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Phylogenetic Affinities of the Ant Genus *Cheliomyrmex* (Hymenoptera: Formicidae)

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Abstract: Field observations of the rarely collected ant, *Cheliomyrmex morosus* (F. Smith), are recorded. The ant is hypogaeic with a majority of its burrows appearing in the upper 6 inches of the soil. Internal and external features of the abdomen considered to be of importance in understanding the phylogeny of this ant are discussed. Included are descriptions of portions of the gastral digestive system, the reproductive system, and the sting apparatus. Malpighian tubule counts in *C. morosus* and 6 other New World dorylines are compared.

INTRODUCTION

The Neotropical ant genus *Cheliomyrmex* was established by Mayr (1870) based on worker specimens of a species that Mayr named *C. nortoni.* Wheeler (1921) indicated that these specimens were "evidently collected by Sumichrast near Mount Orizaba, in the state of Vera Cruz, Mexico." Mayr considered the genus to be morphologically intermediate between the Ponerinae and Dorylinae, and Emery (1895) eventually placed the genus in the Dorylinae. Wheeler (1921) suggested that the genus should constitute an independent tribe, the "Cheliomyrmicini," and Borgmeier (1955), in his massive revision of the New World dorylines, accepted this placement. Numerous other authors have discussed the phylogenetic affinities of the genus. Forel (1893) doubted that *Cheliomyrmex* belonged with the Dorylinae. Ashmead (1906), who placed the genus close to *Dorylus,* indicated that the genus might instead belong near the Ecitonini. Emery (1910) considered the genus to be closely related to *Labidus,* particularly *L. coecus* (Latreille), but this conclusion was later refuted by Wheeler (1921) and by Borgmeier (1954, 1955). Wheeler (1921) characterized the tribe Cheliomyrmecini as a very ancient group, "the most archaic and generalized" of all the tribes of the Dorylinae, and as being very near the ancestral stem from which both the Dorylini and Ecitonini arose in the late Cretaceous. In an examination

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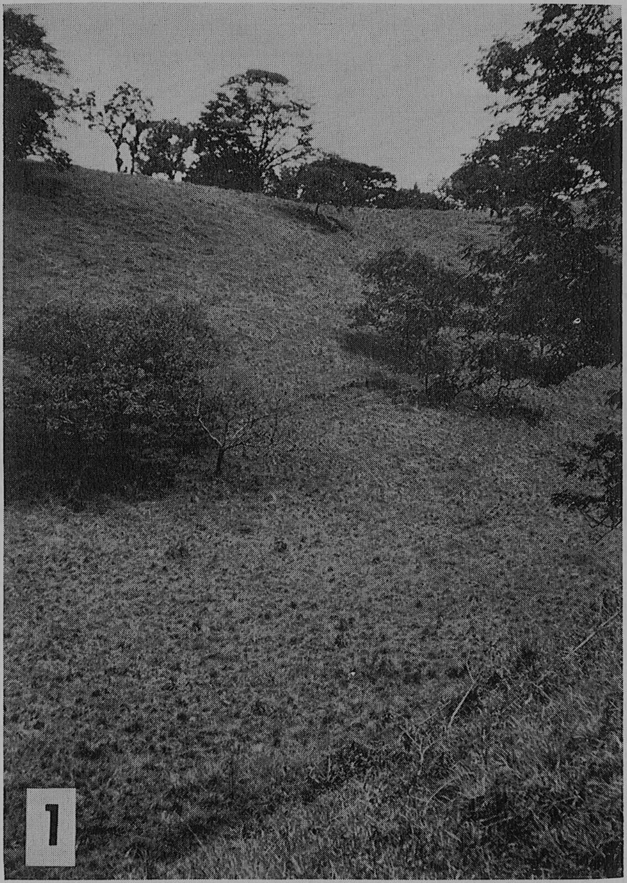

