

***Chroniodiplogaster formosiana* sp. n. (Rhabditida: Diplogastridae) from Chinese populations of *Odontotermes formosanus* Shiraki (Isoptera: Termitidae)**

GEORGE POINAR, JR.,¹ WILLIAM MEIKLE,² GUY MERCADIER²

Abstract: *Chroniodiplogaster formosiana* sp. n. (Rhabditida: Diplogastridae) is described from a population of *Odontotermes formosanus* Shiraki (Isoptera: Termitidae) collected from dead (unidentified) wood at Dinghu Park, China. Characters of *C. formosiana* which separate it from *C. aerivora* (Cobb) are a longer tail, the presence of four micropapillae (quadriform condition), and the adjacent position of the second and third macropapillae on the male tail. The diplogasterid *Pristionchus uniformis* Fedorko & Stanuszek, which is transferred to *Chroniodiplogaster*, can be distinguished from both *C. formosiana* and *C. aerivora* by the position of its excretory pore. Variable results in experimental infection trials suggest that some still unknown factor or factors are important in the infection process. Further studies are necessary to better define these factors before *C. formosiana* can be considered as a biological control agent of the Formosan termite.

Key words: *Chroniodiplogaster formosiana* sp. n., *Coptotermes formosanus*, Diplogastridae, Formosan termite, Rhabditida, systematics, Termitidae, Isoptera.

The Formosan termite (*Coptotermes formosanus* Shiraki: Rhinotermitidae) has become a serious pest in the southern part of the US (Lax and Osbrink, 2003). A USDA/ARS project on the biological control of this termite involved sampling populations of various termites in Australia, China, South Africa, Malaysia, Reunion Island, Singapore, Indonesia, and mainland France. The termites were killed by cooling, placed on agar plates, and inspected daily under quarantine conditions for at least two months for evidence of pathogenic organisms. Nematodes were recovered from the cadavers of representatives from several genera, including *Odontotermes*, *Cryptotermes*, *Postelectrotermes* and *Coptotermes* (Meikle et al., 2003).

Nematodes recovered from *Odontotermes formosanus* Shiraki in Southern China were examined further and evaluated in lab bioassays. The present study describes a new species of *Chroniodiplogaster* from this termite.

MATERIALS AND METHODS

Nematode populations were isolated from *Odontotermes formosanus* (Termitidae) collected from dead (unidentified) wood at Dinghu Park, China (112° 32.523' E and 23° 9.522' N) on 2 March 2002 by G. Mercadier and A. Kirk. They were maintained on nutrient agar plates containing termites (*Reticulotermes banyulensis* Clément) and wax moth (*Galleria mellonella* L.) larvae. Adult and dauer nematodes were heat killed, fixed in TAF and sent to the senior author for identification. Observations and photographs were made with a Nikon Optiphot optical microscope (with magnifications up to ×1,000). All measurements are in micrometers unless otherwise stated.

Four laboratory trials using nematodes obtained from cadavers of *G. mellonella* were conducted to evaluate their virulence against workers of *R. banyulensis*. To obtain the nematodes, droplets of a suspension of nematodes, containing populations of mixed ages, were applied to the cuticle of live, late instar *G. mellonella* larvae that were raised on a diet of honey and wax. After the *Galleria* larvae died, the cadavers were kept for several weeks, by which time most of the nematodes had become third-stage dauers. The dauers were placed in a water suspension and their density determined by counting nematodes in 100 µl of suspension placed in a glass watchglass with a grid underneath.

All trials were conducted using petri dishes (5-cm-diam.) with moist filter paper on the bottom. In the first trial, a group of 10 petri dishes, each of which contained 10 termites, and a second group of 10 plates, each of which contained a single termite, were treated with 10 dauer nematodes/termite. An identical set of control plates contained the same number of termites but no nematodes. After treatment, the dishes were sealed using Parafilm (American National Can, Chicago, IL), to maintain a high humidity level and placed in an incubator at 23°C. The termites were inspected daily for 50 d, and any dead individuals were placed on water agar petri dishes (3.5-cm-diam.) and assayed for associated nematodes.

The second trial was a repeat of the first trial, except that five replicates of grouped termites per treatment were used rather than 10. In the third trial, four replicates of grouped termites were used, and the termites were treated at the rate of 20 dauer stages/termite rather than 10. The fourth trial was similar to the third trial except that termites were treated with a mixed-age population of nematodes, rather than just dauer-stage juveniles, at the rate of 50 nematodes/termite.

