are short. In gynomorphic females, wing muscles replaced by fat body. Fat body usually yellow.
b-females	Young, inseminated, sterile females. No corpora lutea, ovarioles are short, sometimes they contain one or two eggs. In gynomorphic females, wing muscles not yet degenerated, fat body white.
b->A-females	Inseminated, sterile, but eggs in development. Ovarioles more or less elongated, no corpora lutea present.
c-females	Not inseminated, sterile.
C-females	Not inseminated, ovarioles elongated, containing eggs. Corpora lutea present.

Since the color of the fat body, which changes from white in younger females to yellowish in older ones, was not noted in all cases, we do not differentiate between freshly inseminated, sterile females (b) and those which have already been inseminated during a past season (a-females). Likewise, we do not differentiate between older uninseminated females and young uninseminated females, which have not yet started sexual behavior. As sexuals eclose in late June and July in most areas, inseminated females collected in June or July should all have mated already during the last years, and thus be a-females. Whereas all recently eclosed gynomorphic females are winged, it is not possible to tell this year's intermorphic females from older ones without judging the color of the fat body. Only colonies with several A-females were called polygynous; those with

supernumerary a-females in addition to one single queen were called functionally monogynous.

Isoelectric focusing in ultrathin polyacrylamid gels was carried out to estimate relationships of nestmates within some colonies, and to secure conspecifity of allopatric colonies (Heinze and Buschinger, 1988).

Results

Leptothorax spec. A

Fifty four of a total of 206 queenright colonies of *Leptothorax* spec. A collected in June 1983, 1985, and 1988 contained more than one and up to seven females (Table 1). In additional colonies collected in July 1987 and 1988, we counted up to 10 and more females, most of them inseminated. Because at the end of July this year's females have eclosed and may already have mated, it cannot be ruled out, however, that the higher number of females found at that time may be a transient phenomenon and that the young mated females will leave their mothers' nests before hibernation. It is quite certain that all females found in June colonies have hibernated in the nest, and we also found females in July and even August whose fat body color indicated that they had not eclosed recently.

All of the females and some of the workers in 30 colonies collected in June, and in an additional 59 colonies collected in July, were dissected. In all but four colonies only one female was found to be inseminated and fertile and, thus, a queen; the other females, though most were inseminated, did not show any corpora lutea and their ovarioles were only poorly developed (Table 2). In at least two of the four colonies with two A-females, workers engaged in heavy fighting and the queens were attacked. In these cases it is probable that neighboring nests were mixed by error during collection.

Both gynomorphic and intermorphic queens were accompanied by inseminated, sterile females, gynomorphic or intermorphic or both, but the percentage of June colonies with a gynomorphic queen and additional females was distinctly smaller (4.2 percent) than that of comparable colonies with intermorphic queens (28.9 percent). This difference is striking in each of the June collections and it is present in the July collection also. The majority of the supernumerary females (61 out of 80) were inseminated, but sterile. In three queenright colonies all the additional females were uninseminated.

Table 1. Number of gynomorphic (G) and intermorphic (I) females in colonies of some species of the subgenus *Leptothorax* s. str.

Species and date collected	No. of colonies	Number of females: I 0	I 1	I 2	I 3	I 4	I >	G 1	G 2	G 3	G 4	G >	I+G 2	I+G 3	I+G 4	I+G >	Percentage of colonies with >1 female[1]: I	G	Σ
spec. A 6/83	88	18	38	7	2	1	1	18	-	-	-	-	1	1	1	-	22.4	0.0	20.0
6/85	120	40	38	7	1	1	10	16	-	1	1	-	1	-	1	3	33.3	11.1	32.5
6/88	64	8	30	7	4	1	1	12	-	-	-	-	-	-	1	1	30.2	0.0	26.8
7/88	87	13	20	2	3	3	2	36	7	-	-	-	-	1	-	5	33.3	16.3	23.0
spec. B 6/83	39	7						27	3	1	1	-						15.6	
6/85	32	12						13	2	2	-	3						35.0	
7/87	65	15						42	2	3	-	3						16.0	
6/88	6	1						3	1	-	-	1						40.0	
7/88	29	2						12	7	3	1	4						55.6	
retractus 7/88	14	-						11	-	1	-	2						21.4	
8/88	16	2						5	5	1	-	3						64.3	
spec. C 8/88	31	3						13	3	3	1	8						53.6	
Data from the literature:																			
acervorum[2]	754																	48.0	
muscorum[2]	294																	46.3	
gredleri[2]	190																	70.0	
kutteri[2]	22																	27.3	
spec. C[3]	27																	44.4	

[1]Excluding colonies without a female
[2]Buschinger, 1968a
[3]Buschinger, 1979b

Five colonies in the June samples lacked fertile queens, but had one to three intermorphic b->A-females and additional b-females. Of 36 colonies that had only a single female, 10 did not have a fertile queen but did have an intermorphic b->A-female, which in some cases was just ready to lay her first eggs. These presently queenless colonies usually were quite small and consisted of few (1 to 10) workers and some brood. We did not find any queenless colonies with gynomorphic b->A females. All gynomorphic females that were the only female in the colony were found to be fully fertile. (In these evaluations the 12 colonies with both female morphs were not included. Females were dissected in only five of these colonies; in one case the queen was a gynomorph. Genetically mediated queen polymorphism in *Leptothorax* spec. A turned out to be a helpful tool in evaluating the relatedness of the different females in a colony. In one colony from Tadoussac, for example, the intermorphic queen produced only intermorphic female sexuals. One of the supernumerary females, however, was an inseminated gynomorphic female.)

C-females, not inseminated, but fertile females, which produce males, were found in two or three colonies in the field.

Other *Leptothorax*

As the data in Table 2 indicate, colonies of the closely related *Leptothorax* spec. B, of the Western species *C* and of *L. retractus* frequently contained several females. Here dissections proved, however, that all three species regularly have truly polygynous societies. In colonies of spec. B, which were collected in June, usually all inseminated females were fertile. Colonies of *L. retractus* and *L.* spec. C were examined in August; here a certain percentage of the females may have been only recently inseminated and thus not yet fertile.

Colony founding in *L.* spec. A

Of the more than 500 colonies of *Leptothorax* spec. A collected by us since 1979 in North America, only two appeared to be incipient colonies, consisting of a single queen (one gynomorph and one intermorph) and brood. In two or three more cases the colony consisted of two females, one fertile, the other not, and brood. The occurrence of colonies without a fertile queen (see above) but with nearly fertile b->A-females, in June, suggests that colony foundation by budding or colony fission takes place.

Table 2. Dissection results in colonies of *Leptothorax* s. str. with more than one female. AA, two or more fully fertile queens (polygyny); AAb, AAc, AAbc, two or more fully fertile queens, accompanied by one or several b- and/or c-females (polygyny); Ab, Ac, Abc, one fertile queen, accompanied by one or several b-females (functional monogyny) and/or c-females; b, c, bc, one or several b- and/or c-females without queen.

	AA	AAb	AAbc	AAc	Ab	Abc	Ac	bc	b	c	Total	%AA
spec. A June	2[a]	1[a]	-	-	10	4	3	2	2	-	24	8.9
July	-	-	1	-	3	8	4	2	2	3	21	
spec. B	7	3	-	3	1	1	1	1	-	-	17	76.5
retractus	2	1	1	-	1	-	1	-	-	-	6	66.7
spec. C	1	-	-	1	-	1	-	2	2	2	9	22.2
Data from the literature:								bc, b, c				
acervorum[1]	40	2	3	12	3	2	54	5			121	47.1
muscorum[2]	3	-	5	1	17	15	9	6			56	16.1
gredleri[1]	-	-	-	-	26		20	-			46	-
spec. C[3]	2	-	-	-	-	-	-	-			3	66.7

[a]In two of these colonies fighting between workers was observed.
[1]Buschinger, 1968a
[2]Buschinger, 1967
[3]Buschinger, 1979b

In experiments carried out at the TH Darmstadt, *L.* spec. A females were given the chance to mate in arenas containing their maternal colony and in addition, empty nesting sites. Both winged gynomorphic and wingless intermorphic females perform a stationary sexual calling behavior similar to that of other leptothoracine ants, the so called "Locksterzeln" (Buschinger, 1968b). Whereas intermorphic females regularly started sexual display within a short distance of the nest entrance, winged females usually showed some flight activity before they began sexual calling.

