Taxonomic Implications of Doryline Worker Ant Morphology: *Cheliomyrmex morosus* (Hymenoptera: Formicidae)[1]

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ABSTRACT

The external and internal morphology of the worker caste of the doryline ant *C. morosus* (F. Smith) is described, and the taxonomic implications of this morphology for the tribes that compose the subfamily Dorylinae are discussed. Doryline worker ant characteristics of value to phylogenetic and taxonomic interpretation include thoracic suturing, mouthpart morphology and sting apparatus anatomy. Condition of the central nervous system, in particular the number of ganglia present, may also prove useful. Other characteristics such as head configuration, general habitus, Malpighian tubule numbers, and ovarian structure are correlated with worker ant size and difficult to interpret when comparing polymorphic species. A comparative analysis of the characteristics determined to be important as phylogenetic indicators point to a triphyletic origin for the Dorylinae. The tribes Ecitonini and Cheliomyrmecini comprise one lineage, the Dorylini a second, and the Aenictini a third.

The subfamily Dorylinae, or army ants, is currently divided into four tribes. The Aenictini (composed of a single genus, *Aenictus*) and Dorylini (the genus *Dorylus* with its 6 subgenera) are distributed throughout Africa and tropical Asia, and the Ecitonini (including the genera *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrex*) and Cheliomyrmecini (containing the single genus, *Cheliomyrmex*) throughout the New World tropics and subtropics. Monophylogeny for these ants is implied in their placement in a single subfamily, but a polyphyletic origin has been hypothesized (Brown 1954, Gotwald 1969). Comparative morphological studies of the dorylines include those of the thorax (Reid 1941), poison apparatus (Hermann and Blum 1967, Hermann 1969), and mouthparts (Bugion 1930, Gotwald 1969). Other studies of doryline morphology are those by Cohic (1948), Hollingsworth (1960), and Mukerjee (1926, 1933) for the genus *Dorylus;* by Whelden (1963) and Hagan (1954a, b, c) for the genus *Eciton;* and by Gotwald (1971) for the genus *Cheliomyrmex*. Most behavioral observations have been amassed by Schneirla (1971), Rettenmeyer (1963), Topoff (1971, 1972), and Watkins (1964) for New World species and by Cohic (1948), Raignier and van Boven (1955), and Schneirla (1971) for Old World forms. Still, additional comparative morphological and behavioral studies are needed before the polyphyletic hypothesis of doryline origins is securely verified or refuted.

Of the four doryline tribes, the Cheliomyrmecini may be more closely related to the Ecitonini than to the Dorylini and Aenictini (Reid 1941, Borgmeier 1955, Hermann 1969, Gotwald 1969, 1971). In fact, Gotwald (1969) noted that the tribes Dorylini, Aenictini, and Ecitonini form distinctly separate, morphologically homogeneous groups, and that the Ecitonini and Cheliomyrmecini together form a closely related New World group.

It is the purpose of this paper to describe the morphology and histology of the *Cheliomyrmex morosus* (F. Smith) worker and to compare this species with

others in the subfamily. The Neotropical genus *Cheliomyrmex* was chosen because little is known about it and because it represents a monogeneric tribe.

METHODS

Specimens were collected in August 1965 from beneath a decayed log in a pasture near the Fortin de las Flores–Huatusco road at km 38, Vera Cruz, Mexico (Gotwald 1971). All specimens were preserved in Bouin's fluid. Gross dissections were made of numerous workers and soldiers, and measurements were made of 57 workers. These measurements are provided at appropriate points in the paper and represent the size range within the collected series for the structures selected.

Sectioned specimens were prepared with a modified methylsalicylate-parlodin embedding technique and stained with one of three preparations: (1) Delafield hematoxylin I (progressive method); (2) cresyl violet for Nissl substance; and (3) modified Gomoni paraldehyde-fuchsin stain (Lappano-Colletta et al. 1965). All sections were mounted in Permount.

RESULTS

External Morphology.—The workers of *C. morosus* are polymorphic and range in total length from 3.45 to 7.57 mm in the series examined. The habitus is as shown in Fig. 1. The size frequency distribution for the workers was not calculated because the sample was not regarded as random. Morphological discontinuities are not evident when the workers are arranged in a continuous series from the smallest to the largest.

Head.—length 0.72–1.53 mm, width 0.68–1.71 mm, cephalic index (HW/HL × 100) 88–115. Head color ranges from yellowish-brown in the smallest workers to reddish-brown in the largest workers or soldiers. Soldiers or major workers possess cylindrical, falcate mandibles, each with 1 apical and 2 subapical teeth. The worker mandible is typically flattened, somewhat triangular, usually with 1 apical and 2 subapical teeth and a series of denticles (Fig. 2). However, the mandibles of *C. morosus* workers can be arranged in
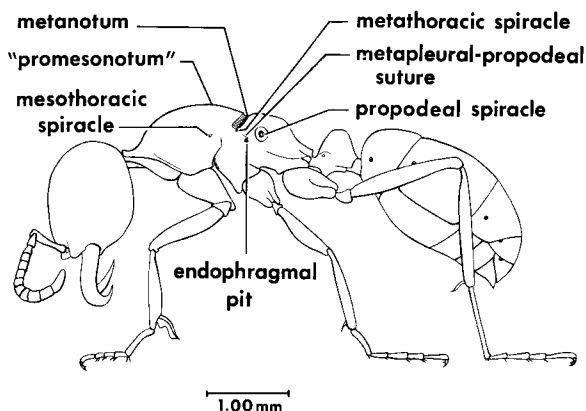
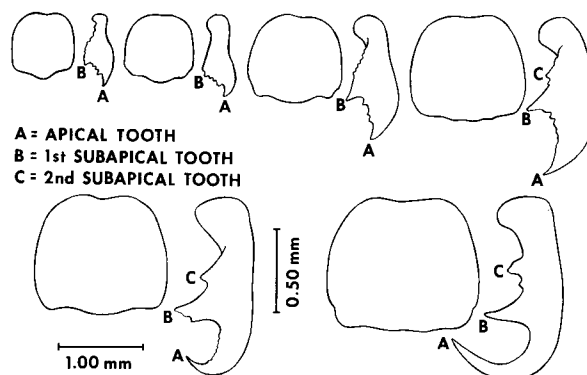FIG. 1.—*C. morosus*, major worker habitus, pilosity omitted.