Data were analyzed using JMP (SAS Institute, Inc., Cary, NC) software. Because the objective of the analysis was to compare termite life spans after treatment rather than survivorship after an arbitrary length of

Received for publication: February 13, 2006.

¹ Department of Zoology, Oregon State University, Corvallis, OR 97331.

² European Biological Control Laboratory, Montferrier sur Lez, France 34980.

E-mail: poinarg@science.oregonstate.edu

This paper was edited by: Zafar Handoo.

time, the Kaplan Meier (KM) method was used since the data were longitudinal (Singer and Willett, 2003). The KM method is a nonparametric method for estimating the "survivor function," or survival probabilities as a function of time (Singer and Willett, 2003) and uses a χ^2 statistic. Average survivorship in days was used to analyze the data of grouped termites. Data were censored for termites kept alone which were alive at the end of the experiment and for groups of termites in which none died.

RESULTS

Chroniodiplogaster Poinar, 1990 (Rhabditida: Diplogastridae)

Emended description: Medium-sized nematodes with smooth cuticle; six lips united at base but distinct at tip; stoma prominent, with both stenostomatous and eury-stomatous types; dorsal metarhabdion with large, movable tooth; subventral metarhabdions with pyramidal, rounded or laciniate teeth; median pharyngeal bulb (metacarpus) distinct, muscular, with distinct valves; basal bulb distinct, glandular; tail shape long and tapering to filamentous; spicules curved; longer-than-body width at cloaca; spicular shaft slender, with or without small rostrum; capitulum small to medium; blade tapering to fine, pointed tip; gubernaculum prominent, with distal portion forming a tubular sheath that surrounds spicule shafts; six pairs of genital megapapillae, four pairs lateral and two pairs subventral; three or four pairs of micropapillae at base of tail just above constricted portion; separate leptoderan bursae associated with megapapillae and micropapillae; tail elongate to filamentous.

Notes: The terms megapapillae and micropapillae are introduced here to differentiate between the large papillae on the lateral and subventral surfaces of the male tail and the small (minute) papillae clustered at the base of the tail constriction. The latter are called "triplets" or "quadriform" when three or four, respectively, occur in a linear series. Weingärtner (1955) referred to these as large and small papillae, however, the large papillae (megapapillae) often include a size range of large and small types which then makes it confusing when differentiating between small megapapillae and the micropapillae. The terms micropapillae and macropapillae are more specific in separating the large, normal-appearing tail papillae from the very minute ones in a completely different location. Also, we prefer not to number the micropapillae since that suggests a pattern of homology that we cannot verify. For instance, we cannot say if the first micropapilla on *C. aevivora* is homologous with the first or second micropapilla on *C. formosiana*. Further ontological studies may answer these questions.