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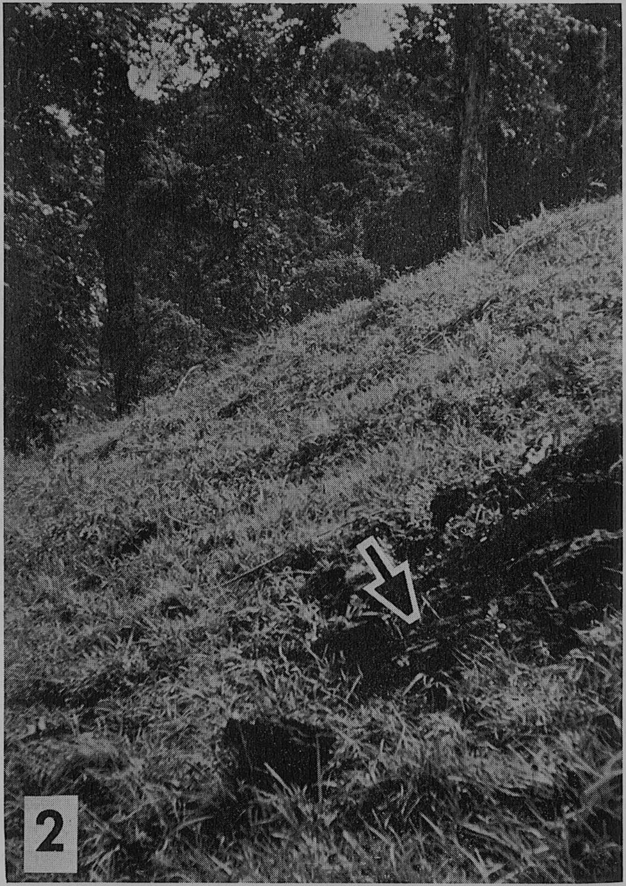

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of ant wing venation, Brown and Nutting (1950) indicated that *Cheliomyrmex* appears as the most primitively veined doryline. Gotwald (1969), in a study of mouthpart morphology, suggested that the Cheliomyrmecini and Ecitonini are closely related and together form a distinct New World group. Reid (1941) pointed out that the thorax of *Cheliomyrmex* is ecitonine in construction, and Hermann (1969) placed the stings of the Cheliomyrmecini and Ecitonini in the same morphological group.

Although Mayr erected the genus *Cheliomyrmex* and described *C. nortoni* in 1870 based on worker specimens, the male of the species was described prior to that date by F. Smith (1859) as *Labidus morosus.* That *C. nortoni* and *L. morosus* were the same species was first suggested by Emery (1910), and later Wheeler (1921) changed the name of the species from *C. nortoni* to *C. morosus.*

C. morosus has been collected only rarely and is recorded from Mexico, British Honduras, and Honduras. Most commonly this species has been collected in the state of Vera Cruz, Mexico, particularly in the vicinity of Orizaba, Cordoba, and Atoyac (Borgmeier, 1955). Because it is rarely seen in the field, little is known of its biology. In addition, the queen for this species, as well as for the entire genus, is unknown. This ant is most probably hypogaeic, but little else is known of its biology.

A colony of *C. morosus* was fortuitously discovered by Dr. Hans Reichardt while participating in a Cornell University Field Expedition to Mexico during the summer of 1965. Subsequent to this discovery and also as a member of this expedition, I observed and collected a large series of workers. In addition a number of males were collected at UV light in the village of Fortin de las Flores, Vera Cruz. The present investigation provides new information on the biology and morphology of this species based on the specimens observed and collected in the summer of 1965.

METHODS

Morphological observations were made both in the field and laboratory. The Malpighian tubule counts were performed in the field on live ants immersed in water. A quick, firm pull on the tip of the gaster with forceps, as described by Ettershank and Brown (1964), is sufficient to pull out and expose the gastral digestive system, whereupon the tubules can be easily counted. The remaining workers of the series collected were placed in Bouin's fluid. A number of these were cut in half between the alitrunk and petiole to assure more complete contact

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FIGS. 1–2. Pasture, east of the Fortin de las Flores—Huatusco road, state of Vera Cruz, Mexico, in which a colony of *Cheliomyrmex morosus* was discovered. Fig. 1. General view of pasture from colony location site. Fig. 2. Colony location site (precise location indicated by arrow).

of the tissues with the fluid. The laboratory dissections were performed on this latter group of specimens. The ovaries were removed from the gaster, stained with acid fuchsin, and mounted on microscope slides in Canada balsam.

OBSERVATIONS

LOCATION AND DESCRIPTION OF THE COLONY: The colony was found beneath a decayed log situated in a pasture on 3 August. This pasture was located approximately one-half mile east of the Fortin de las Flores—Huatusco road at km 38, 2 miles south of Huatusco, in the state of Vera Cruz. This location is within the same general area as Atoyac, the type locality for the species.