Most intermorphic females returned into their mothers' colonies within a few hours after mating, and none of 41 intermorphic females, compared to 13 of 43 gynomorphic females, hibernated outside their mothers' nests. Under laboratory conditions no young, inseminated female, intermorphic or gynomorphic, successfully founded a colony on its own and raised brood during the first following summer. The majority of inseminated females, which were kept separate from workers, were able to survive two, three, or more hibernations. Both intermorphic and gynomorphic females left their

nests to search for food and fed their own larvae. Only one single gynomorphic queen, however, managed to rear her own workers in the second summer after mating; in most cases the brood eventually died.

In the laboratory, supernumerary females have been found to survive for several artificial breeding cycles in the presence of the old queen. Aggression of the workers toward their young inseminated sisters was observed only in colonies with gynomorphs. Here 13 of 19 females, which had been put back into their mothers' nest and were not given the chance to escape, were killed by workers within a few weeks after copulation, their antennae and legs having been cut off. The dissection showed that in most of these females the development of eggs had already started and the ovarioles were elongated. Four other inseminated females were tolerated in this colony for at least one hibernation. Foreign inseminated females were never tolerated by a colony, regardless of the morpha.

In several cases, fission of colonies with two or more inseminated females occurred after hibernation. Old nesting sites were abandoned and workers moved brood and adults into two or even three different new nesting sites. In comparable situations, colonies with only one single female usually gathered in one nesting site after a few days. Spontaneous fission of colonies with several females, however, led in three instances to two independent societies each, which did not exchange brood or workers. One colony fused again after two breeding cycles, but only after one of the two queens had died.

Queen replacement was observed in five colonies, where a hitherto sterile female became fertile after the old queen had died. In two colonies, this event was pursued in electrophoretical enzyme analysis. The esterase locus #7 is variable in *Leptothorax* spec. A and in other related species; its at least four different allozymes can be separated by isoelectric focusing (Heinze and Buschinger, 1988). Queen replacement was reflected in a change of the esterase genotype of worker pupae. A colony from Baie Ste. Catherine, Que., which before had workers with the esterase genotypes BC and BD, now reared diploid brood with the genotype AC, too, thus decreasing the relatedness of workers within the colony. In an additional colony from Rivière Romaine, Que., queen replacement led to a change in the morpha of young females. Whereas the old queen had

reared both morphs, the replacement queen only produced intermorphic females.

Of the 222 colonies of *Leptothorax* spec. B two contained a single queen and brood only, and a third one consisted of two fertile females and brood. Three more colonies might have been incipient, too, but here one worker had already eclosed. However, 7 of 14 colonies of a dark brown ant morphologically similar to *L.* spec. B, which were collected near Vancouver, B.C., in August 1988, were found without workers.

Discussion

The ant tribe Leptothoracini consists of several hundred species of small- to medium-sized ants, which form colonies of several dozen to few hundreds of workers. It exhibits a rich variety of different social structures and colony foundation behaviors. Apart from social parasites, which may be inquilines, degenerate slavemakers, active dulotes, and xenobiotic guest ants, the non parasitic species have been found to be obligatorily monogynous, functionally monogynous, or facultatively polygynous (Buschinger, 1974a).

We here report on functional monogyny and polygyny in some species of the subgenus *Leptothorax* s.str. M. R. Smith (= *Mychothorax* Ruzsky) from North America. Between 20 and 30 percent of the colonies of *L. retractus, L.* spec. B, and *L.* spec. C are truly polygynous. The fertility of several inseminated females has been proven by dissection; in a number of cases, egg-laying has been directly observed. In *Leptothorax* spec. A, about one-fourth of all colonies with intermorphic queens contained additional, inseminated females, again mostly intermorphs, which in almost all cases have been found to be sterile. An occasional polygyny in *Leptothorax* spec. A cannot be ruled out but it seems to be very rare.

There are two important differences between functional monogyny in polistine wasps and in Leptothoracini. In *Polistes gallicus,* Pardi (1940; 1946) had observed that when two females cooperate in colony foundation, the more aggressive one becomes queen, and the subordinate one becomes worker. In colonies with several females, however, ovary size and fertility correspond to the female's rank in a dominance hierarchy. Several females may lay eggs, though in differing degrees, and functional monogyny is sometimes guaranteed only by differential egg consumption by the dominant α-female

(Gervet, 1964). In most cases the coexistence of several inseminated females in one nest is transient, and it resembles the regulation of queen number in obligatorily monogynous ants after colony foundation by pleometrosis (Buschinger, 1974a). In leptothoracine ants, on the other hand, functional monogyny is total and may be a lasting phenomenon. Only the queen has fully developed ovaries; those of the supernumerary females are always undeveloped. The presence of b->A-females with elongated ovarioles in colonies of *Leptothorax* spec. A is restricted to a short period of time and leads to colony fission or, as was observed in the lab, to aggressive behavior toward the young female and finally to her death. Whether dominance hierarchies exist in colonies with several supernumerary females, as in *Polistes,* is not yet known.

Our observations suggest that, comparable to primary and secondary polygyny, functional monogyny in Leptothoracini may arise in two ways. Intermorphic females, and perhaps gynomorphic females also, are easily accepted in their mothers' colonies after mating, and they may stay there for several breeding cycles. The other possibility, a pleometrosis-like colony foundation with several inseminated young females, one of which becomes fertile, has been observed in the field only two or three times. The find of a gynomorphic supernumerary female in a colony with an intermorphic queen which produced only intermorphic female sexuals does not necessarily indicate that foreign females are adopted; the gynomorph might have accompanied a sister during pleometrosis or budding.

According to our results, all species belonging to *Leptothorax* s. str., including *L. acervorum, L. muscorum,* and *L. gredleri* from Eurasia, may have colonies with several inseminated females, as is the fact too in some of the parasitic species, e.g. *L. kutteri* (Buschinger, 1968a), and in the genus *Formicoxenus,* which seems closely related to *Leptothorax* s. str. In the subgenus *Myrafant* and its satellite genera *Epimyrma, Myrmoxenus, Chalepoxenus,* and *Protomognathus,* however, most species are obligatorily monogynous. In *Myrafant* and its parasites, facultative polygyny occurs only occasionally as in the North American species *L. longispinosus, L. ambiguus,* and *L. curvispinosus* (Alloway et al., 1982), or in *Epimyrma algeriana* (Buschinger et al., in prep.). In studies on polygyny in different populations of *L. longispinosus,* a latitudinal cline in the frequency of multiple-queened nests has been suggested;

southern populations seem more likely to be monogynous than northern populations (Herbers, 1986a). Several other factors influence the pattern of polygyny, such as the scarcity of available nest sites (Herbers, 1986b). Neighboring populations, therefore, may differ in the frequency of polygynous colonies, as was shown, e.g., in *L. curvispinosus.* In one population 75 percent of the colonies contained several females, but in a population 7 km away only 38.8 percent were polygynous (Stuart, 1987).

The facultatively polygynous and functionally monogynous species of the subgenus *Leptothorax* s. str. usually live in boreal or alpine coniferous habitats. Of all North American ants, *L. "muscorum",* comprising several species like *Leptothorax* spec. A, B, and C, is the species best able to survive in extreme arctic and alpine conditions (Brown, 1955). With colonies found in north Alaska (Nielsen, 1987) and near the tree line in Nouveau Québec (Francoeur, 1983), both *L. "muscorum"* and *L. acervorum* are among the few species of Formicidae that are found so far north.

