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Redescription of *Chroniodiplogaster aerivora* (Cobb) gen. n., comb. n. (Rhabditida: Diplogasteridae) from Termites

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ABSTRACT: The nematode originally described as *Diplogaster aerivora* by Cobb is redescribed in the new genus *Chroniodiplogaster*. Diagnostic characters of the new genus include (1) the presence of 9 genital papillae, 3 of which are closely associated in a triplet set at the base of the tail, (2) 2 separate bursae, 1 which extends ventrolaterally along the tail, and the second, which is associated with the triplet papillae, and (3) a dorsal metarhabdion with a large mobile tooth and subventral metarhabdions with variably sized teeth. Dauer stages of *C. aerivora* occurred in the heads of worker termites of *Reticulitermes tibialis*. On occasion, the nematodes would enter the body cavity and kill the termites.

KEY WORDS: *Chroniodiplogaster aerivora* gen. n., comb. n., Diplogasteridae, Rhabditida, Nematoda, termite, parasite.

In 1916, Cobb described *Diplogaster labiata* and *Diplogaster aerivora* in a paper by Merrill and Ford (1916) who described the associations of these 2 nematodes with insects. In this study, the latter species was reported by Merrill and Ford (1916) to occur in the heads of the termite, *Leucotermes lucifugus,* with insect death resulting from high numbers of nematodes. Along with his description, Cobb also reported that *D. aerivora* fed on grasshopper eggs. Banks and Snyder (1920) reported juveniles of *D. aerivora* in the heads of active, normal-appearing *Reticulitermes flavipes* and adult nematodes in sick and dead insects.

Davis (1919) found *Mesodiplogaster* (=*Diplogaster*) *aerivora* in dead and dying larvae of the beetle, *Phyllophaga* sp., and suggested that the nematodes were the cause of death. Cobb identified *Mesodiplogaster aerivora* as the nematode responsible for natural mortality of corn earworm larvae, *Heliothis obsoleta* (Winburn and Painter, 1932). Lim et al. (1981) isolated *M. aerivora* from both living and dead grubs of the June beetle, *Phyllophaga anxia.* Recently, the present author received a culture of *M. aerivora* that was isolated from *Reticulitermes tibialis* in Colorado.

Recognition of *M. aerivora* is made difficult by the absence of detailed illustrations and quantitative data in the original description. Neither Weingärtner (1955) nor Goodey (1963) treated *M. aerivora* in their taxonomic presentation of the family Diplogasteridae and the species *M. aerivora* has been treated under the genera *Diplogaster, Micoletzkya,* and *Pristionchus.*

After a detailed morphological study of *M. aerivora,* the present author redescribes the species and places it in a new genus, *Chroniodiplogaster.*

Materials and Methods

Populations of *M. aerivora* studied here were isolated from the heads of worker termites (*R. tibialis*) (Banks) in Colorado in 1987 by John L. Capinera. They were maintained on nutrient agar plates and taxonomic studies were made on adults and dauer juveniles removed from these cultures. All nematodes were killed in hot (55°C) water, fixed in TAF, and processed to glycerin for measurements and drawings. Four of Cobb's original slides (nos. 1–4) containing adult male and female *M. aerivora* were received from A. Morgan Golden, Nematology Laboratory, U.S. Dept. of Agriculture, Beltsville, Maryland, for comparative purposes.

Results

Populations of nematodes removed from the heads of *R. tibialis* in Colorado agreed with the description of *M. aerivora* by Cobb (*in* Merrill and Ford, 1916) and were similar to Cobb's original specimens of *M. aerivora.* Therefore the Colorado population was considered to be *M. aerivora* Cobb.

This reexamination also revealed certain characters that made it difficult to place *M. aerivora* in any of the existing genera of Diplogasteridae. These characters consist of 9 pairs of genital papillae including a posterior set of 3, of which 2 are always reduced, a gubernaculum with ventral processes, which encloses the distal portion of the spicule shafts, a long narrow bursa associated with the 3 ventrolateral papillae, and a separate short bursa associated with the posterior set of

3 unequal papillae. The genus *Diplogaster* Schultze lacks a bursa, the gubernaculum does not encircle the spicule shafts, and there are 8 pairs of genital papillae without a posterior set of 3 (Goodey, 1963). The genus *Micoletzkya* (Weingärtner) contains 10 pairs of genital papillae with the first 2 pairs adjacent (Goodey, 1963). Members of the genus *Mesodiplogaster* Goodey (nec. Weingärtner; see Loof [1976]) possess 2 different stomal forms (Goodey, 1963). The genus *Pristionchus* Kreis, which was not mentioned by Goodey (1963), was originally described as having a small postanal bursa supported by 4 papillae (Kreis, 1933). However, Fedorko and Stanuszek (1971) show a long narrow bursa running posteriorly from the anus to the tail spike in *Pristionchus uniformis*. They illustrate 10 genital papillae pairs but state that only 9 pairs exist.