The pasture was located on two small hillsides which sloped together to form a small hollow (Figs. 1 and 2). It was covered with short grasses and occasional trees. The log under which the colony was found was partially destroyed prior to noting the significance of the discovery. Most observations were made the following day when the colony was found under a fragment of the log. There appeared to be only one tunnel entrance beneath this fragment.

A few workers were observed in the vicinity of the colony entrance, but no organized columns of workers were seen. An unsuccessful attempt was made to attract more workers to the surface by placing fragments of bacon near the tunnel entrance. When one or two workers were lifted with forceps a large number of others would hang together by means of their tarsi, forming a "string" of ants. This is very similar to the behavior of army ants of the genus *Eciton* (see Rettenmeyer, 1963) where it is important in bivouac formation. This suggests that *C. morosus* might similarly cluster in subterranean locations, although such locations would certainly be restrictive to such bivouac formation.

In an effort to locate the queen, the area presumably housing the colony was excavated, eventually resulting in a trench 3 feet long by 1 foot deep and 1 foot wide. Neither the queen nor brood were found, indicating that this area may have been peripheral to the primary colony site. Although the workers had some tunnels at a depth of about 6 inches, most appeared to be located just beneath the surface. The workers sought refuge in these tunnels and could no longer be found. Similarly, Mann (1922) reported locating a small colony of *C. morosus* beneath a stone but the workers quickly disappeared in the ground. He did not attempt to dig in the area.

Upon being disturbed *C. morosus* does not respond as excitedly as do species of *Eciton* and *Labidus*. However, in defending itself, the worker bites and stings simultaneously. When attacked I found that the mandibles penetrate the superficial layers of the skin and must be pulled out. The sting is painful, comparable to a mild bee sting, and results in the formation of a small circular welt about 7 mm. in diameter. Wheeler (1921) described the sting of *C. megalonyx* Wheeler as painful.

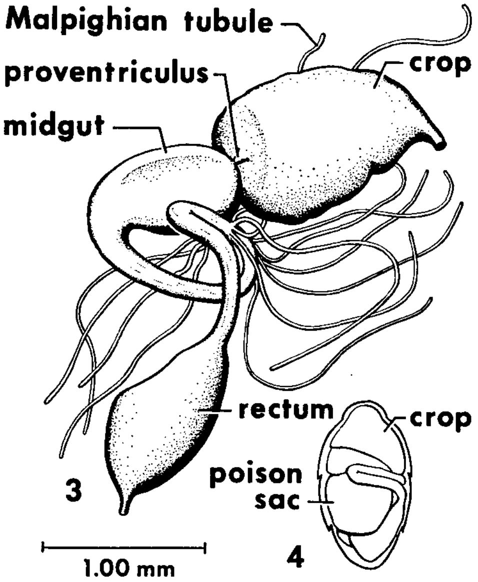
Since little else is known of the biology and behavior of *C. morosus*, it must be assumed that its foraging and emigrating activities resemble those of *C. megalonyx*, for which Wheeler (1921) provided a brief description. His observations indicated that *C. megalonyx* is strongly photophobic. One colony was discovered beneath a pile of logs, and emigrated after being disturbed. Its columns moved beneath leaves, sticks, and boards, where such cover was available. Open spaces were crossed through galleries about four-fifths of an inch wide, which the workers constructed of "small particles of earth." This behavior strongly suggests a hypogaeic lifeway.

MAJOR WORKER MORPHOLOGY: With the exception of descriptive external observations and the work of Hermann and Blum (1967), Hermann (1969), and Gotwald (1969), the morphology of *C. morosus* has not been previously studied. The gross anatomy of portions of the digestive and reproductive systems and of the poison apparatus was studied in this investigation. The structures examined are those considered of potential value in understanding the relationship of this ant to other New World dorylines.

The worker caste of *C. morosus* is described as strongly dimorphic by Emery (1910) and Borgmeier (1955) and is commonly separated into workers and soldiers. Emery (1910) noted, however, that there is a gradual transition between the two groups. The mandibles and overall size form the basis for the distinction between workers and soldiers. The mandible of the soldier is cylindrical and falcate with 1 apical and 2 subapical teeth, while that of the worker is flattened, somewhat triangular, with 1 apical and 2 subapical teeth and a series of denticles. The specimens examined and reported on in this investigation belong to the soldier caste unless otherwise noted. Where possible, the morphology of *C. morosus* is specifically compared to that of other New World Dorylinae.