Species of the subgenus *Myrafant,* on the other hand, are abundant in areas with mild conditions in winter, such as the Mediterranean. Of the numerous species of this subgenus, only five reach Scandinavia, including Denmark (Collingwood, 1979), and among those are the facultatively polygynous *L. tuberum* and *L. interruptus* (Buschinger, 1968a; 1974a) and *L. nylanderi,* of which polygynous colonies have occasionally been found in the field (Chauvin, 1947; Plateaux, 1970). Populations of *Myrafant* in alpine areas, such as *L. tuberum* in the Alps, tend to be facultatively polygynous as well (Buschinger, 1968a), and facultatively polygynous *L. longispinosus* and *L. ambiguus* are the only *Myrafant* to be found in Quebec or Ontario (Creighton, 1950). Some populations of *L. rugatulus* found at higher elevations in the Rocky Mountains apparently are facultatively polygynous, too (S. Cover, pers. comm.).

As Bolton (1986) has pointed out, polygyny and colony fission in certain African and Levantine species of the *Monomorium salomonis* group might be an adaptation to hot and dry summers, which eventually has led to the evolution of apterous or workerlike queens.

Colony structure and intermorphic females in the ant tribe Leptothoracini might be an analogous adaptation to extremely cold climates. In areas with long and severe winters a young female perhaps will have more success in raising offspring if she hibernates in a

conspecific colony (whether becoming fertile there or not) and founding her own colony in one of the following springs either solitarily or by budding or colony fission. Whereas independent colony foundation by young *Myrafant* queens has frequently been observed, females of *Leptothorax* s. str. have only occasionally been found to hibernate solitarily. Buschinger (1968a) collected 13 incipient colonies, consisting of queen and brood only, in a total of 754 nests of *L. acervorum,* and 2 in 319 colonies of *L. muscorum.* Incipient colonies are rare in *L.* spec. A and B, too, far too rare to explain the abundance of mature colonies. Observations made in August 1988 on Mt. Seymour near Vancouver, however, indicate that there is a certain percentage of gynomorphic *Leptothorax* females which do not immediately return to conspecific colonies after mating. A similar behavior was observed in gynomorphic females of *Leptothorax* spec. A. in laboratory experiments. The rarity of incipient colonies in spring might perhaps be due to a low survival rate of solitarily hibernating females or to a return of females into conspecific colonies in late fall.

In *L.* spec. A queen polymorphism, together with differences in mating behavior, may have led to alternative dispersal strategies. Intermorphs mate in the immediate neighborhood of their colonies and are easily accepted back after mating, hence the high percentage of nests with supernumerary intermorphs in the field. Gynomorphic females, on the other hand, show some flight activity before starting sexual calling behavior, and might not be able to find their way home. In constrast to *L. acervorum,* where allozyme data suggest that foreign females perhaps are tolerated in other colonies (Douwes et al., 1987), in *Leptothorax* spec. A workers show aggression toward foreign young inseminated females, and eventually kill them. After hibernation in conspecific nests, females of *Leptothorax* s. str. might found colonies either solitarily, as was assumed for *L. muscorum* (Buschinger and Winter, 1978), or by budding.

In polygynous species, colony fission might increase the kinship in the daughter colonies compared to that in the mother colony by giving the workers the chance to arrange in different matrilines (Crozier, 1981), and indeed the segregation of workers into sororities has been observed in the honey bee (Getz et al., 1982). In functionally monogynous species, however, the overall level relatedness might decrease by budding, similar to the relations in colony fission

in army ants. The evolution of the colony fission mode of reproduction, a phenomenon common in army ants (e.g., Franks and Hölldobler, 1987), was analyzed by Macevicz (1979) both from the kin selectionist and parental manipulationist point of view. Thus, in some cases workers might not suffer a loss in their own inclusive fitness by accompanying their sisters and rearing nieces and nephews instead of brothers and sisters. Workers, e.g., might select the queen with the higher life expectancy, instead of staying with their mother. In honeybees, the old queen leaves the nest and incurs the risks involved with founding a new colony, but almost no details are known about the circumstances of budding in *Leptothorax* ants. Allozyme data (unpubl. results) did not shown any evidence for inbreeding in *Leptothorax* spec. A, which would increase the relatedness between workers and their nieces.

Additional field studies are under way to screen annual changes in colony and population structure of *Leptothorax* spec. A and to find out more about the success of colony foundation behaviors in different habitats.

Summary

Data are given on the colony structure of some North American ant species belonging to the myrmicine subgenus *Leptothorax* s. str. The species studied by now are either functionally monogynous (i.e., sterile, inseminated females may accompany the queen, *Leptothorax* spec. A) or facultatively polygynous (i.e., several fully fertile, inseminated queens may contribute to the offspring). Incipient colonies of these species are rare in the field; young females probably return into conspecific colonies after mating in summer and found their own colonies by budding in spring. The behavior of young intermorphic and gynomorphic females after mating was studied in the functionally monogynous *Leptothorax* spec. A. In this species, queen replacement and colony fission were observed, too.

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A PHYLOGENETIC INVESTIGATION OF *HYDROVATUS*, METHLINI AND OTHER PLESIOTYPIC HYDROPORINES (COLEOPTERA: DYTISCIDAE)*

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Introduction

Phylogenetic relationships of the Dytiscidae are receiving increased attention (*e.g.* Burmeister 1976, 1980; Brancucci and Ruhnau 1985, Dettner 1985). This paper is the fifth in a series on primitive hydroporine genera (Wolfe and Matta 1981; Wolfe 1985; Roughley and Wolfe, in press; and Wolfe and Roughley, in press). The first purpose of this paper is to investigate new discoveries concerning the remarkable abdominal structure of methlines and members of *Hydrovatus* Motschulsky. The peculiar modifications of terminal abdominal terga of members of *Hydrovatus* and Methlini provide good evidence for monophyly of these taxa. The second purpose is to revise a previous hypothesis (Wolfe 1985) of relationships among plesiotypic hydroporines in light of: 1) the new evidence regarding hydrovatine and methline monophyly, 2) more information on *Laccornellus* Roughley and Wolfe, 3) different interpretations of some character systems, and 4) computer generated phylogenies.

Materials and Methods

Analyzed species are listed in Table 1. Authors of species and genera are listed the first time a name is used in text only if the name is not listed in Table 1. Table 2 lists characters used in this analysis but see Wolfe (1985) for complete details and illustrations for characters 1–18.

Dissecting, illustrating, and scanning electron microscope (SEM) techniques are presented in Wolfe (1985). In order to understand the

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derivation of the abdominal structure of specimens of Hydrovatini and Methlini, comparisons were made with members of other hydroporine and nonhydroporine genera listed in Table 1.

Relationships between taxa were determined by phylogenetic techniques (essentially Hennigian) that are outlined in Wiley (1980), and Nelson and Platnick (1981). However, phylogenies in the analysis herein were generated and/or analyzed in part with computer programs developed by Dr. D. Swofford (PAUP, Phylogenetic Analysis Using Parsimony, version 2.4).

Results

Abdominal structure in members of Hydrovatini and Methlini

Three basic abdominal morphotypes (1–3) are recognized. These three types form a spectrum from the unmodified posteriorly rounded, lightly sclerotized terminal tergum found on members of *L. difformis* (Figs. 1A–B) (type 1), to intermediate modifications as found in specimens of *H. pustulatus* Melsheimer (type 2) (Figs. 1C–D), to the most derived condition in methlines (type 3) (Figs. 2A–D).

Morphotype 1. (Fig. 1A). In all examined specimens of *Canthyporus* Zimmermann, *Deronectes* Sharp, *Hydroporus* Clairville, *Laccornis* Gozis, *Oreodytes* Seidlitz and all nonhydroporines, the posterior edge of the eighth tergum is broadly and evenly convex in dorsal view. The eighth tergite is folded ventrally inward as a ventral flap or fold; this folded portion is hereafter referred to as the ventral fold (Fig. 1B). The ventral fold extends anteriorly for about 25 per cent of the length of the last segment. The outwardly visible posterior edge of tergum-8 then, is actually the point at which the tergum folds underneath. This character state is clearly evident in many of the abdominal/genitalic illustrations in Burmeister (1976, 1980).