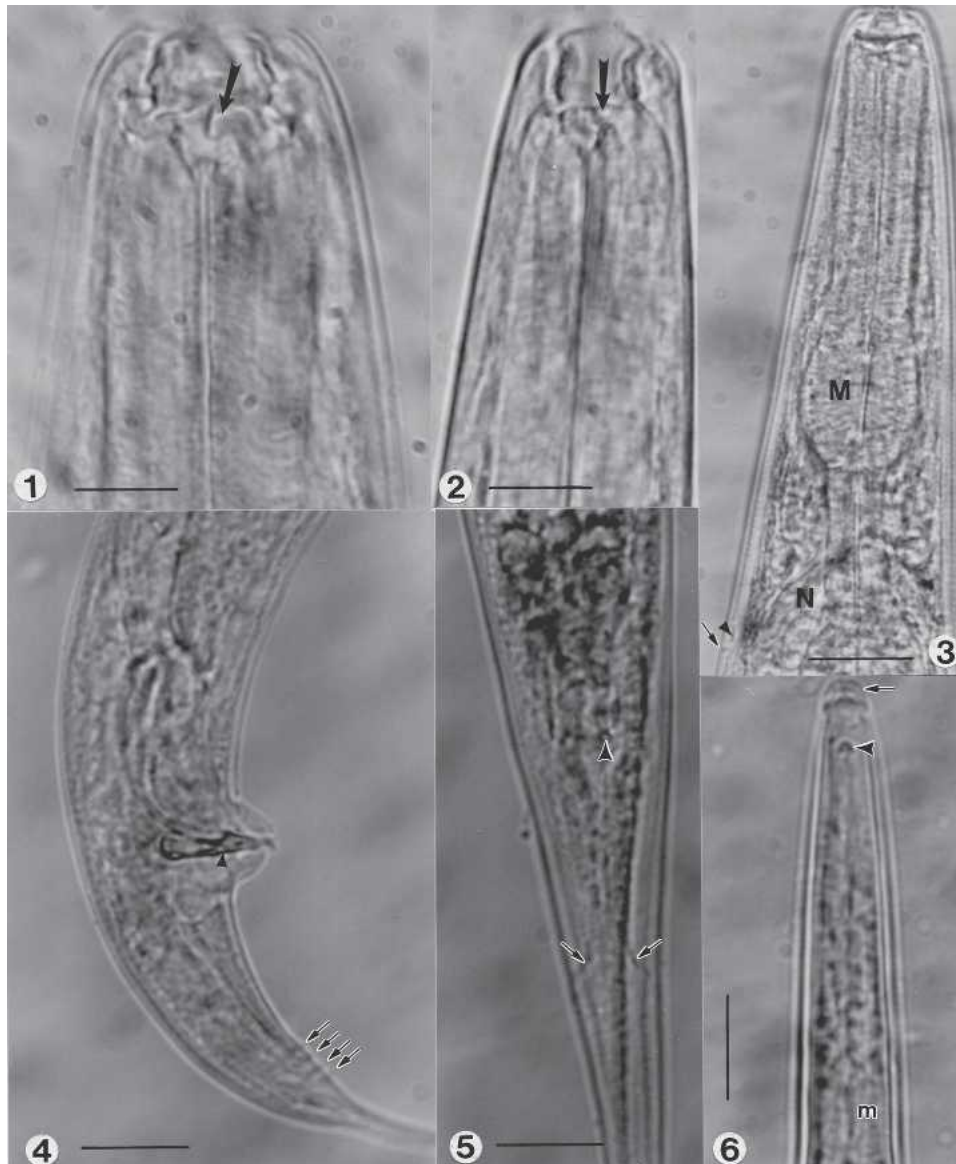
Diagnosis: *Chroniodiplogaster* can be separated from most diplogasterid genera by possessing a gubernaculum in which the distal portion forms an enclosed sheath (or tube) that surrounds the spicule shafts, the number and position of genital megapapillae and micropapillae, separate bursae associated with the megapapillae and micropapillae, and an elongate to filamentous tail. Members of the genus *Diplogaster* Schultzze have eight pairs of genital megapapillae, no micropapillae and the gubernaculum does not enclose the spicule shafts. Species of *Micoletzkyia* (Weingärtner) have 10 pairs of megapapillae, with the first and second pair adjacent, and the gubernaculum does not enclose the spicule shafts (Goodey, 1963; Hirschmann, 1951). In *Mesodiplogaster* Goodey (nec Weingärtner; see Loof, 1976), there are six pairs of megapapillae and three pairs of micropapillae, but the gubernaculum does not encircle the spicule shafts (Hirschmann, 1951; Goodey, 1963). It is obvious that the genus *Pristionchus* Kreis (1933), in which Sudhaus and von Lieven (2003) place *Chroniodiplogaster*, is polyphyletic as conceived by these authors. They describe the basic structure of the gubernaculum "with a paired and an unpaired anteriorly directed process," which is not the condition in *Chroniodiplogaster*. Also, the type species *P. longicaudatus* Kreis (1933) has a straight gubernaculum that does not enclose the spicules, which is a basic character state of the genus *Chroniodiplogaster*.

Chroniodiplogaster formosiana sp. n. Diplogastridae Micoletzky, 1922.

Description: Adults: Cuticle transparent, with transverse and longitudinal striae; lateral lines present, approximately 0.9 apart; anterior end truncated; six lips, each bearing single labial papilla; head not offset, stoma variable, with both stenostomatous (width greater than length and eury-stomatous (length greater than width) forms; large movable tooth on dorsal metarhabdion; smaller irregular shaped teeth on subventral metarhabdions; metacarpus with muscular valvular apparatus; isthmus surrounded by nerve ring; basal bulb glandular, lacking valves; excretory pore opening and hemizonid in vicinity of basal bulb; tail elongate to filamentous.