GASTRAL DIGESTIVE TRACT: (Figs. 3 and 4). The expansible crop is connected to the midgut by means of a membranous proventriculus and occupies a major portion of the first gastral segment. The crop was distended in all specimens examined. The proventriculus closely resembles that of *Eciton hamatum* (Fabricius), which Eisner (1957) described as degenerative. It appears to be reduced to a simple stomodaeal valve with the bulbar cuticle irregularly folded. Eisner (1957) speculated that this type of proventriculus permitted the passage of solid matter through the bulb under muscular pressure.

The midgut is flattened, ellipsoid, shares the first gastral segment with the crop, and usually occupies a transverse position in the gaster. Posteriorly the midgut narrows to form a cylindrical tube anterior to the insertion of the Malpighian tubules. The midgut of the workers of *Eciton hamatum* and *burchelli* (Westwood) are described as pear-shaped (Whelden, 1963a) but lack the well developed tubular, pre-Malpighian tubule tract of *C. morosus*.



FIGS. 3–4. Gastral digestive system of *C. morosus* soldier. Fig. 3. Digestive tract removed from gaster. Fig. 4. Digestive tract *in situ*, dorsal view (drawing not scaled).

Malpighian tubule counts were made on a series of workers. Ettershank and Brown (1964) emphasized the possible value of the tubules as meristic characters in the ants. With this in mind, counts were made in six other species of New World dorylines, during and subsequent to the 1965 field expedition. The results of these counts are summarized in Table 1. Although there is considerable overlap in tubule number range, the mean numbers of tubules are distinct for several species. It appears, however, that the number of tubules is less species specific than it is a function of body size. Indeed, Gray and Lamb (1968) statistically demonstrated a positive correlation between tubule number and head width in *Myrmecia dispar*. It might thus be assumed that the number of tubules is directly correlated with the volume of the individual's hemocoel or at least with overall body size. This appears to be true not only intraspecifically but interspecifically as well. Contrast the mean tubule number for the relatively large ant *L. coecus*, for example, with the mean figure for the smaller *N. nigrescens* (Cresson) (Table 1).

The intestine begins posterior to the insertion of the Malpighian tubules. It continues the alimentary canal as a cylindrical tube. This tube expands to form a thin-walled rectum similar to that of *E. hamatum* and *burchelli* (Whelden, 1963a). Two flattened and elliptical rectal papillae or glands are found in the anterior third of the rectum, one on each side of the opening of the intestine.

Table 1. Malpighian tubule counts in 7 species of New World Dorylinae.

Species		No. Specimens Dissected	Range	Mean	Range for All Workers	Mean for All Workers
Cheliomyrmex morosus (F. Smith)	Soldier	5	11–15	13.20	8–15	11.67
	Media Worker	5	10–15	12.60		
	Minor Worker	5	8–10	9.20		
	Male	1	50	50.00		
Eciton mexicanum Roger	Soldier	1	23	23.00	14–23	19.25
	Media Worker	1	23	23.00		
	Minor Worker	2	14–17	15.50		
Labidus coecus (Latreille)	Soldier	5	15–17	15.80	7–17	10.89
	Media Worker	7	9–12	10.86		
	Minor Worker	7	7– 9	7.43		
Labidus praedator (F. Smith)	Soldier	1	20	20.00	12–20	14.75
	Media Worker	1	15	15.00		
	Minor Worker	2	12	12.00		
Neivamyrmex nigrescens (Cresson)	Major Worker	5	7– 8	7.60	4– 8	6.07
	Media Worker	5	4– 8	5.60		
	Minor Worker	5	5	5.00		
Neivamyrmex opacithorax (Emery)	Media Worker	1	6	6.00	5– 6	5.50
	Minor Worker	1	5	5.00		
Neivamyrmex pilosus (F. Smith)	Major Worker	5	9–12	11.00	6–12	8.31
	Media Worker	6	7– 9	8.17		
	Minor Worker	8	6– 9	6.75		

Whelden (1963a) reported usually three and rarely six rectal papillae in the workers of *E. hamatum* and *burchelli.*

REPRODUCTIVE SYSTEM: (Figs. 5 and 6) Ovaries were found in 4 soldiers. Each ovary consists of a single, polytrophic ovariole. In the polytrophic ovariole, the developing oocytes are separated by groups of trophocytes or nurse cells from which the oocytes receive nutrient molecules. Difficulty was encountered in removing the ovaries from the *C. morosus* soldiers, and in each case, the terminal filaments and portions of the germaria were lost because of their entanglement with surrounding tissues. In most cases the follicular epithelium was clearly evident around each oocyte.

