Taxonomic Implications of Doryline Worker Ant Morphology: *Dorylus* Subgenus *Anomma* (Hymenoptera: Formicidae)

by

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ABSTRACT

The worker caste of two populations of *Anomma* driver ants (genus *Dorylus*) was examined morphologically for characters of potential value in assessing the evolutionary and taxonomic affinities of the Old and New World army ants. Features that thus far appear uniquely developed in the driver ants are the spines on basisternum 2, the pygidial impression and spines, and the anus gland. Other characters that clearly distinguish *Anomma* driver ants from the New World Ecitoninae are the mouthparts, thoracic suturing, sting morphology, condition of certain tergal glands, and the number of ganglionic masses in the ventral nerve cord.

Army ants are primarily tropical and subtropical in distribution and are currently classified in the subfamilies Dorylineae and Ecitoninae. The Old World monogeneric tribes Dorylini and Aenictini, represented by about 100 species in the genera *Dorylus* and *Aenictus*, comprise the Dorylineae (Wilson, 1964, Gotwald, 1979). The genus *Dorylus* consists of six subgenera (*Alaopone, Anomma, Dichthadia, Dorylus, Rhogmus, Typhlopone*). The subfamily Ecitoninae is composed of two tribes, the Cheliomyrmecini with its single genus *Cheliomyrmex* and the Ecitonini with its four genera (*Eciton, Labidus, Neivamyrmex, Nomamyrmex*). The nearly 150 species in this subfamily are distributed in the New World to 40° latitude north and south of the equator (Watkins, 1976).

Recent elevation of the New World forms to subfamily status (Snelling, 1981) reflects the belief among myrmecologists that the true army ants are polyphyletic (Brown, 1954, Gotwald, 1979, 1982, and Gotwald and Kupiec, 1975). In an investigation of the morphology of the workers of *Cheliomyrmex morosus* (F. Smith) and a review of existing comparative morphological studies of doryline and ecitonine ants, Gotwald and Kupiec (1975) concluded that the army ants are triphyletic and that the three lineages of army ants are the

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(1) Ecitonini-Cheliomyrmecini, (2) the Dorylini, and (3) the Aenictini. Furthermore, because army ants disperse poorly, the timing of certain geological events, such as the fragmentation of the supercontinents Laurasia and Gondwana and the appearance and disappearance of land bridges connecting the continents, supports the hypothesis that the army ants arose convergently at three separate tropical loci (Gotwald, 1979). However, additional comparative morphological studies of the army ants should provide an even better basis for understanding army ant origins.

The purpose of this paper is to describe certain morphological features of the workers of two populations of African driver ants, Dorylus (Anomma) nigricans Illiger and D. (A.) molesta (Gerstaecker), and to compare these features to those of other army ants, particularly Cheliomyrmex morosus. Most of the morphological features selected for study and comparison are those that have demonstrated greatest potential to taxonomic decision making and could be included in subsequent phenetic and cladistic analyses of the true army ants. This paper does not claim to be a definitive morphological description of the subgenus Anomma. Although the taxonomy of Anomma is unsettled, it is our opinion that the two forms studied here represent distinct species. These two species are clearly allopatric, with molesta ranging over much of East Africa and nigricans more or less confined to West Africa. Anomma (which is restricted in distribution to sub-Saharan Africa) is the only subgenus of Dorylus containing species that commonly forage on the surface of the ground and are thus more commonly encountered than are other African dorylines.

Methods

The specimens of D. nigricans were collected from a single colony (Gotwald field no. GC-002) on 1 June 1971 at Legon, Ghana. The D. molesta specimens that were sectioned for histological study were taken from two colonies in Tanzania by D. H. Kistner (nos. 1489 and 2310) on 20 April 1966 at Amani and on 17 June 1970 at Arusha National Park. Gross dissections were made in the field on numerous workers of D. molesta (Gotwald field no. KC-086) taken on 27 July 1971 at Karen, Nairobi, Kenya.

Specimens collected for sectioning were preserved in Bouin's fluid and were prepared with a modified methylsalicylate-parlodion embedding technique. Sections were 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.

The terminal segments of the gaster were examined with the scanning electron microscope.
Fig. 1. Dorylus (Anomma) molesta, major worker habitus, legs and pilosity omitted.