FIG. 2.—*C. morosus*, worker head capsules (excluding antennae) and mandibles, dorsal view, selected to illustrate the polymorphic range and allometry of the species.

a continuous morphological series from the smallest to the largest (Fig. 2). In the smallest mandibles, the second (or proximal) subapical tooth is not distinguishable. Head shape changes with total body length and the cephalic index is positively correlated with total body length (Fig. 3). Although these workers are eyeless, two small, light-pigmented "eye-spots" are evident on the head capsule of larger individuals. Innervation of these spots was not detected in the histological preparations. The antennae are 12-segmented in all workers regardless of size. The mouthparts of *C. morosus* were previously described by Gotwald (1969).

Alitrunk.—length 1.15–2.34 mm. Suturing in the alitrunk of *C. morosus* is greatly reduced. Without sutures, the identification of specific sclerites and/or subdivisions is difficult if not impossible. The alitrunk is divided dorsally into anterior and posterior regions by the furrow-like metanotum (Fig. 1). The anterior region, which accounts for 60% of the alitrunk length, consists of the pro- and mesonotum. However, there is no sutural or topological boundary between these nota. The "promesonotum" is flattened dorsally and smoothly rounded anteriorly and laterally. It is continuous with the pleural region and carapace-like. The only distinct morphological feature of the pleural region is the small mesothoracic spiracle located above the first coxa. The posterior region of the alitrunk is composed primarily of the propodeum. The pleural area of this region includes the metathoracic spiracle, the endophragmal pit, the large propodeal (first abdominal) spiracle, and the bulla and orifice of the metapleural gland. The orifice of this gland is shielded dorsally by a cuticular hood. A faint, incomplete metapleural-propodeal suture passes between the endophragmal pit and propodeal spiracle. Ventrally the alitrunk is composed of laterocervical plates and the pro-, meso-, and metasterna (Tulloch 1935) (Fig. 4). The prosternum is situated immediately posterior to the laterocervical plates and is the smallest of the thoracic sterna. It consists of a clearly defined basisternum and furcisternum and bears a pair of furcal pits. The mesosternum and metaster-

num are each marked by a median longitudinal groove, and each is considered to be composed of an extensive anterior basisternum and a small posterior furcisternum. However, these regions are not suturally separated from one another. Unlike the prosternum, the furcasterna of the meso- and metathorax each bear only a single, median furcal pit.

Petiole.—length 0.22–0.56 mm. Lateral aspect of petiole as in Fig. 5. In all workers the petiole bears a ventral median process of triangular shape. The apex of the ventral process projects posteriorly. Viewed dorsally, the petiole is approximately as long as it is wide.

Gaster.—length 1.26–2.61 mm. There are 5 externally visible segments in the gaster of *C. morosus*, and each segment bears a pair of spiracles (Fig. 1). While the color of the gaster is consistent with the color of the head, alitrunk and petiole in any one individual worker, the sting is usually darker.

Internal Morphology.—Alimentary canal and accessory structures: The pharynx is the first region of the alimentary canal. It is characterized by a thick,
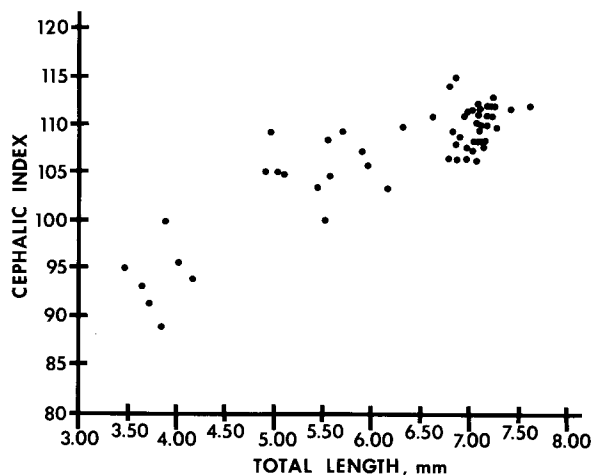

FIG. 3.—Relationship of head shape (cephalic index) to total body length in *C. morosus* workers.

laterocervical plate

basisternum 1

basisternum 2

furcal pit

furcisternum 2

mesosternum

basisternum 3

furcal pit

furcisternum 3

metasternum

1.00 mm   **4**

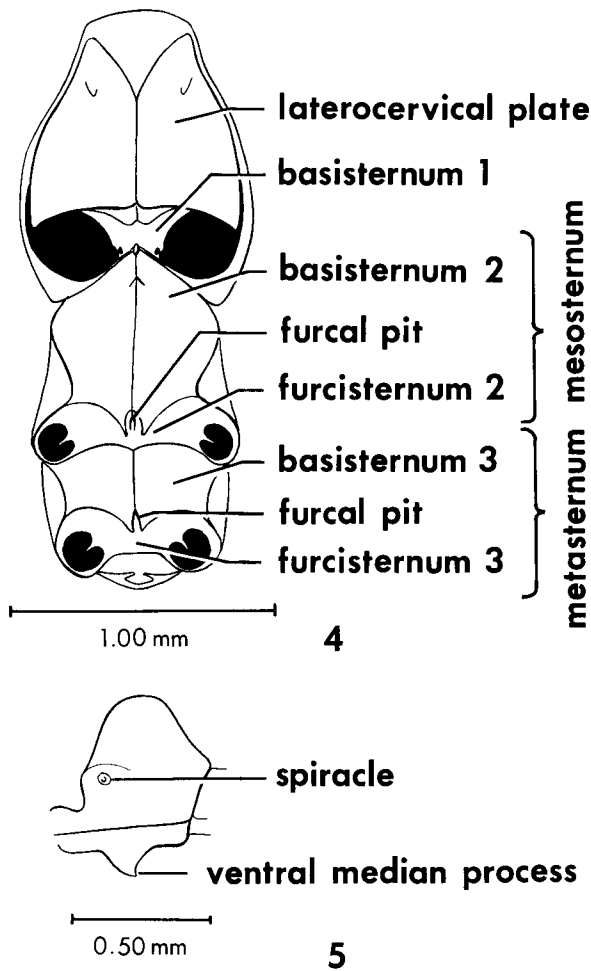spiracle

ventral median process

0.50 mm   **5**

FIG. 4.—*C. morosus*, worker alitrunk, ventral view.
FIG. 5.—*C. morosus*, worker petiole, lateral view.