The generic status of the Diplogasteridae is in a state of confusion and the family needs to be revised. The present author prefers to redescribe the species *M. aerivora* Cobb in a new genus in the family Diplogasteridae, based on the discovery of new morphological characters not reported or seriously considered previously.

In the quantitative portion of the description, all figures are given in micrometers unless otherwise specified. The first number following the character is the mean and numbers in parentheses indicate the range.

Chroniodiplogaster gen. n. (Diplogasteridae (Micoletzky) Steiner)

DESCRIPTION: Medium-sized nematodes with smooth cuticle; 6 lips united at base but distinct at tip. Stoma massive, slightly longer than wide, variable in shape but with only a single basic form, dorsal metarhabdion with large mobile tooth, subventral metarhabdions variable; right subventral bearing tooth usually wide and pointed or notched at tip; left subventral bearing smaller pyramidal or lacinate tooth; median bulb of pharynx distinct, with strong crescent-shaped valves; female didelphic; female and male tails variable, short and acute or long and tapering or long and offset leading to filamentous tip; spicules large (length greater than body width at cloaca), slender, with small but distinct capitulum; gubernaculum with proximal (terminal) portion bent up and enclosing spicule tip region; with 9 pairs of genital papillae including 3 pairs located together in an off-ventral position near base of tail constriction; 2 bursae normally present; 1 extending ventrolaterally along tail region and second smaller ventral 1 associated with the triplet papillae at base of tail.

The genus *Chroniodiplogaster* can be separated from previously described genera in the Diplogasteridae having a similarly shaped stomal opening with the dorsal metarhabdion containing a distinct movable tooth by the normal presence of 2 separate bursae, a gubernaculum that surrounds the terminal spicular tips, and the presence of 9 basic genital papillae always including a postanal set of 3 (triplet).

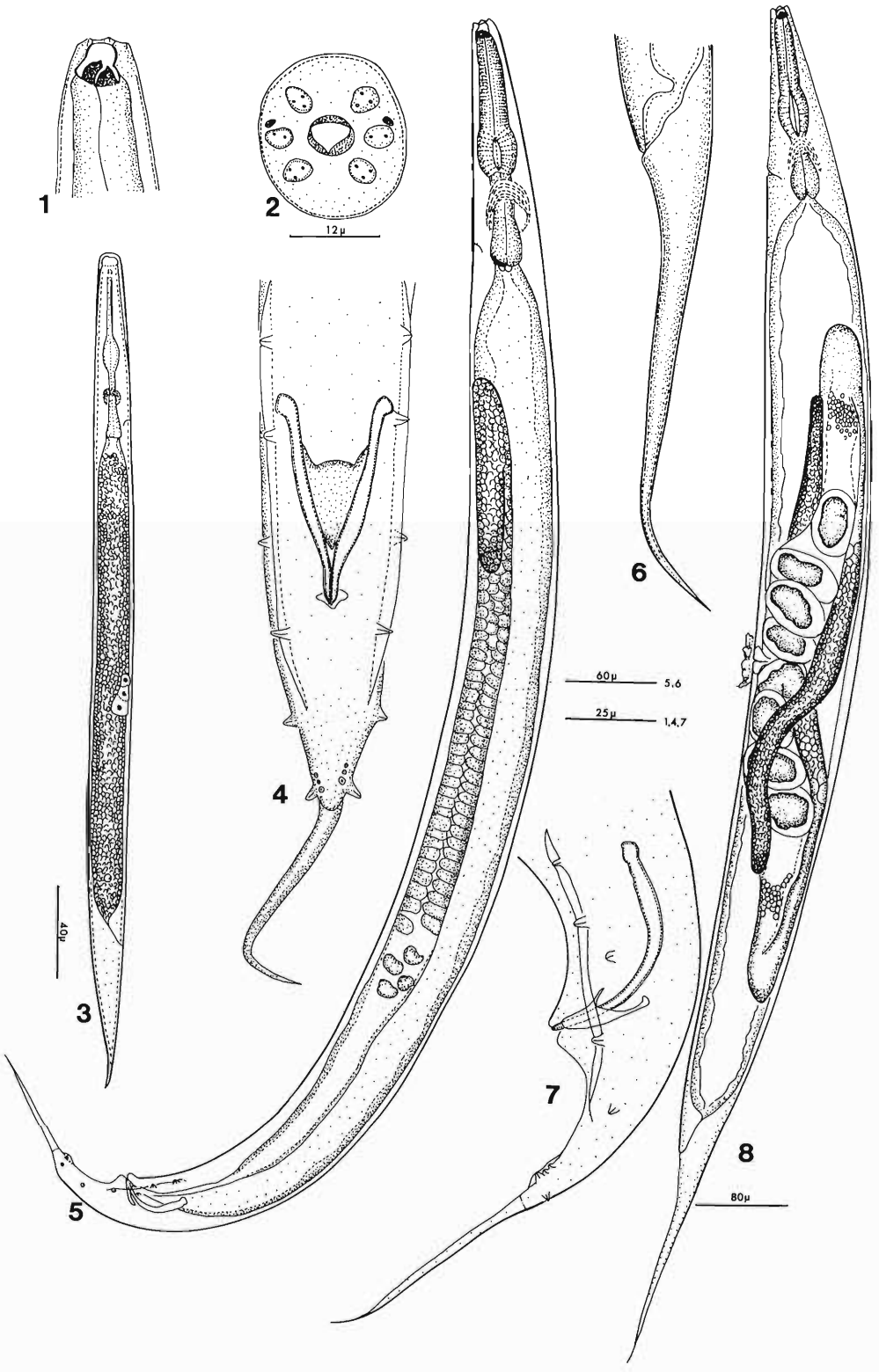
Chroniodiplogaster aerivora (Cobb) 1916 comb. n.