Results

External Morphology

The workers of *D. (A.) nigricans* and *molesta* are polymorphic, and morphological discontinuities are not evident when the workers of either species are arranged in a continuous series according to size. The range of total body lengths for the *nigricans* series examined was 3.64 to 12.25 mm and for the *molesta* series 2.70 to 12.02 mm. The habitus is as shown in Fig. 1.

Head: length 0.90-3.37 mm, width 0.80-3.70 mm, cephalic index (HW/HL x 100) 78-124.7 for *nigricans* and length 0.72-2.96 mm, width 0.72-3.14 mm, cephalic index 86.2-114.3 for *molesta* (Fig. 2A). Soldiers of both species possess cylindrical, falcate mandibles, each with 1 apical and 1 subapical tooth. Media and minor workers possess a flattened mandible with 1 apical and 2 subapical teeth and a series of denticles, particularly prominent in minors, along the masticatory margin between the subapical teeth. The mandibles of both species can be arranged in a continuous morphological series from the smallest to the largest. In the large media workers, the first (or distal) subapical tooth is inconspicuous (Fig. 3). In both species the distal margin of the labrum is smoothly curved without a median cleft (Fig. 2B). The major workers possess a single, median tubercle near the distal margin of the labrum. The maxillary palpus is 2-segmented and a prominent transverse stipital groove is present on the stipes (Fig. 2E). In (Fig. 2C) the majors, the galeal crown is produced into a conical prominence bearing numerous setae. The lacinal comb is conspicuous and is composed of many stout setae (Fig. 2C). The labial palpus is 2-segmented (Fig. 2D). All workers are eyeless and without "eyespots." The antennae are 12-segmented in both species.
Fig. 2. *Dorylus (Anomma) molestata*. A. Head of major worker, dorsal view, right antenna and pilosity omitted. B. Labrum of major worker, external surface. C. Left galea and lacinia of major worker, maxillary comb drawn as seen through transparent galea. D. Left labial palpus of major worker. E. Left stipes, maxillary palpus of major worker. Scales in mm.
Fig. 3. *Dorylus (Anomma) nigricans*, left mandibles from a (A) major, (B) media, and (C) minor worker, dorsal aspect.

Alitrunk: length 1.12-3.75 mm for *nigricans*; 0.90-3.97 mm for *molestas* (Fig. 1, 4A). The pronotum and propleurae together form a prothoracic carapace that is clearly separated from the remainder of the alitrunk by a pro-mesonotal and pro-mesopleural suture (Fig. 1, 4A). These sutures join laterally to form a caudally directed point. A meso-metanotal suture can be detected in major workers as a faint line or depression approximately 0.5 mm posterior to the pro-mesonotal suture (Fig. 1). No other suturing on the dorsum is evident. The meso-metapleural and metapleural-propodeal sutures are conspicuously impressed but incomplete; the latter suture passes ventral to the large propodeal spiracle and through a small endophragmal pit. The pleura of the metathoracic-propodeal region includes the bulba and orifice of the metapleural gland. The orifice of the gland is shielded dorsally by a cuticular hood whose arched free margin extends cranially almost to the meso-metapleural suture. Ventrally, the alitrunk is composed of the laterocervical plates and the pro-, meso-, and metasterna. The prosternum is small and composed of a poorly defined basisternum 1 and furcisternum 1. The meso- and metasternum each include an extensive anterior basisternum and small posterior furcisternum, although these regions are not sutturally separated. Two conspicuous, caudally directed spines arise from the posterior margin of basisternum 1 (Fig. 4A, B).

Petiole: length 0.36-1.03 mm, width 0.30-0.90 mm for *nigricans* and length
0.36-1.08 mm, width 0.31-0.96 mm for *molestata* (Fig. 4C, D). The petiole of each species bears a ventral median process or tooth that is directed posteriorly (Fig. 4C). This subpetiolar tooth is present in all workers, although in minor workers, it is proportionately smaller and is placed at the extreme anterior end of the petiole. The lateral posterior angles of the petiole, as viewed dorsally, form bulbous processes (Fig. 4D). In the case of *molestata*, these angles are especially conspicuous and may constitute a diagnostically significant characteristic for the species.