chitinous ventral plate. Muscle fibers attach to both the ventral and dorsal pharyngeal surfaces, and the ventral pharyngeal plate bears two projections that may serve in muscle attachment. The chitinous lining or intima of the pharynx is progressively thinner as it approaches the beginning of the esophagus. Anterior to the "brain," the intima of the esophagus produces numerous hair-like spines that project into the lumen (Fig. 6). The esophagus is invested with a circular layer of muscle. Longitudinal muscle fibers were not apparent in our preparations. The esophagus is devoid of internal spines but subsequently associated ventrally with two bundles of longitudinal musculature as it passes between the supra- and subesophageal ganglia. Posterior to the brain the longitudinal muscles disappear, while a sparse circular musculature remains. Underlying the chitinous intima of the pharynx and esophagus is a continuous epithelial layer of varying thickness.

In the alitrunk the esophagus expands and both the intima and epithelium become thinner and cause the esophageal wall to appear more membranous. A layer

of circular musculature surrounds the esophagus at this point, but a longitudinal layer is not apparent.

The arrangement of the gastral digestive structures of *C. morosus* was described by Gotwald (1971). Briefly, the crop and midgut (ventriculus) lie juxtaposed and occupy the anterior half of the gastral cavity. They are connected by a reduced membranous proventriculus. The midgut tapers posteriorly to form the intestine which expands posteriorly to form the rectum. The Malpighian tubules attach approximately at the junction of the midgut and intestine.

In the gaster the esophagus expands to form the crop. The intima and epithelium are both more distinct in the crop than in the esophagus. The intima is thrown into a series of irregular folds (Fig. 7). The crop is invested with a circular layer of muscle, but longitudinal muscle fibers were not evident.

The midgut is a thick-walled structure composed of columnar digestive cells and smaller underlying regenerative cells. The intima ends with the proventriculus and is present again in the intestine. Small spherical bodies occurred in the lumen close to or adhering to the digestive cells in all midgut sections. The midgut is surrounded by a circular layer of muscle.

The intestine and rectum are histologically similar to the crop except that the epithelium is reduced. Circular muscle fibers are sparse. Rectal papillae were not detected in the histological preparations, although Gotwald (1971) reported the presence of two flattened, elliptical papillae in the anterior third of the rectum. The Malpighian tubules, whose insertion theoretically marks the beginning of the intestine, are composed of cuboidal cells arranged in a single layer around the lumen. The nuclei of these cells are distinct, and the smooth-walled lumen runs the entire length of each tubule. The Malpighian tubules range in number from 8 to 10 in minor workers, 10 to 15 in media workers, and 11 to 15 in soldiers (Gotwald 1971).

Glands.—There are six paired glands and one unpaired gland in *C. morosus*. The paired glands are the mandibular, maxillary, and pharyngeal in the head, the labial (salivary) and metapleural in the alitrunk, and the poison filaments in the gaster. The Dufour's gland is an unpaired gland in the gaster.

The mandibular glands are situated near the antennal sockets, against the basement membrane of the cranial hypodermis. Each gland is composed of only a few irregularly shaped cells with distinct nuclei. Presumably each cell empties its products into a common duct that terminates at the base of its corresponding mandible.

The maxillary glands are located laterad of the infrabuccal pocket, ventrad of the anterior tentorial arms. Each is composed of numerous pyramidal cells with distinct nuclei, and each cell tapers at one end to form a small duct (Fig. 9). These ducts empty into a larger common duct for each gland, and each of the common ducts opens into its corresponding lateral wall of the infrabuccal pocket.

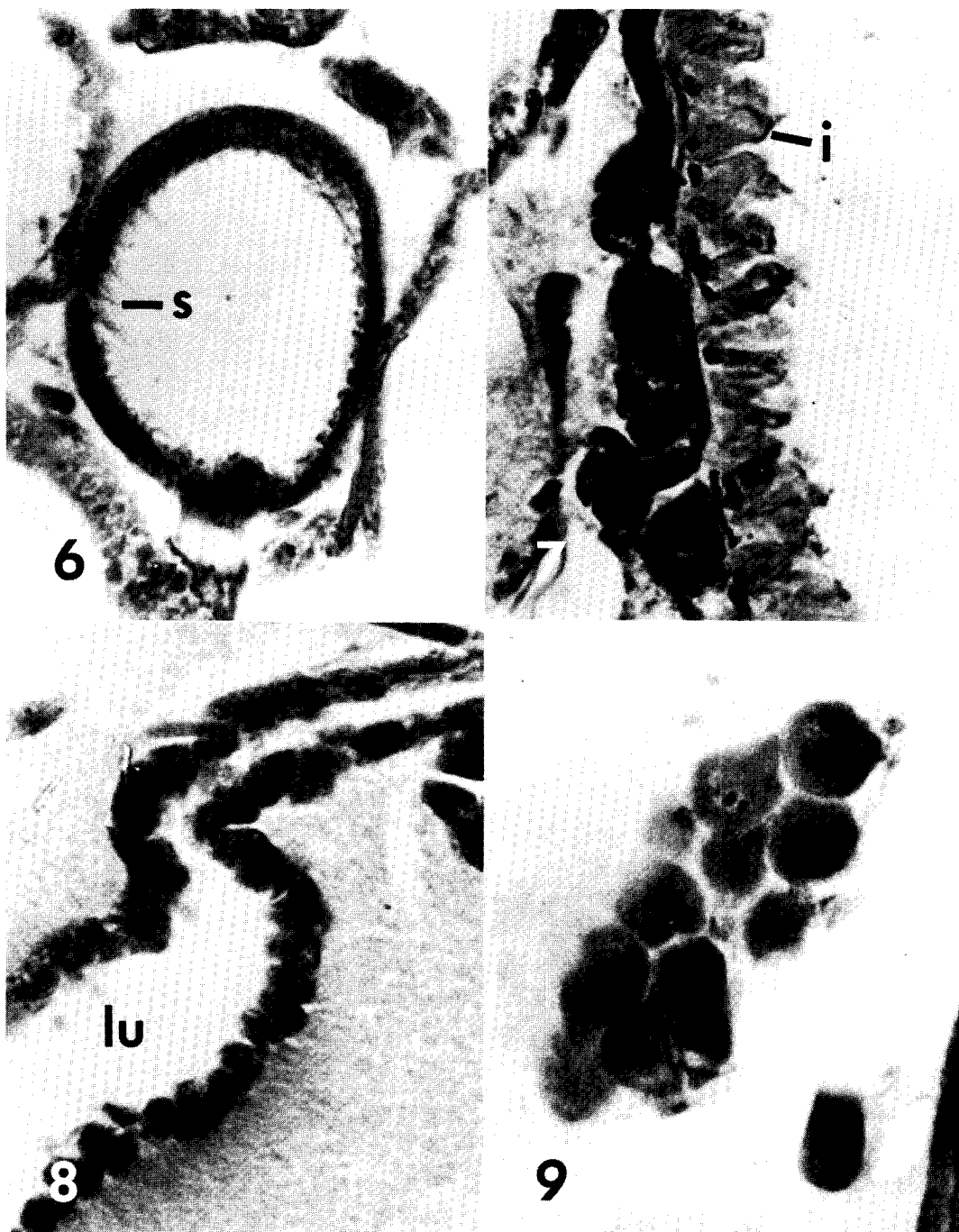The pharyngeal glands are located anterior to the