Morphotype 2. (Figs. 1C–D). On males and females of *Hydrovatus,* only the apical tergum is distinctly modified; it is narrow, acutely pointed, and it is differentiated into a dorsal and ventral lamina (Fig. 1C). Neither lamina is distinctly sclerotized, but the ventral lamina is more membranous than the dorsal lamina (Fig. 1D). Dissections were difficult but it appeared that the dorsoapical portion of the ventral lamina possessed a slight inward fold and no ventral fold was evident on the dorsal lamina.

Table 1. List of species of Dytiscidae examined only for abdominal structure.

Hydroporinae
Canthyporus hottentotus Gemminger and Harold
Celina grossula J. LeConte
Celina hubbelli Young
Celina imitatrix Young
Deronectes striatellus J. LeConte
Hydroporus aulicus J. LeConte
Hydrovatus pustulatus Melsheimer
Hydrovatus sp. (from Sri Lanka)
Laccornis conoideus J. LeConte
Laccornis deltoides Fall
Laccornis etnieri Wolfe and Spangler
Laccornis lugubris (Aubé)
Laccornis copelatoides Sharp
Methles cribatellus Fairmaire
Oreodytes quadrimaculatus (Horn)
Queda compressa Sharp
Colymbetinae
Agabus spinipes Sharp
Colymbetes sculptilis Harris
Lancetes sp.
Dytiscinae
Dytiscus fasciventris Say

The terminal tergum of specimens of *Q. compressa* Sharp is most similar to morphotype 1.

Morphotype 3. (Figs. 2A–D). In this morphotype, the seventh and eighth terga are modified in both males and females. Tergum 8 is extremely acutely pointed posteriorly and also consists of a dorsal and ventral lamina. The ventral lamina (Fig. 2B) is a thin, flexible, triangular structure that is similar to that of *Hydrovatus;* the lateral edges are fringed with setae and curved dorsally thus forming a broad channel into which the dorsal lamina rests.

The dorsal lamina (Fig. 2A) is quite sclerotized, rigid, and overall rather wishbone-shaped. Posteriorly, the structure is somewhat trifid with the medial portion extremely prolonged, laterally compressed, and apically acute; the apicolateral portion is densely setose. Anteriorly, the dorsal lamina extends as a pair of diverging thin apodemes. Each apodeme expands anteriorly into a club shaped apex and extends anteriorly underneath the seventh tergum all the way to the posterior edge of the sixth tergum (Fig. 2D).

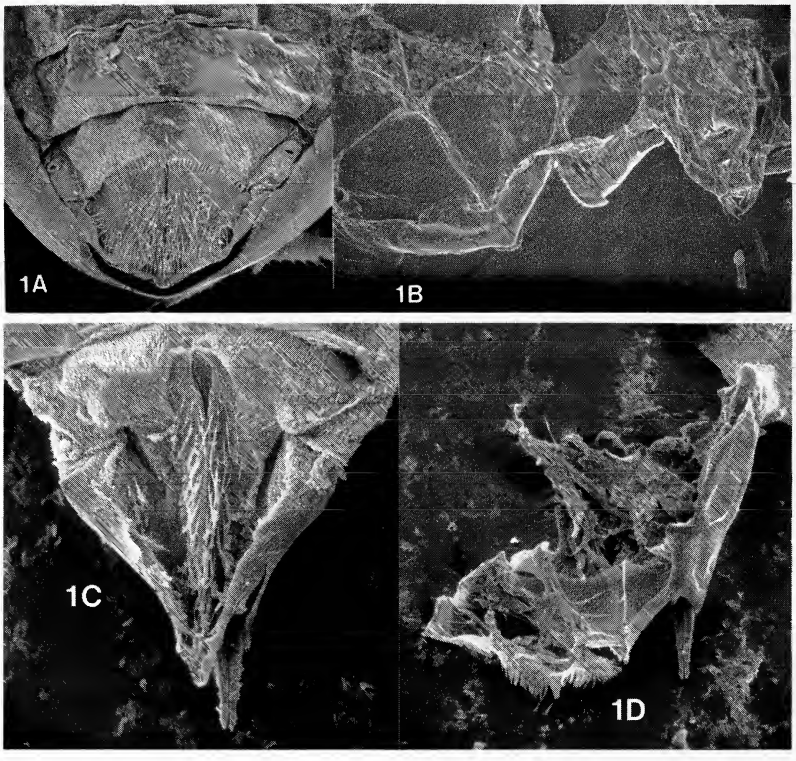

Figure 1. Terminal abdominal structure in *Laccornis* and *Hydrovatus*. A) Dorsal view of terga 6–8 of *Laccornis difformis* (40×) B) Dissected abdominal apex of *L. difformis* (40×). Tergum 8 is folded back (all the way to the left) so that ventral surface is exposed revealing ventral fold (indicated by arrow); tergum 8 is not bilaminar. C) Acutely pointed eighth tergum of *Hydrovatus pustulatus* (80×). D) Dissected abdominal apex of *H. pustulatus*. Tergum 8 is folded so that dorsal lamina (left arrow) is separated from ventral lamina (right arrow) (60×).

The anterior edge of tergum 7 (Fig. 2C) is expanded anteriorly as a broad, bisinuate flange with a short anterolaterally extended apodeme at each anterolateral corner. Apodemes of tergum 7 extend anteriorly for 75 per cent of the length of tergum 6.

The function of the modified methline abdominal structures has not been observed. Ovipositional function is ruled out because modifications are identical in males and females. Perhaps, the acutely pointed and sclerotized apex is a device for puncturing plant tissue to obtain trapped air. It is interesting that a similar behavior has

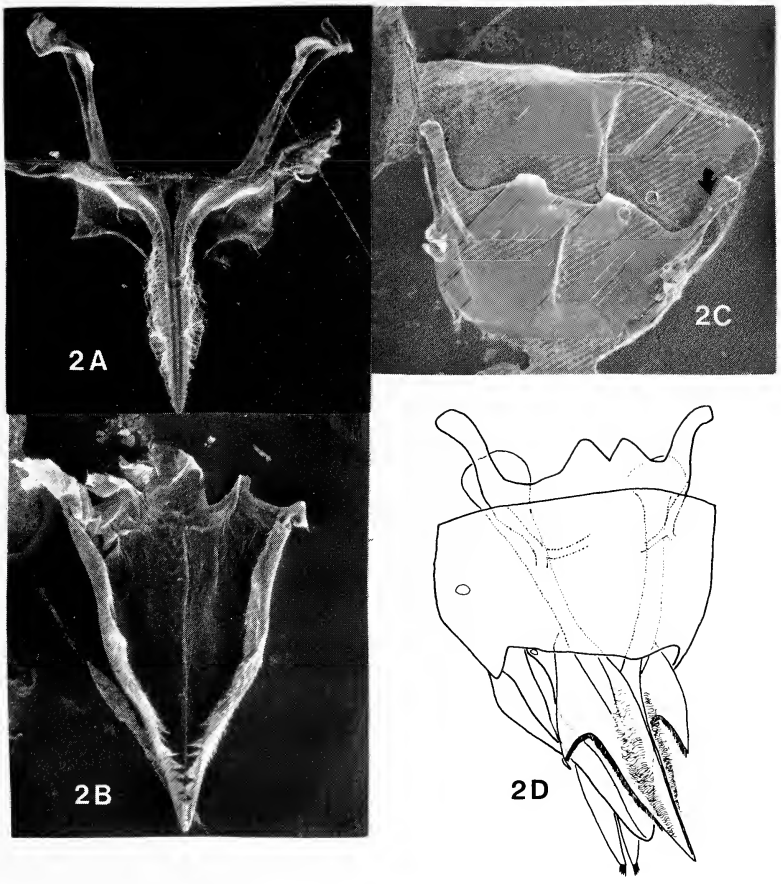

Figure 2. Abdominal structure of *C. hubelli* (60×) A) Acute, pointed, spear-shaped dorsal lamina of tergite 8. B) Ventral lamina. C) Ventral view of terga 6 and 7 showing apodemes on tergum 7. D) Composite illustration of terga 7 and 8.

been postulated for larval methlines because of the peculiar posteriorly extended lateral tracheal trunks located at the abdominal apex (Spangler 1973).