Gaster: length 1.26-4.02 mm for *nigricans*; 0.94-4.25 mm for *molestata*. The gaster consists of 5 visible segments and is unremarkable except in its caudal extremity where the terminal tergite or pygidium (abdominal segment VII) is impressed with a circular concavity. This pygidial impression is circumscribed by a sharply produced and elevated margin and is armed at each side with a single pygidial spine (Fig. 5). Distally the spines are commonly simple, but they may also be bi- or tripartite and may vary from spine to spine on the same individual worker (Fig. 6). For example, *nigricans* workers were found with the following combinations: both simple, simple-bipartite, both bipartite, and simple-tripartite; and *molestata* workers: both simple, simple-bipartite, both tripartite. Each pygidial spine is a cuticular process with a clearly impressed boundary between the body of the spine and the apex or apices. However, this apparent articulation appears fully sclerotized and inflexible. In some workers the apices bear parallel, longitudinal striae that closely
Fig. 5. *Dorylus* (*Anomma*) *molest*a, major worker. A, Pygidium, oblique dorsal view. B, Pygidal spine, lateral view. Scales in mm.

resemble the striae that mark some of the pygidial setae (Fig. 6B). Because the sclerites that compose the sting apparatus of army ants were examined in detail by Hermann (1969), they were not examined in this study.

**Internal Morphology**

Alimentary canal and accessory structures: the pharynx is the first region of
the alimentary canal and is characterized by a chitinous ventral plate. Muscle fibers attach to both the ventral and dorsal pharyngeal surfaces. The intima or chitinous lining of the pharynx thins abruptly as it becomes the esophagus. Anterior to the brain the intima of the esophagus produces numerous hair-like spines that project into the lumen. These spines decrease
Fig. 7. *Dorylus (Anomma) molesta*, media worker, liquid-filled crop, lateral view as exposed in dissection.

in number as the esophagus enters the "brain" and are absent after a short distance. The esophagus is invested with a circular layer of muscle fibers anterior to the brain; these fibers persist into the alitrunk. Longitudinal muscle fibers are apparently absent, except for the section of the esophagus that passes through the brain (technically between the circumesophageal commissures). These longitudinal fibers begin anteriorly on the ventral surface of the esophagus as two discrete bundles that eventually unite to form a single flattened sheet. This sheet terminates at the point where the esophagus exits from the brain. Posterior to the brain, the esophageal lumen enlarges and the wall become membranous.

In the gaster, the esophagus expands to form the crop which is invested with a circular layer of muscle fibers. The intima of the crop, midgut, intestine and rectum is smooth, and nowhere is it produced into a series of irregular folds. Circularly arranged muscle fibers are evident throughout the remainder of the canal. If longitudinal fibers are present, they were not apparent in the sections examined. The proventriculus, situated between the crop and mesenteron, is membranous. Field dissections of *molesta* revealed that when closed the proventriculus causes the crop to expand with accumulated liquid until it occupies the anterior half of the gaster (Fig. 7). Also revealed in field dissection were two dorsal air sacs in the anterior half of the gaster. These sacs extend from the 1st to the middle of the 3rd gastral segment and straddle and partially cover the crop and anterior part of the
Fig. 8. \textit{Dorylus (Anomma) molest}, relationship of head width to numbers of Malpighian tubules.

Malphighian tubules, whose insertions approximate the beginning of the intestine (proctodeum), are composed of a single layer of cuboidal cells arranged about a small lumen. The nuclei of these cells are distinct in the preparations examined. Gross dissections of \textit{molest}a workers showed the tubules to range in number from 6 to 28. The numbers of tubules are positively correlated with worker size (Fig. 8). Rectal papillae were not evident in the histological preparations, although in gross dissection they are easily identified. The number of papillae in \textit{molest}a is constant at two.

Glands: there are 4 paired glands, not counting the paired poison filaments, and 2 unpaired glands, excluding the convoluted gland of the poison sac. The mandibular, maxillary, labial and metapleural glands are
Fig. 9. *Dorylus* (*Anomma*) *molestata*, major worker, mandibular gland, dorsal view as exposed in dissection.

paired; the pharyngeal and Dufour's glands unpaired. While other glands are present (e.g., pygidial, postpygidial, and anus glands), they were not identified in the sections examined.