FIG. 6.—Esophagus of *C. morosus* worker, cross section anterior to brain (400×); s, esophageal spines.
FIG. 7.—Crop wall of *C. morosus* worker, cross section (400×); i, intima.
FIG. 8.—Pharyngeal gland of *C. morosus* worker, longitudinal section (400×); lu, lumen.
FIG. 9.—Maxillary gland of *C. morosus* worker, cross section (400×).

brain and dorsad of the anterior tentorial arms. They are composed of numerous cylindrical lobes, each of which has an irregularly shaped lumen (Fig. 8). The wall of each lobe is composed of a single layer of polyhedral cells.

The labial glands are located immediately posterior to the mesothoracic spiracles and are composed of small cylindrical lobes. Each lobe is composed of a single row of cells, each of which appears to possess an intracellular duct that continues from one cell to another. The lobes converge to form a duct-like reservoir on each side of the alitrunk, slightly anterior

and dorsad to each gland. Each reservoir empties into a cuticular duct which proceeds antero-medially until they unite to form a common duct at the anterior end of the alitrunk. This common salivary duct passes through the cervical region into the head capsule, ventrad of the brain and terminates in the labium. The salivary duct orifice provides a marker for the boundary between the hypopharyngeal and premental regions of the labium (Gotwald 1969).

The metapleural glands are located in the posterior third of the alitrunk, one on each side. Each gland is composed of numerous ellipsoidal cells with conspicuous nuclei (Fig. 10). Each cell gives rise to a small duct intracellular in origin. These ducts unite in each gland to form a bundle of ducts. The cell products are secreted through these ducts onto sieve plates located at the apex of an accessory metapleural structure, an invagination of the metapleuron (Tulloch et al. 1962). The accessory structures open on the posterior-lateral margins of the metapleuron.

The poison filaments arise from the poison duct anterior to the sting bulb. These ribbon-like structures are unbranched and are randomly distributed in the area of the poison sac (Gotwald 1971).

Distinct dorsal abdominal glands were not identified in the histological preparations, although a cluster of small gland-like cells was discovered in dissection attached to the membrane of the anterior margin of the 7th abdominal tergite.

Dufour's gland is situated in the last two visible segments of the gastral cavity at the apex of the joining ovarioles (Gotwald 1971). The duct of this small, spherical gland enters the sting bulb ventrad to the poison sac duct. The wall of the gland is composed of a profuse number of small cells detectable only through the presence of their conspicuous nuclei.

A gland-like tube, ventrad and histologically similar to the Dufour's gland is distinguishable in section, but has not been located in gross dissection.

Nervous System.—In the head, the nervous system consists of a supraesophageal and a subesophageal ganglion. These ganglia are fused into a single mass of nervous tissue, or brain, penetrated by the esophagus and its associated musculature (Fig. 11–12). Several structures and regions can be distinguished histologically within the supraesophageal ganglion. These structures include the four corpora pedunculata, two within each half of the protocerebral area of the ganglion. Each corpus pedunculatum, or "mushroom body," is composed of a calyx at one end of a "stem" or pedunculus of nerve fibers. The corpora pedunculata of each side consist of a medial calyx and pedunculus and a lateral calyx and pedunculus (Fig. 11–12). The two peduncula fuse and then divide to form an α and a β lobe (see Vowles 1955). The antennal lobes, one to each half of the deuterocerebral area, are located ventrad of the corpora pedunculata. A reduced optic center is situated laterad of each antennal lobe (Fig. 11). The central body is located between the antennal lobes.

The ventral nerve cord of the alitrunk, petiole, and gaster consists of six ganglia successively connected by paired interganglionic connectives. These connectives enter the alitrunk from the subesophageal ganglion and join the first of the three ganglia located in the alitrunk. The first ganglion is housed, in part, by portions of the prosternum and is connected to the second ganglion which, with the third ganglion, is situated in the posterior half of the alitrunk. There is a single ganglion contained in the petiole and two in the gaster. The first of the gastral ganglia is located in the first gastral segment, and the second extends through parts of the next two segments. Histologically, the connectives and peripheral nerves are composed of nerve fibers, while the ventral ganglia consist of a core of fibers surrounded by conspicuously nucleated neuron cell bodies. The last ganglion of the ventral nerve cord is conspicuously compound.