Discussion

Wolfe (1985) presented considerable evidence that Hydroporinae is monophyletic. Among taxa examined (Table 3), *Laccornis,* Methlini, Hydrovatini, *Canthyporus,* and *Lioporeus* were considered the

most plesiotypic lineages. It also was suggested that: 1) Hydrovatini and Methlini were sister taxa, 2) Bidessini, *Oreodytes,* and *Hygrotus* Stephens were relatively more plesiotypic than *Hydroporus, Deronectes* s.l., Vatellini, and *Graptodytes* Seidlitz, and 3) *L. lugubris* and *L. copelatoides* were related more closely to *Canthyporus* than to *Laccornis.*

Since that information was published, several studies have increased significantly our understanding of plesiotypic groups. First, information provided herein more definitely supports monophyly of *Hydrovatus* and Methlini. Second, Roughley and Wolfe (1987) definitively demonstrated generic status of *L. copelatoides* and *L. lugubris* and assigned those species to a new genus, *Laccornellus;* evidence supporting a close relationship between *Laccornellus* and *Canthyporus* was reviewed. Third, Wolfe and Roughley (in press) completely revised *Laccornis* and described a new tribe, Laccornini, for the genus.

In light of this new information, the phylogeny of plesiotypic hydroporines proposed by Wolfe (1985) is re-evaluated below. The analysis herein is facilitated by phylogenetic computer programs (PAUP) not previously available to me. I have found that use of these programs supplements interpretation of hypotheses by: 1) more accurately and repeatedly revealing the number of equally parsimonious trees derivable from a character matrix, 2) permitting rapid calculation of consensus trees so that similarities between equally parsimonious trees can be ascertained, 3) more definitively allowing assessment of assumptions used in tree construction (*e.g.* character weighting, character ordering, and addition and elimination of taxa), and 4) allowing easier comparison of trees in terms of homoplasy and tree length.

In summary, it must be stressed that computer generated phylogenies are not intrinsically better than mentally computed trees. However, I think that singular reliance on mental computations can be biased too easily by preconceived notions/hypotheses concerning one or two trees that investigators often have in mind before in depth analyses even begin. Compared to purely mentally constructed hypotheses, computerized constructions (and associated kinds of output) reveal in a more definable and consistent way the frailties of a given hypothesis(es). Although various assumptions/limitations that are explicitly exposed through computer analysis

Table 2. Synopsis of plesiotypic and apotypic characters used in analysis. Unless otherwise indicated characters are from the adult stage. See Wolfe (1985) for complete details and illustrations for characters 1–18. Character 19 illustrated herein.

Character	Plesiotypic state	Apotypic state
1. Mandibles	ventral medial setae present	ventral medial setae absent
2. Labial spines	in multiple rows, spines smaller	in single (at most double) row, spines larger
3. Larval nasale	absent	present 1—without notch 2—with notch
4. Larval galea	present	absent (reduced in Methilini)
5. Prosternum	not declivous	declivous
6. Prosternal pore	absent	present
7. Scutellum	exposed	concealed
8. Elytral ridge	reduced, not carinate	present 1—carinate 2—slightly posteriorly elevated 3—distinctly posteriorly elevated 4—ligulate
9. M4 vein	contacting oblongulum	not contacting oblongulum
10. Base of metafurca	not produced and cleft	produced and dorsally cleft 1—indistinctly developed 2—distinctly developed
11. Proventriculus	sclerites of sulci with longitudinal ridge and/or teeth	sclerites of sulci with transverse teeth
12. Protarsomere	pentamerous	pseudotetramerous 1—indistinctly pseudotetramerous 2—distinctly pseudotetramerous
13. sublateral row of spines of mesotibia	sparser (state 0)	states 1 to 3, indicate increasing density
14. Proximity of metafemur to metacoxal process	touching to scarcely separated	distinctly separated
15. Valvifer	present	absent
16. Apodeme of genital valves	absent	present
17. Posterior apex of body	not acuminate	acuminate
18. Larval urogomphi	short	long
19. Posterior tergite	not apically acute and bilaminar	1-tergum-8 only modified; acute and bilaminar 2-tergum-7 and 8 modified; tergite-8 sclerotized, trifid and spear shaped

may require that data be much more conservatively interpreted (see below), it no way implies that the only good character data is that data which produces one (or a few) easily interpreted, most parsimonious tree(s). Furthermore, many assumptions (*e.g.,* character-weighting, assumed monophyly of subgroups, occurrence of equally parsimonious trees) that require explicit enumeration with a computerized approach are used implicitly (sometimes ignored) in mentally produced hypotheses.

Hydrovatini-Methlini monophyly

Polarizing the character states of members of *Hydrovatus* and Methlini is rather straight forward. Morphotype-1 occurs in members of *Hydroporus, Deronectes, Oreodytes, Canthyporus, Laccornis,* and all non-hydroporines (see Table 1). It is logical to postulate a morphocline that proceeds from morphotype-1, through morphotype-2 and culminating in morphotype-3. Thus the structural modifications of morphotype-2 are a synapotypy unifying *Hydrovatus* and Methlini and the apotypic modifications associated with morphotype-3 phylogenetically cluster *Methles* and *Celina.* These latter facts help offset the conflict created by the exposed scutellum in members of *Celina* and concealed condition in *Methles.*

There are potential synapotypies for *Queda* and *Hydrovatus:* the prosternal process is extremely broad, the metafurca is reduced in size and wishbone shaped, an elytral humeral carina is present, and the internal elytral ridge is expanded throughout its length in members of both genera. However, I had hoped that the unification of *Queda* and *Hydrovatus* in Hydrovatini (Zimmerman 1920) could be supported further through this analysis; unfortunately this is not the case. As stated above, abdominal modifications are plesiotypic in members of *Queda,* so much so that inclusion in Hydrovatini based on the structure of tergum 8 is not obvious. Furthermore, the metafemoral apices are distinctly separate from the metacoxal lobes in members of *Queda* (apotypic) while in *Hydrovatus* and methlines the metafemora almost attain or do reach the metacoxal lobes (plesiotypic). In summary, recent studies are making the phylogenetic relationship of *Queda* more enigmatic rather than more understandable and this genus requires further study.

Phylogenetic re-evaluation of plesiotypic Hydroporines

The analysis below is based on a modified version (Table 3 herein) of the character state matrix of Wolfe (1985, Table 2, pp. 136–137).

Previously there were tabular errors associated with two characters. Character-2 (arrangement of labial spines) for members of *Q. compressa* should have read 0, not 1. For character-14, I intended proximity of the metafemoral base to the metacoxal lobes to be coded dichotomously; therefore, each 2 in that column should have been 1 and the 1 recorded for specimens of *L. lugubris* and *L. copelatoides* should have been 0. These were tabular errors only and were not incorporated into the phylogeny proposed by Wolfe (1985). It was indicated that medial mandibular setae were absent in all hydroporines; however, there is a reduced row on specimens of *M. mexicanus* Sharp and *O. rivalis* (Gyllenhal) that is difficult to see; therefore, character 1 should have read 0, not 1, for these two species. The discovery of medial mandibular setae in *M. mexicanus* and *O. rivalis* did not alter their phylogenetic placement; these two taxa still are regarded as rather apotypic.

Previously, I was not sure about the status or placement of *L. lugubris* and *L. copelatoides.* However, further study (Roughley and Wolfe, 1987) adequately demonstrated that those species formed a distinct unit and they were assigned to a new genus, *Laccornellus,* and *Laccornellus* is included in the analysis below.

Before analysis with PAUP was conducted, groups of identical taxa were identified and each group was represented by one species. With these modifications, computer analysis revealed more than 100 equally parsimonious trees: however, it is interesting to note that a consensus tree of these first 100 trees showed the same basic patterns as previously proposed in Wolfe (1985).