The mandibular glands are situated near the bases of the mandibles adjacent to each antennal socket (Fig. 9). These relatively large glands are composed of numerous spherical cells arranged about a cavity that most likely serves as a reservoir. Each cell appears to possess its own duct that empties individually into the central cavity. A single large duct leads from this reservoir to the base of the mandible.

The maxillary glands are small and are composed of pyramidal to ovoid cells. They are located dorsal to the antero-lateral corners of the buccal cavity. Each cell empties directly into the cavity via its own duct that opens through the lateral wall of the cavity.

Centered on the midsagittal line dorsal to the brain, the pharyngeal gland consists of a series of irregularly shaped lobes that radiate from a common center. Each lobe is composed of a single layer of polyhedral cells arranged about a central lumen.
The labial glands lie in the alitrunk and each produces a duct that proceeds anteriorly until both ducts unite to form a common salivary duct. This duct opens onto the membranous dorsal surface of the labial prementum and theoretically serves as a marker for separating the hypopharyngeal region from the prementum area of the labium (Gotwald, 1969).

Numerous cells with prominent nuclei and nucleoli compose the metapleural glands, which are located at the posterior end of the alitrunk. Each cell is provided with its own duct that appears to arise intracellularly.

The Dufour's gland, whose wall is composed of numerous small cells with clearly defined boundaries, is sac-like and possesses a duct that enters the sting bulb ventral to the poison sac duct.

Nervous System: since Gotwald and Kupiec (1975) found that the nervous system yields little in the way of phylogenetic information, except for the numbers of ganglia incorporated into the ventral nerve cord, only the ganglia were examined. In molesta, these include 3 thoracic ganglia, 1 petiolar ganglion, and 4 gastric ganglia. The ventral nerve cord of the alitrunk and gaster thus consists of 8 ganglia successively linked by paired interganglionic connectives. In the gaster, the first of the 4 ganglia located there is situated at the boundary between the first and second gastric segments, the second within but near the posterior margin of the second gastric segment, and the last 2 within the third gastric segment.

Reproductive System: gross dissections of molesta workers with head widths ranging from 0.75 to 3.50 mm revealed ovaries in 9 of 10 individuals examined. Each ovary consists of a single polytrophic ovariole, some containing maturing oocytes measuring up to 0.84 mm in length.

Discussion

The workers of Anomma and of the other 5 subgenera of Dorylus are polymorphic. This is also true of the Ectoninae, except for some species of the genus Neivamyrnex and Ecton rapax F. Smith. Aenictus is the only genus of true army ants in which all of the species are essentially monomorphic. Worker polymorphism is a derived characteristic that gives rise to assorted degrees of division of labor among workers (Wilson, 1953).

The workers of Anomma occupy a continuous size range but exhibit allometrically determined differences correlated with size. Mandible shape, in particular dentition, is but one such feature. The lack of demonstrably discrete size classes among the workers is consistent with the conclusions of previous investigations of polymorphic army ant species (Hollingsworth, 1960; Gotwald and Kupiec, 1975). Allometrically produced differences in mandible morphologies may be variously adapted to different tasks (Gotwald, 1978). In the evolution of polymorphism, these differences were probably
preadaptive to an eventual division of labor among workers in such behaviors as foraging, retrieving prey, defense, transporting brood, queen and brood care, trail wall construction, nest building, and "housekeeping" activities.

The reduced palpal segmentation of *Anomma* is characteristic of all true army ants in which the maxillary palpus ranges from one to two segments and the labial palpus from two to three segments. This reduction in palpal segmentation is correlated with the hypogaeic life style of most species and supports the hypothesized subterranean existence for the ancestors of those species, such as many *Anomma*, that lead a largely epigaeic life style (Gotwald, 1982). The mouthparts of army ants were previously examined and compared by Gotwald (1969). Among the unique features of the mouthparts of *Anomma* and at least some other species of *Dorylus* are the conically produced galeal crown and the entire distal margin (i.e., the absence of a median cleft) in the labrum. In the Ecitoninae the galeal crown is flattened and the labrum is always bilobed. This is also true of *Aenictus*. The mandibles of *Anomma* and *Cheliomymrmex* soldiers resemble one another more closely than they do other species (there is one subapical tooth in *Anomma*, two in *Cheliomymrmex*). This similarity in mandible morphology between Old and New World army ants is a convergent development.