Reproductive System.—The worker reproductive system, when present, consists of two ovaries, each consisting of a single, polytrophic ovariole (Gotwald 1971), and a common oviduct. Located in the terminal segments of the gaster, the ovarioles extend anteriorly from the common oviduct and end in the terminal filament. Each ovariole consists of a series of oocytes (the largest of which is less than 0.25 mm in diameter) separated from one another by groups of polyhedral trophocytes.

Poison Apparatus.—The poison apparatus consists of a poison sac and duct, poison filaments, and sting bulb and associated sclerites. Dufour's gland is also associated with the sting apparatus. Hermann and Blum (1967), Hermann (1969), and Gotwald (1971) discussed the poison apparatus of C. morosus morphologically and histologically, so it is not included in detail here.

DISCUSSION

All worker ants of the subfamily Dorylinae are polymorphic, except the genus Aenictus, some species of the genus Neivamyrmex, and Eciton rapax Fr. Smith. The size differential, in terms of total length, between the smallest and largest C. morosus workers in the series measured, is 4.12 mm. Differentials calculated from data presented by Schneirla (1971) for a variety of doryline species are: 8.1 mm for Eciton burchelli (Westwood); 8.0 mm for Dorylus (Anomma) wilverthi Emery; 2.8 mm for Neivamyrmex nigrescens (Cresson); and 0.5 mm for Aenictus gracilis Emery. Thus the degree of polymorphism exhibited by C. morosus lies midway between the quasi-monomorphic (sensu Topoff 1971) Aenictus and the strongly polymorphic Eciton. While it is convenient to refer to individuals of a worker-polymorphic species as belonging to major, media, and minor subcastes, such designations are often arbitrary since workers may form a continuous gradient size series. This is true of Cheliomyrex, of most Eciton (Schneirla 1971), and of the Dorylus subgenus Anomma (Huxley 1927, Hollingsworth 1960, Raignier and van Boven 1955). Wilson (1953) considered worker polymorphism as a special adaptive character that resulted "in various types and degrees of division of worker labor." There are many examples in the ants
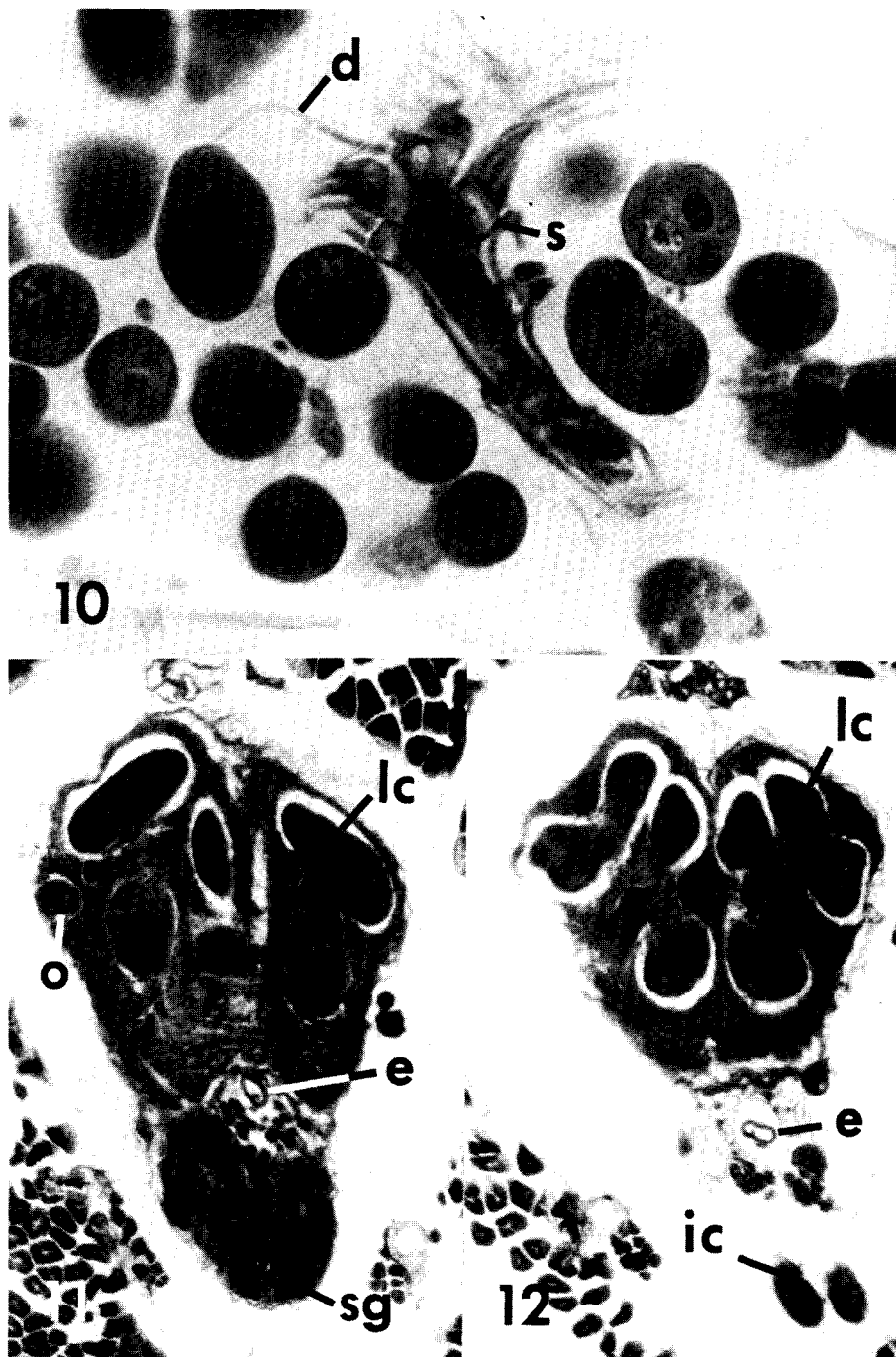
FIG. 10.—Metapleural gland of *C. morosus* worker, cross section through posterior portion of gland (400X); d, duct; s, sieve plate.