Female (Figs. 1,3,5,8). Stoma usually wider than long (stenostomatous); vulva located slightly anterior to mid-body; gonads paired, opposite with ovaries normally reflexed past vulvar opening; tail tapering to filamentous tip; phasmids elongate, eggs ellipsoidal with smooth and relatively thick shell; embryonation occurs within female uterus with up to 10 eggs present at one time; hatching not observed inside uterus.

Male (Figs. 2,4,7,9,10,11). Stoma usually longer than wide (eury-stomatous); testis reflexed; tail tapering to fine hairline terminus posterior to quadruple group of micropapillae; spicules slender, transparent, curved al-



FIGS. 1–6. *Chroniodiplogaster formosiana* sp. n. Fig. 1. Head of female showing stenostomatous stoma (wider than long). Arrow shows large, movable tooth on dorsal metarhabdion. Bar = 9 μ m. Fig. 2. Head of male with eurystomatous (longer than wide) stoma. Arrow shows large movable tooth on dorsal metarhabdion. Bar = 10 μ m. Fig. 3. Anterior end of female. Arrow shows excretory pore opening adjacent to basal bulb. Arrowhead shows hemizonid. N = nerve ring. M = metacarpus. Bar = 22 μ m. Fig. 4. Lateral view of male tail. Arrows show micropapillae at base of tail. Arrowhead shows gubernaculum. Bar = 14 μ m. Fig. 5. Ventral view of upper portion of female tail. Arrows show tube-like phasmids. Arrowhead shows anal opening. Bar = 20 μ m. Fig. 6. Anterior portion of dauer juvenile. Arrow shows loose cuticle protruding from top of head. Arrowhead shows collapsed metarhabdions. m = collapsed metacarpus. Bar = 17 μ m.

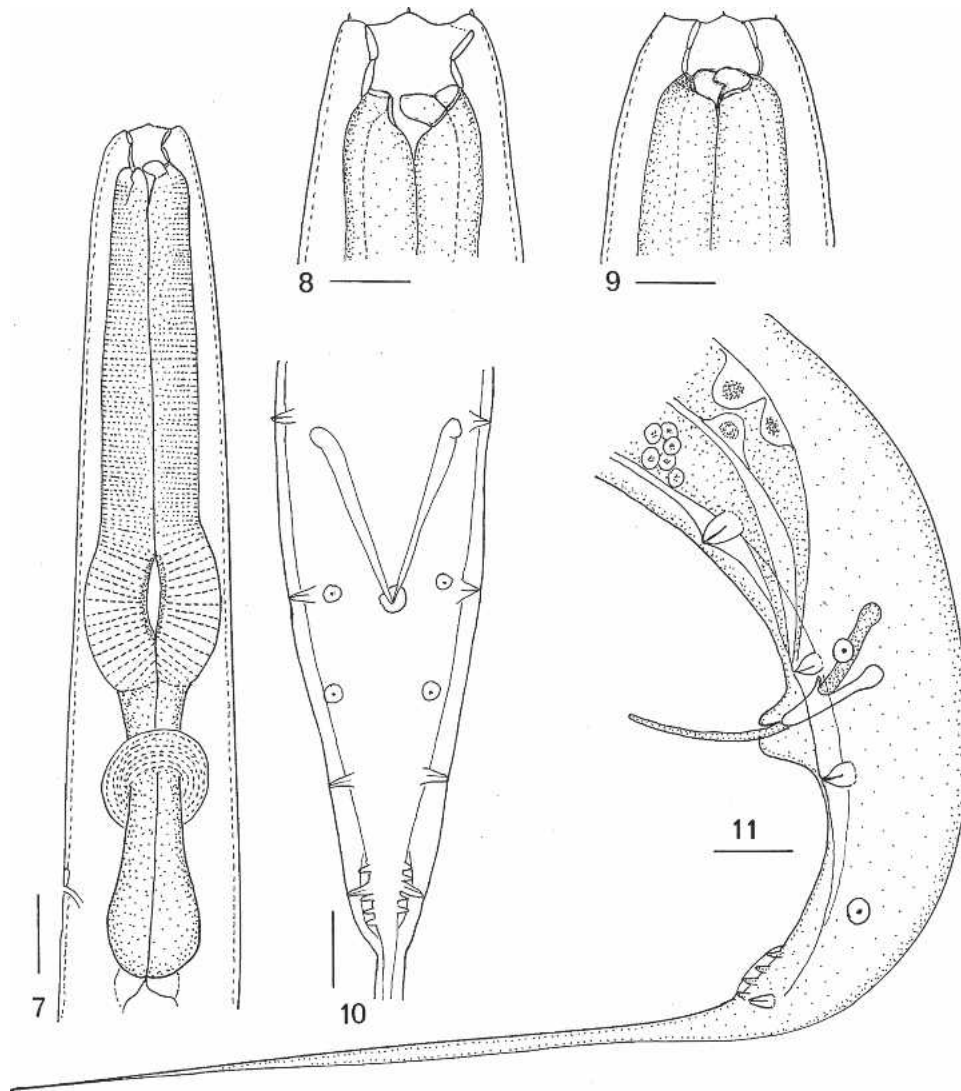
most 90°, with distinct capitulum, slender shaft and pointed tips; gubernaculum with lateral crurae; distal portion forming a tube that encloses spicule shafts; genital papillae consisting of six pairs of megapapillae (one pair precloacal, two pairs adcloacal, three pairs postcloacal) and four pairs of micropapillae (quadri-form) just anterior to tail constriction; elongate bursa associated with three pairs of megapapillae; minute bursa associated with four pairs of micropapillae.