Little taxonomic importance can be attached to the fact that most army ants are eyeless or in possession of greatly reduced eyes, since this condition is arrived at convergently (Gotwald, 1982). The workers of *Dorylus*, *Aenictus*, and *Cheliomymrmex* are eyeless, while with few exceptions, those of *Eciton*, *Labidus*, *Neivamyrnex*, and *Nomamyrmex* possess greatly reduced (to a single facet) compound eyes. Like reduced palpal segmentation, reduced eyes and eyelessness are correlated with hypogaeic life ways. The adoption of epigaeic foraging, emigration, and nesting behaviors by some species, notably *Anomma*, *Eciton*, and *Neivamyrnex*, is a secondary and rather recent evolutionary development. These species retain their hypogaeically produced morphological characteristics.

The alitrunk (= mesosoma) of *Anomma* and the other *Dorylus* subgenera is fundamentally different from that of *Aenictus* and the Ecitoninae, in that it is divided in half dorsally and laterally by the pro-mesonotal and pro-mesopleural sutures. The absence of thoracic suturing shared by *Aenictus* and the Ecitoninae is the derived or apomorphic condition but little can be inferred phylogenetically about lost character states, because parallel losses are common in species not closely related. The spines on basisternum 2 in *Anomma* may be unique among the army ants but their absence in other species will have to be observationally confirmed.

In *Anomma*, the rest of *Dorylus*, and *Cheliomymrmex*, the waist consists of a single segment, the petiole, and represents the plesiomorphic state. Among the Ecitonini and *Aenictus*, the waist consists of two segments, the petiole
and postpetiole. Some investigators have suggested that the binodal waist variously facilitates stinging, laying chemical trails, and carrying brood and prey (Gotwald, 1982).

The pygidial impression and spines of Dorylus, including Anomma, constitute the most clearly diagnostic feature that the genus possesses. To our knowledge, pygidial spines such as these are found nowhere else among the ants. The longitudinal striae present on the well marked apices of the spines suggest that the apices themselves were derived from setae similar to those found on the pygidium that also possess such striae. The function of the pygidial spines is unknown, but their presence may be correlated with the absence of stinging in the genus or with the secretory activities of the pygidial and postpygidial glands. Although we have observed Anomma extensively in the field, nothing in its behavioral repertoire suggests a function for these spines.

Although we have not examined the sting apparatus in this study, it is relevant to note that Dorylus workers do not sting (Gotwald, 1978). Hermann (1969) encountered nothing in his investigation of the Dorylus sting apparatus that would theoretically affect employment of the sting, except that the sting sclerite itself is widely spatulate at its base. Among the New World army ants and Asian Aenictus, apparently all of which sting, the sting bulb is not spatulate but slender. Gotwald (1978) observed that at least one non-stinging species of African Aenictus also possesses a spatulate sting. An alternative function for the sting in Dorylus has not been observed, although an adaptive "trade-off" for the loss of stinging might be anticipated in these highly predaceous ants where stinging can be of such great value in capturing prey. Certainly among the Ecitoninae, stinging appears to be as important as biting in subduing prey (Schneirla, 1971). It is noteworthy that the furcula, a sclerite located anterior to the sting bulb, is common to all ants except the ecitonines, dorylines, cerapachyines, and one ponerine species that behaves like an army ant. Evidence suggests a convergent loss of this sclerite in ants that evolve the army ant adaptive syndrome (Hermann, 1968).

Observations on the internal morphology of Dorylus workers are few in number and scattered throughout the literature. Only Mukerji's (1933) small paper on certain internal features of D. (Alaopone) orientalis Westwood is devoted exclusively to Dorylus.

The alimentary canal of army ants is of little consequence to evolutionary and taxonomic interpretation. The pharynx and esophagus are more or less uniformly developed throughout the Formicidae. Bugnion (1930) observed that the pharynx of Anomma is reduced and proposed that this reduction is correlated with the assumed absence of trophallaxis among army ants. However, the fact that Anomma workers return to the nest with liquid-filled crops (Gotwald, 1974) indicates that the regurgitative exchange of prey fluids between workers, workers and larvae, and workers and the queen may
indeed occur. Because the proventriculus is reduced and membranous in *Anomma* as well as in other army ants, it too is of little value to the study of army ant systematics. Because the damming of this type of proventriculus requires continuous muscular contraction, crop storage in army ants may be of relatively short duration (Eisner, 1957).