FIG. 11.—Brain of *C. morosus* worker, cross section (100X); e, esophagus; lc, lateral calyx; o, optic center; s.g., subesophageal ganglion.

FIG. 12.—Brain of *C. morosus* worker, cross section posterior to subesophageal ganglion (100X); e, esophagus; ic, interganglionic connective; lc, lateral calyx.

of caste polyethism (Wilson 1971), including the dorylines (Topoff 1971, Schneirla 1971). The biology of *C. morosus* is too poorly known to say that caste polyethism occurs. Curiously, there is a decline in polymorphism with increasing latitude (i.e. coldness of climate) everywhere in the world except the Indo-Australian region (Wilson 1968). This is of considerable interest when examining the dorylines.

for the only group that is not polymorphic is *Aenictus* and this genus is more diverse in tropical Asia than it is in Africa (Wilson 1964). This suggests that most *Aenictus* species have dispersed from Asia to Africa rather than the reverse.

The gradual size and morphological (allometric) transition in worker-polymorphic dorylines is demonstrable in the worker mandibles and heads. Hollingsworth (1960) illustrated this gradual change in *D. (A.) nigricans* Illiger, and *C. morosus* is a good example as well (Fig. 2). Certainly head shape in *C. morosus*, as evidenced in cephalic index, is correlated with total body length (Fig. 3).

The workers of *Dorylus, Aenictus,* and *Cheliomyrmex* are eyeless, while those of *Eciton, Labidus, Neivamyrmex,* and *Nomamyrmex,* with a few exceptions possess at least a reduced compound eye. Schneirla (1971) noted that the "visual equipment" of workers is best developed in epigaeic (i.e., surface-adapted) species and most poorly developed in hypogaeic or subterranean species. This observation apparently holds true for New World forms; for example, *C. morosus* is strongly hypogaeic and eyeless (Gotwald 1971) and *Labidus,* also hypogaeic, has poorly developed eyes (Werringloer 1932). However, the observation is not so applicable to a number of *Aenictus* and *Anomma* species which, in foraging and emigrating behavior, although eyeless, are relatively epigaeic. Epigaeic habits in blind species are probably secondary or tertiary developments. The compound eye of doryline workers is highly modified and ocellus-like, and even in "blind" forms, such as *Dorylus,* there is an integumental or subdermal light scense (Werringloer 1932). "Eyelessness" has developed convergently in numerous hypogaeic ant species and is of little use in interpreting the relationships of the doryline tribes.

When the pedicel or waist of an ant is uninodal, the segment is called the petiole (abdominal segment II); when the waist is 2-segmented, the segments are referred to as petiole and postpetiole respectively. The pedicel is binodal in the Ecitonini and Aenictini and uninodal in the Dorylini and Cheliomyrmecini. If the Dorylinae are monophyletic, the condition of the waist is much less conservative than it is in such subfamilies as the Myrmicinae (binodal) and Formicinae (uninodal). Pullen (1963) suggested that a binodal waist produces flexibility in such actions as stinging, and Schneirla (1971) added that the binodal condition is an important adaptation for epigaeic species when subduing strong, fast-moving prey. Schneirla (1971) further noted that this flexibility is advantageous in carrying brood and booty and in laying chemical trails.

Although the Cheliomyrmecini are similar to the Dorylini in possessing a uninodal waist, they are clearly dissimilar in thoracic suturing. Reid (1941) found that the doryline worker thorax is bipartite in the Dorylini and suturally undivided in the Cheliomyrmecini and Ecitonini. His conclusions support a polyphyletic origin for the doryline tribes, although he also noted that the thorax of *Aenictus* is similar to that of *Eciton.*

The pharynx of *C. morosus* and all other ants is preceded by the infrabuccal pocket. Janet (1894, 1905) noted that the infrabuccal pocket (poche gnathale) in ants serves as a filter by collecting grooming debris and solid particles from food. This collected debris is periodically ejected as small, discrete pellets (Janet 1894, 1904, Bugnion 1924, 1930, Wheeler and Bailey 1920). Eisner and Happ (1962) suggested that this filtering action was preadaptive to the development of passive crop storage and regurgitative food transmission in dolichoderine and formicine ants. Although the infrabuccal pockets of the *C. morosus* specimens dissected and sectioned did not contain debris, Whelden (1963) found infrabuccal debris in nearly all *E. hamatum* and *burchelli* workers examined. Bailey (1920) also reported infrabuccal pocket debris in *E. burchelli* and, in addition, found animal tissue debris in the infrabuccal pocket of *D. (A.) nigricans.*

The pharynx and esophagus of *C. morosus* are similar to those of *E. hamatum* and *burchelli* (Whelden 1963). Indeed, these portions of the alimentary canal appear to be structurally uniform throughout the Formicidae (e.g., see Walker and Clower 1961, and Forbes 1938). However, Bugnion (1930) described the pharynx of *Dorylus (A.) wilverthi* and *nigricans* as reduced and hypothesized that this reduction is correlated with the absence of trophallaxis in the dorylines. While the crop and midgut are also relatively uniform histologically in all ants, the proventriculus that connects them is not . The proventriculus of *C. morosus* closely resembles that of *E. hamatum,* which Eisner (1957) described as degenerative. Damming of the doryline proventriculus is probably dependent on muscular contraction (Eisner 1957), and crop storage may be of relatively short duration. While trophallaxis is apparently weakly developed or absent in the Dorylinae (Wilson 1971), foraging *Anomma* workers do return to the nest with their crops filled with liquids probably of prey origin (Gotwald 1974). Because the doryline proventriculus is degenerative it is not useful in delineating the tribal relationships.

The presence of columnar digestive cells and smaller regenerative cells in the ventricular wall of *C. morosus* is characteristic also of non-doryline ants (Walker and Clower 1961, Forbes 1938). Although Whelden (1963) noted the columnar digestive cells in *Eciton,* he failed to mention the regenerative cells. However, these latter cells are most likely present in all dorylines.