Whelden (1963b) described the reproductive system of workers of *E. hamatum* and *burchelli* as simple in structure and unlike that of the queens. He found as many as 3 ovarioles in each ovary, but in many minor workers, only one per ovary was found, thus appearing similar to *C. morosus.* To contrast the worker and queen ovaries, it should be noted that Hagan (1954) found each ovary of the queen of *E. burchelli* to contain at least 1200 ovarioles.

In the *C. morosus* soldier, the ovaries and common oviduct are ventral to the ducts of the poison sac and Dufour's gland in the terminal segments of the gaster

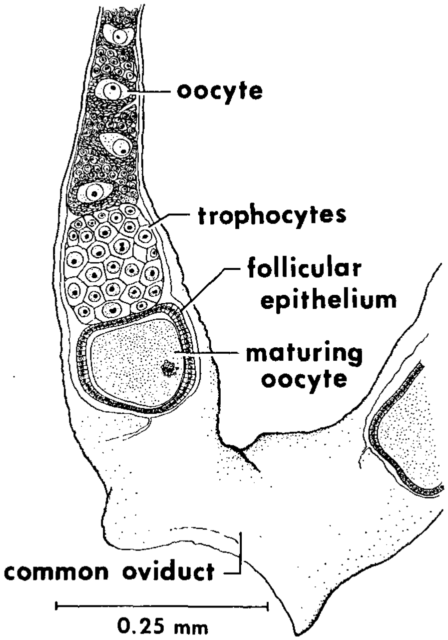


FIG. 5. Right ovary of *C. morosus* soldier, ventral view, terminal filament not shown, portions of drawing diagrammatic.

(Fig. 6). Several oocytes can be seen in each ovariole, and in each case, the oocyte closest to the common oviduct is in an advanced stage of growth and maturation (Fig. 5). Usually the nucleus is not discernable in these latter cells. The trophocytes are polyhedral cells.

POISON APPARATUS: (Figs. 6 and 7) Although the entire sting apparatus was examined, only the glandular elements are reported on here. The poison sclerites have been discussed and illustrated by Hermann (1969). The poison sac is the most conspicuous structure in the gaster and is situated between the midgut and rectum. The sequential order of major gastral organs along the longitudinal axis is constant (see Fig. 4). Some positional variation, however, is encountered in the skewing of the organs to the right or left.

The poison sac is generally spherical with its conspicuous duct ending in the sting bulb (Fig. 7), and is similar to the poison sac of *Eciton hamatum* (Whelden, 1963a; Hermann and Blum, 1967). The posterior face of the sac usually bears a concave impression probably created by pressure from the rectum. This often gives the sac a much more cylindrical appearance.

The free poison filaments (Figs. 6 and 7) arise from the poison sac duct, and their origin is similar to that found by Hermann and Blum (1967) in *E. hamatum* [although Whelden (1963a) reported that the filaments arose from the anterior