The following description also incorporates features cited by Cobb (*in* Merrill and Ford, 1916) in his original description.

DESCRIPTION: Adults: Cuticle transparent, with faint transverse striae and 24 longitudinal striae; lateral lines present; anterior end truncated; not offset, lips 6, fused at base, each bearing single inner labial papilla, submedial lips also bearing 2 additional papillae, lateral lips with single additional papilla, amphids located at base of lateral lips (on dorsal side), stoma walls highly cuticularized; dorsal metarhabdion with large protruding movable tooth, the inner contour of which fits into the contour of the protruding tooth on the right subventral metarhabdion, which may be notched at apex; left subventral metarhabdion bearing a smaller, conoid-lacinate tooth, which is closely associated with that of the right subventral metarhabdion: pharynx extending from base of stoma, gradually widening, until reaching swollen metacorpus containing elongated valvular apparatus, followed by isthmus surrounded by nerve ring; pharyngeal base expanding into pyriform bulb lacking distinct valve; excretory pore opening in vicinity of basal bulb; small, 2-celled pharyngeal–intestinal valve present; intestine forming narrow rectum before leading to anus or cloacal vent.

FEMALE (Figs. 1, 2, 6, 8): Vulva located in midbody region, roughly spherical in shape in ventral view; gonads paired and opposite with ovaries reflexed past vulvar opening; tail tapering gradually to fine hairline terminus; eggs ellipsoidal with smooth and relatively thick shell; embryonation occurs within female uterus.

MALE (Figs. 4, 5, 7): Similar to female in respect to cuticle, stoma, pharynx and intestine; tail tapering abruptly posterior to cloaca; tail tapering uniformly to small hairline terminus pos-



terior to triplet group of ventrolateral genital papillae, faint constriction present just posterior to triplet group of ventrolateral papillae; spicules slender, light brown, and curved almost to 90° angle, with distinct, but variably shaped capitulum, slender shaft and sharply pointed tips; gubernaculum with lateral crurae enclosing tips of spicules; extended proximal portion of corpus frequently, but not always, hooked; pair of ventral processes extending anteriorly from surrounding corpus-crurae portion; genital papillae consisting of 3 preanal pairs, 2 ventrolateral (submedian), 1 lateral (or sublateral), and 6 postanal pairs, 1 of which is ventrolateral just posterior to anus, another lateral and another dorsolateral just anterior to constricted tail area; another 3 pairs (triplet) are in a ventrolateral group just anterior to tail constriction; these latter 3 pairs of papillae not uniform in structure, the anterior 2 reduced and show little cuticular support with posterior pair larger; this set of 3 papillae is placed more anteriorly on left side than on right side of tail; single testis reflexed; 2 bursae present, ventrolateral bursa extends preanally and postanally in association with 3 ventrolateral papillae; another smaller bursa associated with posterior set of 3 (triplet) papillae.