The Malpighian tubules of *C. morosus* are histologically identical to those of *Eciton,* but variation in terms of tubule and lumen diameter occurs within a single species (Whelden 1963). Ettershank and Brown (1964) suggested that the number of Malpighian tubules might serve as an important meristic character in the taxonomy of ants, and Gotwald (1971) compared the number of tubules in *C. morosus* with 6 species in three genera of New World dorylines. There was considerable overlap in tubule number ranges between the species. The number of tubules present is probably a function of body size in many

ants (Gray and Lamb 1968, Gotwald 1971), but is constant in some genera.

Since the intestine and rectum constitute the proctodeum, they are lined with a cuticular intima similar to that of the stomodeum (pharynx, esophagus, crop, and proventriculus). The rectal papillae may be of potential value as meristic characters. Whelden (1963) reported a range of 3 to 6 rectal papillae in *E. hamatum* and *burchelli*, and Mukerjee (1933) noted 2 papillae in the worker of *Dorylus (Alaopone) orientalis* Westwood. There are two such papillae in *C. morosus* (Gotwald 1971).

The mandibular gland of *C. morosus* does not have the conspicuous reservoir of some ants, for example like that shown by Janet (1898a) for *Myrmica rubra* L. In *Eciton* this reservoir is reduced, and although Whelden (1963) described it as a chamber, it appears more duct-like. In numerous myrmicine and formicine ants, mandibular gland secretions serve as alarm substances (Wilson 1963, 1971, Cavill and Robertson 1965, Regnier and Wilson 1968, Wilson and Regnier 1971), and field experiments with New World army ants of the genera *Eciton, Nomamyrmex,* and *Labidus* suggest that the mandibular gland of doryline ants also produces alarm substances (Brown 1960).

While the maxillary glands of *C. morosus* are composed of cells like those found in *Eciton,* the maxillary gland ducts open directly into the buccal tube and not into a special diverticulum of the buccal tube as in *Eciton* (Whelden 1963). Additionally, the maxillary glands of *C. morosus* are much smaller than those of *Eciton,* which Whelden (1963) described as sometimes forming a single compact gland "from the base of one mandible all the way across the front of the head to the base of the other mandible." The ducts of the maxillary gland cells of *C. morosus* unite to form a single common duct in each gland which in turn open into the buccal tube, while those of *Eciton* do not form a common duct but instead open individually into the buccal tube (Whelden 1963).

The pharyngeal glands of *C. morosus* differ little from those of *Eciton* (Whelden 1963). The structure of the glandular walls and the irregular nature of the lumen of each lobe in *Cheliomyrmex* and *Eciton* are identical. However, the spines that characterize the lining of the main chamber of each gland in *Eciton* were not identified in *C. morosus.* These glands are peculiar to the ants and evidence indicates that pharyngeal gland products are transferred with regurgitated crop liquids from workers to queens and larvae (Wilson 1971).

Although the labial glands of *C. morosus* and *E. burchelli* and *hamatum* are similar, the cuticular wall of the common labial duct is much thicker in *C. morosus.* The absence of an expanded reservoir in each gland in *Cheliomyrmex* and *Eciton* is typical also of nondoryline ants, although Forbes et al. (1961) described a large, thin-walled reservoir for the labial gland of *C. pennsylvanicus* (subfamily Formicinae). While such a development is not surprising, *C. pennsylvanicus* possesses two pairs of tracheal air sacs in the region of the labial gland (Keister 1963),

either of which might have been mistaken to be salivary reservoirs.

Detailed morphological descriptions of the metapleural gland, a gland found only in the ants, were provided by Janet (1898a, b), Tulloch (1936), and Tulloch et al. (1962). The openings of the secretory cell ducts into the accessory structure or chamber in *Eciton* occur singly or in groups (Whelden 1963), similar to the condition found in *Myrmecia nigrocincta* F. Smith (subfamily Myrmeciinae) (Tulloch et al. 1962). In *C. morosus* the openings are similarly distributed over several sieve plates. The metapleural glands are structurally consistent in those ants examined, although the glands are absent in some castes of some species, including the males of the Dorylinae (Brown 1968). The metapleural glands have been traditionally regarded as a source of colony odor, an hypothesis recently modified by Brown (1968). Maschwitz et al. (1970) found that metapleural secretions of some species are effectively antibiotic against certain bacteria and fungi and that the secretions protect the body surface and nest against microorganisms.

The gross morphology of the poison filaments and Dufour's gland of *C. morosus* was examined by Gotwald (1971). The Dufour's gland in *C. morosus* and *Eciton* (Hermann and Blum 1967) is a simple, elongated, terminally-bulbous structure. It does not show the same potential as a taxonomic character among the doryline tribes as it does in some Formicinae, where it is often variably bilobed (Wilson and Regnier 1971). Dufour's gland is the source of chemical trail substance in some ants [e.g., *Solenopsis* (Wilson 1959, 1962)]. In others, such as the formicines, its secretions serve to spread and enhance penetration of formic acid from the poison gland and to act as alarm pheromones (Wilson and Regnier 1971). Although the function of the Dufour's gland in the dorylines has not been established, trail substance in *Neivamyrmex* and *Eciton* is of hindgut origin and not from Dufour's gland (Watkins 1964, Blum and Portocarrero 1964).

Even though the poison apparatus (i.e., the glands, muscles, and sclerites of the sting) was not examined in detail in this investigation, its taxonomic potential must be noted. Interpretations of ant phylogeny based on poison apparatus morphology were offered by Hermann and Blum (1967), Hermann (1969) and Robertson (1968). The phylogenetic scheme for the ants provided by Robertson (1968) refuted the durable arrangement proposed by Brown (1954), but included an unrepresentative sample of ant species (e.g., the dorylines were not included). Hermann (1969) noted some morphological variations in the sting apparatus within the subfamily Dorylinae which support, to some extent, the polyphyletic hypothesis for the origin of the dorylines.