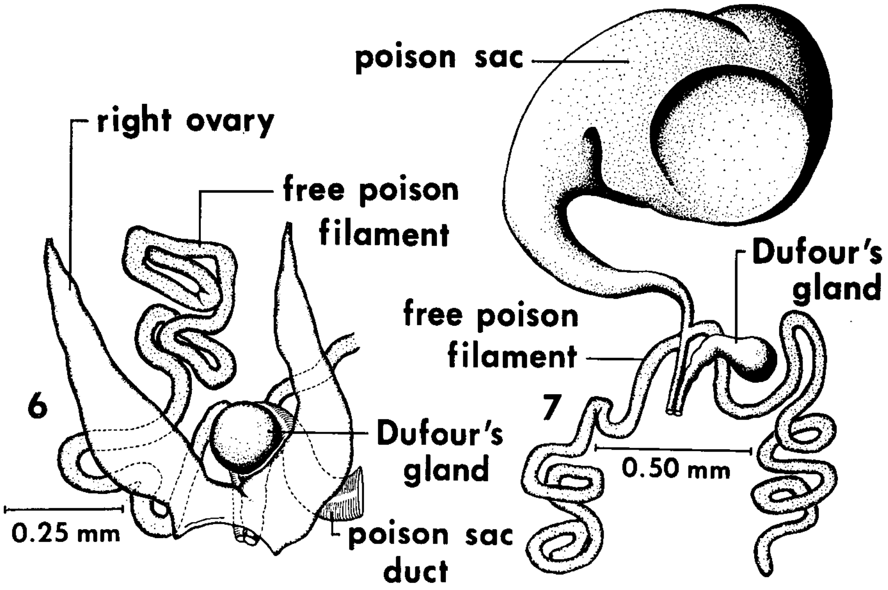


Fig. 6. Ovaries and portions of poison apparatus of *C. morosus* soldier, ventral view. Fig. 7. Glandular elements of poison apparatus of *C. morosus* soldier.

end of the sac in this species]. The filaments appear to arise much farther down the duct from the poison sac in *C. morosus* than they do in *E. hamatum*. These ribbon-like filaments are unbranched and appear to be randomly distributed within the vicinity of the poison sac.

The Dufour's gland is spheroid, sac-like, and much smaller than the poison sac. This gland is situated at the apex of the joining ovarioles (Fig. 6). As in *E. hamatum* (Hermann and Blum, 1967), its duct enters the sting bulb ventrad to the duct from the poison sac.

Hermann and Blum (1967) have examined the sting apparatus, especially the skeletal components, of *Cheliomyrmex* and report that this genus lacks the furcula, a sclerite absent in all dorylines. Hermann (1969) has recently provided a more detailed examination of the poison sclerites.

DISCUSSION

Preliminary evidence suggests that *C. morosus* and *megalonyx* are hypogaeic, i.e., they maintain subterranean bivouacs and forage either beneath the surface of the soil and/or on the surface of the soil beneath debris. When such debris is absent the workers (*C. megalonyx*) fashion surface galleries of soil particles, thus avoiding exposure to the light or perhaps other factors. Similar hypogaeic behavior patterns, including the construction of surface galleries, also occur in the New World doryline, *Labidus coecus* (Borgmeier, 1955). *Labidus praedator* (F. Smith), on the other hand, is intermediate between the hypogaeic *coecus* and the epigaeic ecitonines such as *Eciton hamatum*. Wheeler (1921) reported that while *L. praedator* constructs surface galleries, it does, on occasion, forage in the open on the soil surface. I have also observed a column of *L. praedator* crossing a path, in the open, without constructing galleries (Mexico, 1965). A range of behavior patterns, then, exists in the New World Dorylinae, and it is not unusual to see behavioral variation within a single genus (e.g., *Labidus*). Of the Old World Dorylinae, species of the genus *Dorylus* are primarily hypogaeic (Wheeler, 1922). The subgenus *Anomma*, however, contrasts sharply with other *Dorylus* subgenera, being strongly epigaeic in its foraging habits (Wheeler, 1922; Raignier and van Boven, 1955). *Aenictus* likewise contains both hypogaeic and epigaeic forms (Schneirla and Reyes, 1966).

The intrageneric variation in bivouac formation and foraging patterns suggests that the nature of these phenomena (i.e., whether they are hypogaeic or epigaeic) is not particularly helpful in establishing phylogenetic relationships within the Dorylinae.

Hypogaeic conditions, however, may significantly affect other generic-specific behavior patterns. Schneirla (1957, 1964) suggested that variable nomadism (as opposed to regular nomadic-statary cycles) is correlated, in part, with communicative processes as they occur in diffuse subterranean bivouacs (in *Dorylus*, *Anomma*, *Labidus*, and *Nomamyrmex*). Again, variable nomadism occurs in both New and Old World genera, and it may be presumed that *Cheliomyrmex*, as a hypogaeic form, exhibits variable nomadism, a condition of group predatory behavior (see Wilson, 1958).