Measurements

FEMALES (N = 10) (from nutrient agar cultures): Length, 1.39 (1.22–1.60) mm; greatest width, 82 (69–95); length stoma, 9 (6–11); width stoma, 7 (5–8); distance from anterior end to base of metacorpus, 116 (98–133); distance from anterior end to excretory pore, 159 (139–184); distance from anterior end to nerve ring, 144 (133–152); distance from anterior end to base of pharynx, 177 (152–200); length tail, 215 (162–273); width at anus, 36 (32–41); percent vulva, 49 (47–52); length of eggs in utero, 57 (48–64); width of eggs in utero, 32 (28–35).

MALES (N = 10) (from nutrient agar cultures): Length, 960 (832–1,120); greatest width, 62 (57–70); length stoma, 9 (8–10); width stoma, 7 (5–8); distance from anterior end to base of metacorpus, 104 (88–120); distance from anterior end to excretory pore, 152 (147–160); distance from anterior end to nerve ring, 119 (109–136); distance from anterior end to base of pharynx, 162 (142–181); reflexion of testis, 155 (120–192); length tail, 112 (88–138); width at cloaca, 36 (30–40); length tail posterior to constriction, 63 (35–90); length spicules, 56 (48–69); width spicules, 4 (2–4); length gubernaculum, 18 (14–22); width gubernaculum, 3 (2–4).

DAUER JUVENILES (Fig. 3) (N = 15): Length, 337 (284–397), greatest width, 15 (12–19); mouth and pharynx collapsed, head slightly offset, third-stage juvenile surrounded by second-stage cuticle.

Discussion

The population of *C. aerivora* redescribed here originated from colonies of *R. tibialis*. Dauer stages occurred in the heads of workers and when the termites were stressed or weakened, the nematodes entered the insect's body cavity and initiated development (Capinera, pers. comm.). The original population of *C. aerivora* was recovered from the heads of *L. lucifugus* where they occurred in the immediate region of the mouth parts and in the upper part of the head cavity (Merrill and Ford, 1916). The latter authors mentioned that the nematodes were usually found in masses, feeding upon the bodies of dead termites or other available decaying matter. In laboratory infection experiments where *L. lucifugus* workers were placed in moist soil containing cultures of the nematodes, the average number of nematodes in each termite head increased from 3 (natural infection) to 46 over a period of 4 days. After 12 days, all the termites had died and their bodies were being consumed by nematodes. Nutrients were probably obtained from bacteria and insect breakdown products.

In studies on *C. aerivora* in the scarabaeid beetle, *Phyllophaga anxia,* by Lim (1979) and Lim et al. (1981), nematodes were recovered from moribund field-collected second- and third-instar grubs. Measurements provided by Lim (1979) of the white grub population of *C. aerivora* agree in general with the measurements cited in the present study. However, Lim (1979) recorded a female tail length of 169 (128–176) (N = 10), which is somewhat shorter than that of the termite population. Also the distance from the anterior end to the base of the pharynx was given as 185 (176–191) (N = 4) for the male and 194

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Figures 1–8. ***Chroniodiplogaster aerivora*** **(Cobb): 1. Lateral view of female head. 2. En face view of female. 3. Dauer juvenile. 4. Ventral view of male tail. 5. Male. 6. Lateral view of female tail. 7. Lateral view of male tail. 8. Female.**

(178–223) (N = 10) for the female of the white grub population (Lim, 1979), which are larger values than noted in the present study. These quantitative differences could be attributed to strain differences or availability of nutrients, and both nematodes are considered the same species by the present author.

Detailed studies on events leading to the actual infection and death of any insect with *C. aerivora* are lacking. Earlier studies with *Mesodiplogaster lheritieri* (Maupas) and *Pristionchus uniformis* Fedorko and Stanuzek indicated that mortality of *Galleria mellonella* larvae resulted from reproducing nematodes breaking through the intestinal wall and entering the hemocoel (Poinar, 1969). Thus, these latter nematodes as well as *C. aerivora* are facultative parasites (Poinar, 1972) whose dauer stages enter the natural openings of insects and remain quiescent or begin to develop in the alimentary tract, head glands, or other body areas. This behavior causes the rupture of protective membranes, allowing the nematodes, together with their microbial associates, to enter the insect's hemocoel, resulting in immediate or eventual death. Insects undergoing stress from starvation, physical factors, or other disease-producing agents are probably more susceptible to infection by *C. aerivora* and related species. In the case of *C. aerivora* and termites, the nematodes may remain for relatively long periods of time in the head glands of the insects before initiating development and invading the hemocoel. Thus the insect may also serve as a refuge against adverse environmental conditions as well as being a potential food source and/or culture medium for edible bacteria.

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Errata

In a recent issue of this journal, the following corrections should be made:

July 1989, 56(2):201–203, in the article by Canals and Gasbarre:

In Table 1, all the protein concentrations of the ES given as mg/ml should be μg/ml.