To reduce the number of equally parsimonious trees below 100, I represented several groups considered to be monophyletic by one species. *L. triangularis* (Fall) was used for *Lioporeus, L. kocai* (Ganglebauer) for *Laccornis, U. lacustris* (Say) for Bidessini, and *M. cribatellus* Fairmaire for the clade that includes Methlini and Hydrovatini. Justification for monophyly of *Lioporeus* and *Laccornis* is based on information in Wolfe and Matta (1981) and Wolfe and Roughley (in press) respectively. Bidessini is considered monophyletic based on metacoxal process structure. Justification for monophyly of Methlini and Hydrovatini is not conclusive, as long as *Queda* is included in Hydrovatini; however, until more characters are discovered to clarify the phylogenetic position of the enigmatic *Queda,* I assume it shares a most recent common ancestor with *Hydrovatus* and that the distinct gap between metafemora and

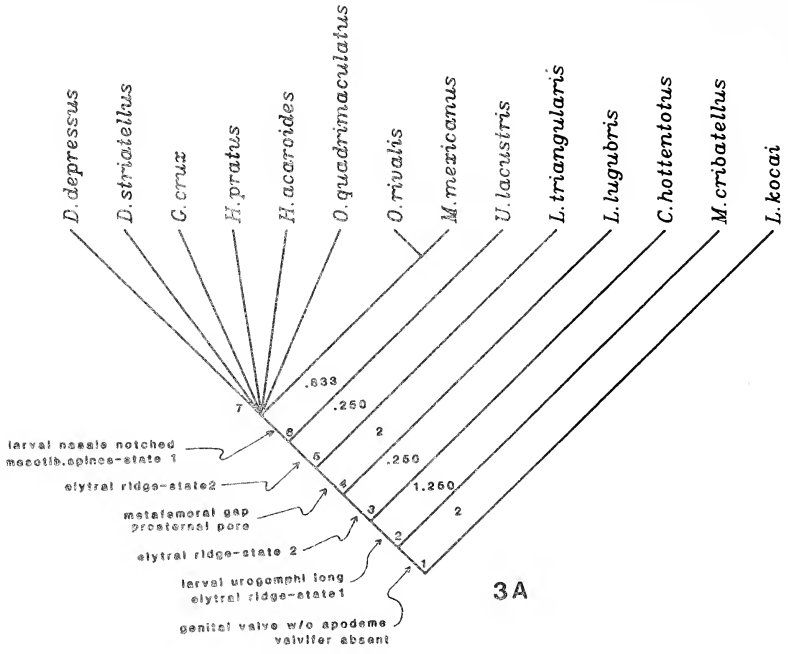

Figure 3, above and opposite. Phylogenies discussed in text. A) Consensus tree produced from 99 equally parsimonious trees after all characters were scaled. Species names are used for taxa actually used in analysis. Numbers 1–7 are node numbers; numbers .250, .833, etc. are branch lengths for each proximate HTU. The indicated character state changes are derived directly from computer analysis and are interpreted/evaluated in text. B) and C) More conservative phylogenetic hypotheses. See text for discussion. Generic and tribal names are used in place of species names.

metacoxal lobes is secondarily derived in members of *Q. compressa.*

Even with the above specified reduction in species number, more than 100 equally parsimonious trees still are produced. Rather than immediately further decrease the number of species, I next elected to scale all characters; scaling is useful because it equalizes the influence of 2-state and multi-state characters by decreasing weights of character states of multi-state characters so that character states of all characters are on an interval from 0 to 1. For example, a 3-state character would be coded 0–.5–1 instead of 0–1–2 and a 4-state character recoded 0–.333–.666–1 (see Swofford 1985). With all characters scaled, 99 equally parsimonious trees are produced. The consensus tree (Fig. 3A) continues to show the same basic set of relationship proposed in Wolfe (1985).

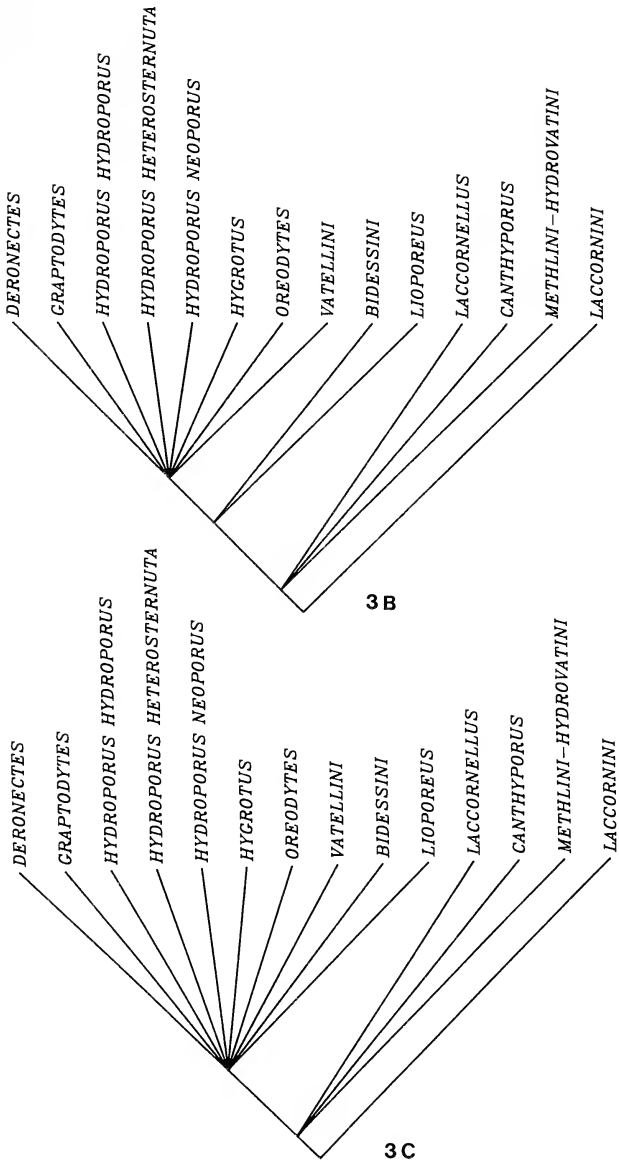
DERONECTES
CRAPTODYTES
HYDROPORUS HYDROPORUS
HYDROPORUS HETEROSTERNUTA
HYDROPORUS NEOPORUS
HYGROTUS
OREODYTES
VATELLINI
BIDESSINI
LIOPOREUS
LACCORNELLUS
CANTHYPORUS
METHLINI-HYDROVATINI
LACCORNINI
3B
DERONECTES
CRAPTODYTES
HYDROPORUS HYDROPORUS
HYDROPORUS HETEROSTERNUTA
HYDROPORUS NEOPORUS
HYGROTUS
OREODYTES
VATELLINI
BIDESSINI
LIOPOREUS
LACCORNELLUS
CANTHYPORUS
METHLINI-HYDROVATINI
LACCORNINI
3C

Table 3. Character states used in phylogenetic analysis (modified from Wolfe [1985]). See Table 2 for character description.