The structure of the cheliomyrmecine pedicel is of particular interest since it consists of a single node (i.e., the postpetiole is not separated from the 4th abdominal segment by a constriction), whereas the remaining New World dorylines (the tribe Ecitonini) are binodally pedicellate. Phylogenetically this condition may be viewed in two ways: (1) it may be considered an extremely important morphological discontinuity within the New World Dorylinae, or (2) it may be regarded as a relatively unimportant development, attributable to the lability of the abdomen. The structure of the pedicel in other subfamilies appears conservative. It is, for instance, uninodal throughout the Dolichoderinae and Formicinae and binodal in the Pseudomyrmicinae and Myrmicinae. Brown (1954a) placed these latter two groups in two different formicid complexes and considered the binodal pedicellate condition in each subfamily to be evolutionarily convergent. The condition of the pedicel is least conservative in the Dorylinae, as it is presently constituted, with the binodal condition in the Ecitonini and Aenictini, and the uninodal condition in the Cheliomyrmecini and Dorylini. Considering the evidence of Reid (1941), Hermann (1969), and Gotwald (1969), *Cheliomyrmex* is phylogenetically closer to the Ecitonini than is suggested solely by the condition of the pedicel.

The proventriculus in *Cheliomyrmex* is predictably reduced and consists only of a stomodeal valve. It is like the proventriculus of *E. hamatum* (Eisner, 1957). The proventriculus of other dorylines has not been thoroughly examined and comparison to *C. morosus* is impossible. Mukerjee (1933) provided a brief description of the proventriculus of *Dorylus* (*Alaopone*) *orientalis* Westwood, indicating that "the longitudinal folds or ridges projecting within its lumen are ill-developed." This description applies equally well to the cheliomyrmecine proventriculus.

The presence of ovaries containing maturing ova in *C. morosus* workers suggests that these workers lay unfertilized eggs. Egg laying in many ant species, of course, is not confined to the queen, and worker eggs, although in most cases not reared, are used as larval food (Wallis, 1965). Also, Weyer (1927) reported that maturing ova in two species of Formicinae are reabsorbed. Ovaries were not found in all workers of *C. morosus* dissected, nor are they always found in all individuals of other species involving ovary-bearing workers. Mukerjee (1927) in a study of *Myrmicaria brunnea* Saunders, found ovaries in only four specimens of nearly 100 examined. In addition to Whelden's (1963b) description of worker ovaries in *Eciton,* Mukerjee (1933) provided a description of the worker ovary in *Dorylus* (*A.*) *orientalis.* Structural and histological variation between doryline worker ovaries is minimal, except for the number of ovarioles making up a single ovary.

It is the function of such ovaries that stimulates the most intriguing questions. In some species of *Rhytidoponera, Diacama,* and *Leptogenys,* queens are not known and the queen function is assumed by workers (Brown, 1954b; Brown and Taylor, 1970). The frequency and function of egg laying (if it occurs at all) in the workers of *C. morosus,* however, can only be speculated upon, and precise answers clearly await discovery of the queen and exacting studies of colony behavior.

Literature Cited

ASMEAD, W. H. 1906. Classification of the foraging and driver ants, or family Dorylidae, with a description of the genus *Ctenopyga* Ashm. Proc. Entomol. Soc. Wash., **8:** 21–31.

BORGMEIER, T. 1954. Aenictini n. trib. und die Tribus-Einteilung der Dorylinen (Hym. Formicidae). Zool. Anz., **153:** 211–214.

———. 1955. Die Wanderameisen der Neotropischen Region. (Hym. Formicidae). Stud. Entomol. **3**, 717 pp.

BROWN, W. L., JR. 1954a. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. Insectes Sociaux. **1:** 21–31.

———. 1954b. Systematic and other notes on some of the smaller species of the ant genus *Rhytidoponera* Mayr. Breviora. **33:** 1–11.

BROWN, W. L., JR., AND W. L. NUTTING. 1950. Wing venation and the phylogeny of the Formicidae (Hymenoptera). Trans. Amer. Entomol. Soc., **75:** 113–132.

BROWN, W. L., JR., AND R. W. TAYLOR. 1970. Superfamily Formicoidea, in The Insects of Australia. Melborne Univ. Press, Melborne, 1029 pp.

EISNER, T. 1957. A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). Bull. Mus. Comp. Zool., Harvard, **116**: 437–490.

EMERY, C. 1895. Die Gattung *Dorylus* Fab. und die systematische Einteilung der Formiciden. Zool. Jahrb. Syst., **8**: 685–788.

———. 1910. Subfam. Dorylinae. In Genera Insectorum. Fasc. **102**, 34 pp.

ETTERSHANK, G., AND W. L. BROWN, JR. 1964. The Malpighian tubules as meristic characters in ants (Hym., Formicidae). Entomol. Mon. Mag., **100**: 5–7.