The nervous system of the ants has not been examined in a phylogenetic context. Certainly numerous morphological and functional studies exist, including those of Janet (1899), Vowles (1955), Markl (1966), and Bernstein and Bernstein (1969). The

corpora pedunculata have received much attention because the idea persists that the size of these bodies, relative to the rest of the brain, is an indication of mental capacity (Wilson 1971). Among those ants examined by Vowles (1955) and Bernstein and Bernstein (1969), the corpora pedunculata are smallest in *Eciton hamatum* and largest in *Formica rufa* L., but the size differential in this case is related in part to the reduced size of the optic ganglia in *Eciton* (Vowles 1955). The optic centers in *C. morosus* are also reduced. Obviously, the relative size of the doryline brain in all species is predictably smaller than in ants with well-developed eyes (Werringloer 1932).

The worker nervous systems of *C. morosus* and *E. burchelli* and *hamatum* are similar in most respects. *C. morosus* does not have a conspicuous optic nerve like that of *Eciton* (Whelden 1963). Also, because *Eciton* is binodally waisted and *C. morosus* uninodal, the gaster of *Eciton* contains only one ventral compound ganglion. Wheeler (1910) indicated that the central nervous system of the adult ant "presents only eleven ganglionic masses," but it is now evident that there may be even fewer ganglia in some species. In the case of *C. morosus* there are only 8 such ganglia (including the fused supra- and subesophageal ganglia).

Ovaries have been described for the workers of *D. (Alaopone) orientalis* (Mukerjee 1933), *E. hamatum* and *burchelli* (Whelden 1963), and *C. morosus* (Gotwald 1971). These ovaries are composed of polytrophic ovarioles. In *D. orientalis* and *C. morosus* each ovary (i.e., on each side) consists of a single ovariole (Mukerjee 1933, Gotwald 1971), but in *Eciton,* the number of ovarioles per ovary ranges from 1 to 3 (Whelden 1963). Whether or not these workers actually lay eggs remains unknown. Ovaries may not be present in all doryline workers, for Holliday (1904) failed to find ovaries in *Neivamyrmex nigrescens* (Cresson) and Mukerjee (1933) and Gotwald (1971) each dissected a number of workers of *D. orientalis* and *C. morosus* respectively in which no ovaries were discovered. Inter- and intraspecific variation in doryline worker ovaries is generally limited to the number of ovarioles composing an ovary, and Whelden's (1963) data implies that ovariole number is positively correlated with worker size, thus reducing its value in relating the tribes phylogenetically.

CONCLUSIONS

While variations in conservative characters are of considerable importance to phylogenetic interpretation, most taxonomists ultimately rely on a potpourri of characters of moderate lability and must risk the chance of phylogenetically grouping together species or species groups whose similarity was arrived at convergently. Army ant behavior patterns (i.e., nomadism and group predation), for instance, have arisen convergently, to some extent, in nondorylines such as *Simopelta* (Gotwald and Brown 1966) and *Leptogenys* (Wilson 1958) and concomitant convergence

in some morphological characteristics should be anticipated. Indeed, Hermann (1968, 1969) found that the ponerine *Simopelta oculata* Gotwald and Brown lacks a furcula among its sting sclerites, a character it shares with all the dorylines and with none of the other ponerines examined thus far.

Certain doryline worker characteristics have a predictably higher taxonomic value than others. In external anatomy the suturing of the thorax (Reid 1941) and the structure of the mouthparts (Gotwald 1969) are taxonomically useful features and point to a polyphyletic origin for the dorylines. ·The sting apparatus is equally important in supporting the polyphyletic hypothesis. Head shape and habitus configuration, on the other hand, are allometrically determined in highly polymorphic species, and the utilization of such characters depends on the intelligent use of ratios (e.g. cephalic index) in comparative studies. The condition of the doryline waist may also be a poor indicator of phylogenetic relationships. Based on the number of segments in the waist, it is certainly easier to believe that the dorylines consist of four phyletic lines (the Aenictini, Dorylini, Ecitonini, and Cheliomyrmecini) than to assume that the Cheliomyrmecini and Dorylini, both uninodal, are closely related.

The alimentary canal is of little use to taxonomic interpretation within the Dorylinae. Proventricular structure is degenerative and the numbers of Malpighian tubules, rectal papillae, and ovarioles are often size-correlated and not dependable as meristic characters.

While the glands are, for the most part, structurally and quantitatively uniform throughout the dorylines, the identification of glandular secretions must be rated as an important target for functional and phylogenetic research. Interspecific differences in glandular secretions and functions may ultimately contribute in a significant manner to an understanding of evolutionary relationships in the Dorylinae.

The ant nervous system morphologically yields little phylogenetic information and is subject to such convergent variation as the reduction of optic centers in species which are poorly equipped visually (a condition which is, in turn, related to the convergent development of hypogaeic lifeways). However, a comparative analysis of the numbers of central nervous system ganglia within the Dorylinae and the other ant subfamilies may be useful in establishing some phylogenetic relationships.

An analysis of the geographical distribution of the doryline tribes and of existing morphological and behavioral studies indicates that (1) the subfamily Dorylinae, as presently constituted, is triphyletic; that (2) the 3 lineages composing the Dorylinae are the Ecitonini-Cheliomyrmecini, the Dorylini, and the Aenictini; that (3) the Aenictini arose in tropical Asia and dispersed toward and eventually reached and spread in the Ethiopean Region; that (4) the Dorylini arose in tropical Africa and weakly dispersed toward Asia, with only a few species established in the Indo-Australian region; that (5) the

Ecitonini and Cheliomyrmecini arose from a common ancestor that possessed a single-segmented waist; and that (6) the Ecitonini and Cheliomyrmecini diverged from one another early in their evolution; the genus *Cheliomyrmex* retained the primitive single-segmented waist and the Ecitonini, through a constriction between abdominal segments III and IV, developed a two-segmented waist.

The taxonomic implications are clear. If we cannot justify the placement of the current doryline tribes in any of the existing ant subfamilies, they should be given subfamily status. The subfamily Dorylinae should be retained for the Dorylini and a good case for subfamily status for the Ecitonini-Cheliomyrmecini can be made [the subfamily Ecitoninae has already appeared in the literature (Brown 1973)]. The status of the Aenictini remains for continuing investigation.

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