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Colymbetinae (out-group)																			
*Matus ovatus**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporinae																			
Methlini																			
Methles cribatellus	1	1	1	1	1	0	1	0	1	1	1	1	0	0	1	1	1	0	2
Celina hubbelli	1	1	1	1	1	0	0	0	1	1	1	2	0	0	1	1	1	0	2
C. imitatrix	1	1	1	1	1	0	0	0	1	1	1	2	1	0	1	1	1	0	2
C. grossula	1	1	1	1	1	0	0	0	1	1	1	2	1	0	1	1	1	0	2
Hydrovatini																			
Hydrovatus pustulatus	1	1	1	1	1	0	1	3	1	2	1	2	1	0	1	1	1	0	1
Queda compressa	1	0	?	?	1	0	1	3	1	0	1	2	1	1	1	1	1	?	0
Bidessini																			
Uvarus lacustris	1	1	1	1	1	1	1	3	1	2	1	2	0	1	1	1	0	1	0
Bidessonotus inconspiciuus	1	1	?	?	1	1	1	4	1	2	1	1	0	1	1	1	0	?	0
Hydroporini *sensu latu*																			
Laccornis kocae	1	1	1	1	1	0	1	0	1	2	1	2	0	0	0	0	0	0	0
L. conoideus	1	1	1	1	1	0	1	0	1	2	1	2	1	0	0	0	0	0	0
L. etneiri	1	1	1	1	1	1	1	0	1	2	1	2	1	0	0	0	0	0	0
L. deltoides	1	1	1	1	1	1	1	1	1	2	1	2	1	0	0	0	0	0	0
Laccornellus copelatoides	1	1	?	?	1	0	1	2	1	2	1	2	0	0	1	1	0	?	0
L. lugubris	1	1	?	?	1	0	1	2	1	2	1	2	0	0	1	1	0	?	0
Canthyporus hottentotus	1	1	1	1	1	0	1	1	1	2	1	2	0	0	1	1	0	0	0
Lioporeus pilatei	1	1	?	?	1	1	1	1	1	2	1	2	0	1	1	1	0	?	0
L. triangularis	1	1	?	?	1	1	1	1	1	2	1	1	0	1	1	1	0	?	0
Hygrotus acaroides	1	1	2	1	1	1	1	4	1	2	1	2	1	1	1	1	0	1	0
H. nubilis	1	1	2	1	1	1	1	4	1	2	1	2	1	1	1	1	0	1	0
Oreodytes quadrimaculatus	1	1	?	1	1	1	1	3	1	2	1	2	3	1	1	1	0	1	0
O. rivalis	0	1	?	1	1	1	1	2	1	2	1	2	1	1	1	1	0	1	0
O. snoqualmie	1	1	?	1	1	1	1	2	1	2	1	2	1	1	1	1	0	1	0
Graptodytes crux	1	1	2	1	1	1	1	3	1	2	1	2	3	1	1	1	0	1	0
Deronectes depressus	1	1	2	1	1	1	1	3	1	2	1	2	1	1	1	1	0	1	0
D. striatellus	1	1	2	1	1	1	1	2	1	2	1	2	3	1	1	1	0	1	0
Hydroporus (Hydroporus rufilabris	1	1	2	1	1	1	1	2	1	2	1	2	3	1	1	1	0	1	0
H. (Neoporus) clypealis	1	1	2	1	1	1	1	3	1	2	1	2	3	1	1	1	0	1	0
H. (N) undulatus	1	1	2	1	1	1	1	3	1	2	1	2	3	1	1	1	0	1	0

Table 3. *continued*

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
H. (N) pratus	1	1	2	1	1	1	1	2	1	2	1	2	2	1	1	1	0	1	0
H. (N) tennetum	1	1	2	1	1	1	1	2	1	2	1	2	2	1	1	1	0	1	0
H. (Heterosternuta) pulcher	1	1	2	1	1	1	1	3	1	2	1	2	3	1	1	1	0	1	0
Vatellini																			
Macrovatellus mexicanus	0	1	2	1	1	1	1	4	1	2	1	1	3	1	1	1	0	1	0

The number of equally parsimonious trees can be reduced more by eliminating more species. For example, if *O. quadrimaculatus* (Horn) is removed and characters still are scaled, 27 equally parsimonious trees are produced. It is interesting that except for the omission of *O. quadrimaculatus,* the consensus tree of those 27 trees remains identical to that shown in Fig. 3A.

As indicated previously, it is obvious that there are not enough characters to resolve the phylogenetic relationship of all taxa listed in Table 3. Phylogenetic problems seem particularly acute in "higher" hydroporines (*Deronectes, Hydroporus,* etc). This is borne out by the fact that eliminating taxa from among more apotypic groups (*e.g. O. quadrimaculatus*) significantly decreases the number of equally parsimonious trees (from over 100 to 99 to 27) without affecting relationship among plesiotypic clades. Even treating all characters as unordered did not perturb relationship among primitive groups.

Despite apparent stability of relationship among primitive groups, there still are only a few synapotypies to support proposed relationships and not all synapotypies are equally important, especially after decreasing weight of some characters by scaling. Weaknesses and strengths of various parts of the phylogenetic hypothesis in Fig. 3A overall are reflected by computed branch lengths (length = number of character state changes or synapotypies per line segment), after *Laccornellus* is added to the analysis and characters are scaled. For example the lengths of the branches connecting node three to node four and from node five to node six is only 0.250 for each. The length of the branch connecting node six to node seven is 0.833. These problems are elaborated further below.

Evaluation of synapotypies

All trees show *Laccornis* as the most primitive clade followed by successive divergence of *Methles, Canthyporus, Laccornellus, Lioporeus, Uvarus* Guignot, and finally a large polychotomy containing *Hydroporus s.l., Deronectes, Oreodytes, Hygrotus, Macrovatellus* Sharp, and *Graptodytes. Oreodytes rivalis* is shown as the sister taxon to *M. mexicanus;* however, this sister group relationship was based on a character loss (loss of mandibular setation) and I feel confident future studies will not support this close relationship between *M. mexicanus* and *O. rivalis.* Relationships among *Deronectes, Oreodytes,* etc. are not known and obviously require considerably more study.

The primary character involved in arraying the more primitive lineages is development of the elytral ridge which is homoplasious (consistency index [CI] = .444). Characters that are homoplasious can be phylogenetically useful, but only if polarities for the character states are worked out more comprehensively at and below the generic level so that the plesiotypic states can reasonably be predicted for each genus; unfortunately, this kind of meticulous work is only finished for *Lioporeus, Laccornis* and *Laccornellus.* While I am confident that the trend for the internal elytral ridge is generally from the non-ridged condition to the more ligulate state, I am not sure of the exact plesiotypic condition for all genera analyzed; therefore, excessive reliance on this character is not justified.

Relationships among the plesiotypic groups also are in part established by nasale structure and length of the larval urogomphus. Larval characters often are rather conservative and therefore useful for higher level phylogenetic analysis. However, no larvae are described for any members of two critical genera, *Lioporeus* and *Laccornellus.* Furthermore, Watts (1970) demonstrated considerable variation in length of larval urogomphus in members of *Hygrotus.* Also, character states for urogomphal length and lateral notch of the nasale are not clearly dichotomous. For these reasons, decreased reliance on these characters is appropriate.

The most reliable characters available are presence/absence of a valvifer, presence/absence of the prosternal pore, and degree of separation of base of the metafemora and metacoxal lobes. Within the Hydroporinae, the prosternal pore has evolved at least twice, once in *Laccornis* and then in taxa above node 4. Wolfe and Rough-

ley (in press) clearly showed that the pore is secondarily derived in *Laccornis.* Although this character needs to be analyzed in more taxa, among species examined, it is dichotomous and appears to be a reliable phylogenetic indicator.

In all examined members of *Laccornis,* Methlini, *Hydrovatus, Laccornellus,* and *Canthyporus,* metafemora touch or almost touch the metacoxal lobes. All taxa beyond node 4 have a distinct gap between the metafemoral base and metacoxal lobes. I think that this character is important; however, as long as *Queda* is retained in Hydrovatini the presence of the metafemoral gap will be homoplasious in Hydroporinae.

Presence of a valvifer in members of *Laccornis* indicates a plesiotypic position for that genus (Burmeister 1976, Wolfe 1985). This is an internal character that is part of a complex muscular/structural system (see Burmeister 1976) and I consider it very significant. Furthermore, according to the phylogeny (Fig. 3A) this character is perfectly consistent.

One important final point is that if historical zoogeographic implications previously proposed concerning Northern and Southern hemisphere taxa (Wolfe 1985) are correct, increased homoplasy in all characters will have to be accepted. Synapotypies associated even with valvifer, metacoxae and prosternal pore may have evolved twice: once in northern hemisphere hydroporines and once in hydroporines of the southern hemisphere (see Wolfe 1985 for more complete discussion).

Conclusions. Information provided herein substantiates the hypothesis that *Hydrovatus* and Methlini are sister taxa; however, inclusion of *Queda* in Hydrovatini is questioned and requires further study.