FOREL, A. 1893. Sur la Classification de la famille des Formicides, avec remarques synonymiques. Ann. Soc. Entomol. Belg., **37**: 161–167.

GOTWALD, W. H., JR. 1969. Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). Cornell Univ. Agr. Exp. Sta. Mem. 408, 150 pp.

GRAY, B., AND K. P. LAMB. 1968. Some observations on the Malpighian tubules and ovarioles in *Myrmecia dispar* (Clark) (Hymenoptera: Formicidae). J. Aust. Entomol. Soc., **7**: 80–81.

HAGAN, H. R. 1954. The reproductive system of the army-ant queen, *Eciton* (*Eciton*). Part 1. General anatomy. Amer. Mus. Novitates. 1663, 12 pp.

HERMANN, H. R 1969. The hymenopterous poison apparatus: evolutionary trends in three closely related subfamilies of ants (Hymenoptera: Formicidae). J. Georgia Entomol. Soc. **4**: 123–141.

HERMANN, H. R., JR., AND M. S. BLUM. 1967. The morphology and histology of the hymenopterous poison apparatus. III. *Eciton hamatum* (Formicidae). Ann. Entomol. Soc. Amer., **60**: 1282–1291.

MANN, W. M. 1922. Ants from Honduras and Guatemala. Proc. U. S. Nat. Mus., **61**: 1–54.

MAYR, G. 1870. Neue Formiciden. Verh. Zool.—Bot. Ges. Wien, **20**: 939–996.

MUKERJEE, D. 1927. Notes on the occurrence of ovaries in the worker of *Myrmicaria brunnea* Saunders. J. Dep. Sci., Calcutta Univ. **8**: 21–24.

———. 1933. On the anatomy of the worker of the ant *Dorylus* (*Alaopone*) *orientalis* Westw. Zool. Anzeiger. **105**: 97–105.

RAIGNIER, A., AND J. VAN BOVEN. 1955. Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). Ann. Mus. Roy. Congo Belge, Sci. Zool. **2**: 1–359.

REID, J. A. 1941. The thorax of the wingless and short-winged Hymenoptera. Trans. Roy. Entomol. Soc. London, **91**: 367–446.

RETTENMEYER, C. W. 1963. Behavioral studies of army ants. Univ. Kansas Sci. Bul., **44**: 281–465.

SMITH, F. 1859. Catalogue of the hymenopterous insects in the collection of the British Museum. VII. Dorylidae and Thynnidae., 76 pp.

SCHNEIRLA, T. C. 1957. A comparison of species and genera in the ant subfamily Dorylinae with respect to functional pattern. Insectes Sociaux. **4**: 259–298.

———. 1964. Cyclic functions in genera of legionary ants (subfamily Dorylinae). XII Int. Congr. Entomol. (mimeographed copy of abstract). 5 pp.

SCHNEIRLA, T. C., AND A. Y. REYES. 1966. Raiding and related behaviour in two surface-adapted species of the Old World doryline ant, *Aenictus*. Anim. Behav. **14**: 132–148.

WALLIS, D. I. 1965. Division of labour in ant colonies. Symp. Zool. Soc. London No. 14. pp. 97–112.

WEYER, F. 1927. Die rudimentären Keimdrüsen im Lebensablauf der Arbeiter von *Formica rufa* L. und *Camponotus ligniperda* Latr. mit Berücksichtigung der übrigen sozialen Hymenoptera. Zool. Anzeiger. **74**: 205–221.

Wheeler, W. M. 1910. Ants. Their structure, development and behavior. Columbia Univ. Press, New York. 663 pp.

———. 1921. Observations on army ants in British Guiana. Proc. Amer. Acad. Arts Sci., **56:** 291–328.

———. 1922. Ants of the Belgian Congo. Bull. Amer. Mus. Natur. Hist. **45:** 1–1139.

Whelden, R. M. 1963a. The anatomy of the adult queen and workers of the army ants *Eciton burchelli* Westwood and *Eciton hamatum* Fabricus [*sic*]. J. New York Entomol. Soc., **71:** 90–115.

———. 1963b. The anatomy of the adult queen and workers of the army ants *Eciton burchelli* Westwood and *Eciton hamatum* Fabricus [*sic*]. J. New York Entomol. Soc., **71:** 158–178.

Wilson, E. O. 1958. The beginnings of nomadic and group-predatory behavior in the ponerine ants. Evolution. **12:** 24–36.