The number of Malpighian tubules is positively correlated with body size, so that overlap in tubule numbers can be expected, particularly when comparing polymorphic species. The number of tubules in *D. (A.) molest* overlaps considerably at the lower end of the range with the numbers of tubules in 7 species of New World army ants for which these numbers have been determined (Gotwald, 1971). However, *molest* soldiers possess 5 more tubules than the largest of these 7 species, *Eciton mexicanum* Roger, reflecting *molest*’s even greater size. The number of rectal papillae, on the other hand, may be relatively constant for any one species. Whelden (1968) reported a range of 3 to 6 papillae in two species of *Eciton* and Mukerji (1933) observed 2 papillae in *D. (Alaopone) orientalis*. Two papillae are also present in *Anomma* and in *Chelomyrmex* (Gotwald, 1971).

The presence or absence of specific exocrine glands may be of significance to evolutionary interpretation, but extensive comprehensive surveys of ant glands are few in number. Still, numerous exocrine glands have been examined and the behavioral consequences of their pheromonal secretions determined (e.g., see Hölldobler, 1978). Among the newest to be discovered are a series of tergal and sternal glands. Conspicuous among the tergal glands are the pygidial and postpygidial glands. The pygidial glands open through the intersegmental membrane connecting abdominal terga 6 and 7 (Kugler, 1978). The postpygidial glands open between the 7th and 8th abdominal terga (Hölldobler and Engel, 1978). Large pygidial glands with distinct reservoirs are present in *Eciton* and *Neivamyrmex*. Postpygidial glands are also present in these genera. Because the 7th tergum is small in these ants, the reservoirs of the pygidial and postpygidial glands “open directly above the anus at the abdominal tip,” and preliminary tests with *Eciton* workers suggest that these tergal glands are involved in chemical trail communication (Hölldobler and Engle, 1978). Interestingly, Hölldobler and Engle (1978) found that the pygidial gland in *D. (A.) molest* is rather different from that of *Eciton* and *Neivamyrmex*. They also found that the reservoirs of the *Anomma* pygidial glands do not open at the abdominal tip and that *Dorylus* possesses an “anus gland,” a feature not discovered thus far in other ants examined.

Like *Chelomyrmex morosus*, *D. (Anomma) molest* possesses 3 thoracic ganglia and a single petiolar ganglion. However, the gaster of *Chelomyrmex* houses 2 distinct ganglionic masses and that of *D. (A.) molest* 4 such masses. Thus the fusion of ganglia has occurred to a greater extent in *Chelomyrmex*. *Eciton* has the same number of ventral ganglionic masses as *Chelomyrmex*, although their distribution is different, because the waist of *Chelomyrmex* is uninodal
and that of *Eciton* binodal (Whelden, 1963).

Ovaries are apparently common in army ant workers. Most often each ovary consists of a single polytrophic ovariole. This is true of *D. (Anomma) molesta*, *D. (Alaopone) orientalis* (Mukerji, 1933), and *C. morosus* (Gotwald, 1971). In *Eciton*, the number of ovarioles per ovary ranges from 1 to 3 (Whelden, 1963). The extent of variation in numbers of ovarioles per ovary within and between species has not been determined. However, based on the survey of *D. (A.) molesta*, the number of ovarioles does not appear to be a function of worker size. Whether army ant workers produce trophic eggs upon which larvae and other colony members feed remains to be investigated.

Conclusions

Morphological features of *Anomma* driver ants that are unique or that show promise in evaluating the evolutionary origins and taxonomic affinities of the true army ants include:
1. Condition of the galeal crown and labrum.
2. Presence of the pro-mesonotal and pro-mesopleural sutures.
4. Presence of pygidial spines and impression.
5. Spatulate sting bulb and the concordant absence of stinging.
6. Number of rectal papillae.
7. Arrangement and structure of the pygidial and postpygidial glands and their reservoirs.
9. Number of ganglionic masses in the ventral nerve cord.

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Literature Cited