The overall phylogenetic hypothesis proposed in Wolfe (1985) is overextended. After re-interpretation of specified characters, phylogenetic analysis facilitated by PAUP reveals well over 100 equally parsimonious trees. By using one representative species for each of Bidessini, *Lioporeus, Laccornis,* and Methlini/Hydrovatini, and scaling all characters, 99 equally parsimonious trees were produced; the consensus tree of the 99 equally parsimonious trees very closely approximates the tree in Fig. 45 of Wolfe (1985). However, re-evaluation of synapotypies between nodes 1–4 in Fig. 3A herein suggests that relationships between *Laccornellus, Canthyporus,* and

Methylini-Hydrovatini cannot be conclusively resolved and the phylogeny in Wolfe (1985) should be adjusted. At best (Fig. 3B), structural data indicates *Laccornis* is the most plesiotypic clade followed by a polychotomy that includes *Laccornellus, Canthyporus,* and Methlini-Hydrovatini. Most characters indicate Bidessini and *Lioporeus* are more plesiotypic than remaining hydroporines. However, the primary characters suggesting this are either variable or gradational; although character trends are evident it is difficult to polarize these characters (e.g. internal elytral ridge, mesotibial spines) on a node by node basis.

It seems that the best hypothesis for now is that of Fig. 3C, at least until immature stages of *Lioporeus* and *Laccornellus* are described and/or more synapotypies are discovered. For example, if members of *Lioporeus, Laccornellus,* and/or all had distinctly long urogomphi, I would be more confident about using that character as a synapotypy to separate *Canthyporus* etc. from Methlini-Hydrovatini-Laccornini. Further resolution of phylogeny of hydroporines will require analyses emphasizing more African and Australian genera so that an alternate hypothesis involving independent evolution of the northern and southern hemisphere hydroporine faunas can be investigated adequately.

Summary

The eighth abdominal tergum of most hydroporines is evenly convex posteriorly and ventrally is folded inward for about 0.25 the length of the tergum. On males and females of *Hydrovatus* and Methlini (*Celina* and *Methles*), tergum 8 is posteriorly acute and consists of a dorsal and ventral lamina that are about equal in size. In methlines, terga 7 and 8 are modified. On tergum 8, the dorsal lamina additionally is modified posteriorly into a distinct, trifid, highly sclerotized, spearlike structure with two long, diverging, anteriorly extended apodemes. Shorter anteriorly extended apodemes also are present on the anterior edge of tergum 7. These modifications suggest that *Hydrovatus* and Methlini form a monophyletic unit and also support the contention that Methlini (which includes *Celina* and *Methles*) is monophyletic. Specimens of *Queda compressa* do not possess these distinctive abdominal modifications and that genus may be improperly assigned to Hydrovatini.

Relationships among *Laccornis,* Methlini-*Hydrovatus, Canthyporus, Laccornellus,* and *Lioporeus* proposed by Wolfe (1985) are reviewed. Based on structural considerations only, *Laccornis* still is recognized as the sister to all other Hydroporinae, and the next most plesiotypic group is represented by a polychotomy of *Canthyporus, Laccornellus,* and Methilini-*Hydrovatus;* however, the specific relationships between the latter three clades cannot be as confidently predicted as previously thought. Members of *Lioporeous,* Bidessini, *Deronectes, Oreodytes, Hygrotus, Graptodytes,* and *Hydroporus sensu latu* are relatively more apotypic than *Canthyporus* etc. Characteristics of the internal elytral ridge and mesotibial chaetotaxy suggest *Lioporeus* and Bidessini are more primitive than the latter five groups, but these latter relationships cannot be established conclusively.

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CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month, October through May, at 7:30 p.m. in Room 154, Biological Laboratories, Divinity Avenue, Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

BACK VOLUMES OF PSYCHE

Requests for information about back volumes of Psyche should be sent directly to the editor.

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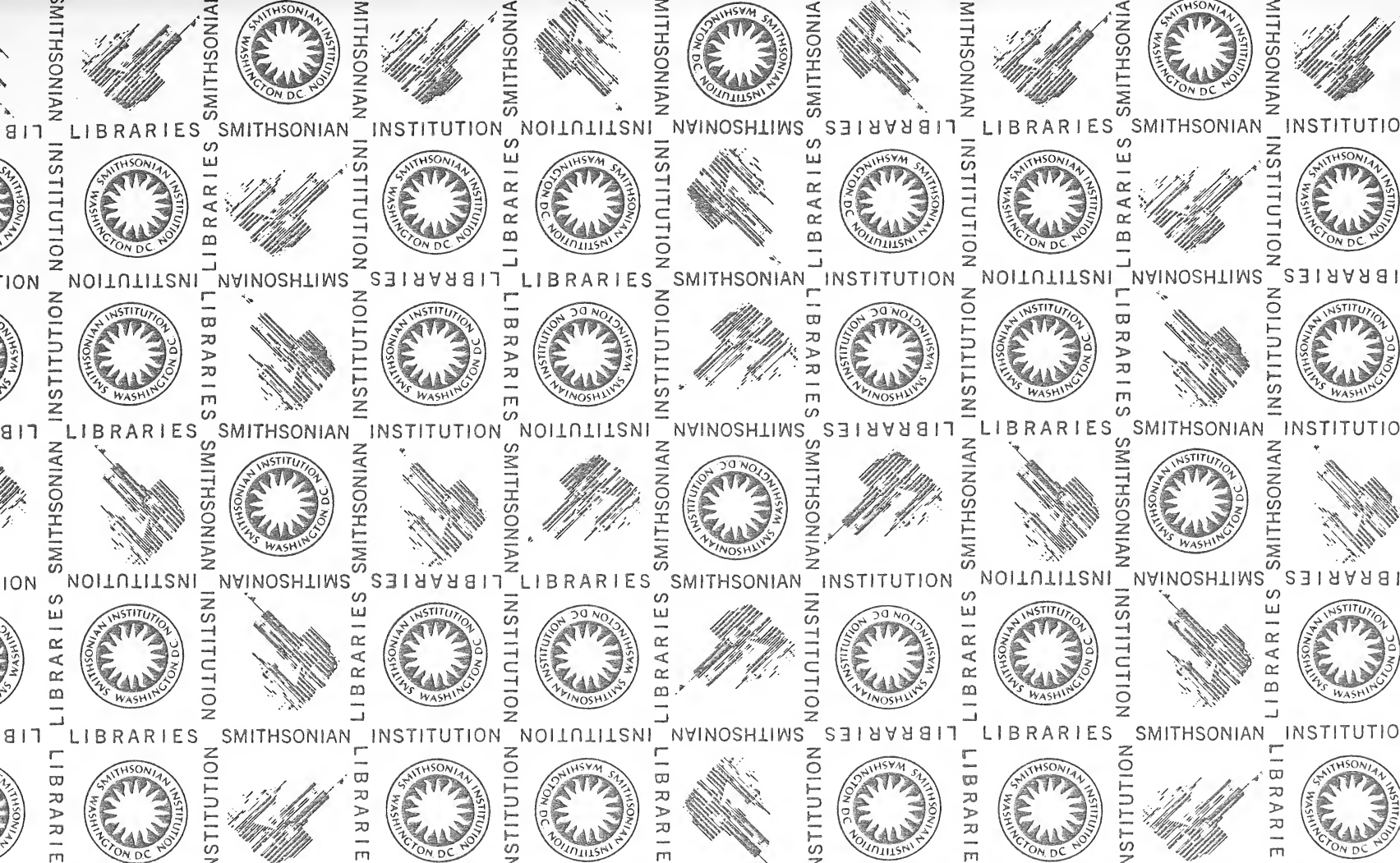
Eagle Hill Wildlife Research Station

The Eagle Hill Wildlife Research Station, Steuben, Maine, has announced a series of thirteen advanced and professional seminars in biology during the coming summer. Each seminar will be a week long and the program will extend from May 21 to September 18. Two seminars will be on insects. One, on moths, will be led by Dr. Charles V. Covell, of the University of Louisville, and author of the Field Guide to the Moths of Eastern North America. The other is on forest entomology, and will be conducted by Richard Dearborn, Senior Entomologist of the Maine State Forest. For information write or call: Eagle Hill Wildlife Research Station, Steuben, Maine, 04680; telephone, (207) 546-2821.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