Measurements

Females: (N=20) (From nutrient agar cultures): Length, 993 \pm 202 (695–1301); width at vulva, 62 \pm 13 (35–73); length stoma, 7 \pm 0.7 (6–8); width stoma,

8 \pm 0.7 (7–9); distance from anterior end to base of metacarpus, 103 \pm 6 (92–120); distance from anterior end to hemizonid, 129 \pm 13 (110–148); distance from anterior end to excretory pore, 133 \pm 13 (112–152); distance from anterior end to nerve ring, 114 \pm 5.3 (104–120); distance from anterior end to base of pharynx, 152 \pm 10 (141–170); length tail, 240 \pm 27 (158–282); body width at anal opening, 25 \pm 5.3 (15–33); percentage of vulva, 45 \pm 3 (40–49); length of eggs in utero, 55 \pm 16 (46–65); width of eggs in utero, 31 \pm 4.3 (22–36).

Males (N = 20) (from nutrient agar cultures): Length, 660 \pm 23 (624–708); greatest width, 30 \pm 3 (23–



FIGS. 7–11. *Chroniodiplogaster formosiana* sp. n. Fig. 7. Anterior end of male. Bar = 14 μ m. Fig. 8. Head of female. Bar = 7 μ m. Fig. 9. Head of male. Bar = 12 μ m. Fig. 10. Ventral view of male tail showing all macropapillae and micropapillae. Bar = 10 μ m. Fig. 11. Lateral view of male tail showing spicules, gubernaculum, two bursae and genital papillae. Bar = 9 μ m.

35); length stoma, 7 ± 0.67 (6–8); width stoma, 5 ± 0.33 (5–6); distance from anterior end to base of metacarpus, 93 ± 2.7 (84–97); distance from anterior end to excretory pore, 117 ± 3.6 (109–124); distance from anterior end to nerve ring, 99 ± 4.3 (92–108); distance from anterior end to base of pharynx, 137 ± 4 (128–150); reflexion of testis, 92 ± 10 (68–110); length of tail, 111 ± 5.6 (101–127); length of tail filament (posterior to constriction), 79 ± 6 (65–92); width at cloaca, 23 ± 0.67 (21–28); length spicules, 37 ± 3.3 (32–44); width spicules, 3.5 ± 0.33 (3–4); length gubernaculum, 14 ± 0.48 (10–17); width gubernaculum, 3 ± 0.67 (2–4); length tubular phasmids, 4 ± 0.33 (4–5); length phasmids from cloacal opening, 42 ± 3 (36–48).

Dauer juveniles: (N= 20) (Fig. 6). Third-stage juvenile enclosed in second-stage cuticle; stoma and pharynx collapsed, indistinct; length of third-stage with surrounding second-stage cuticle, 328 ± 13 (300–345);

length of third-stage without surrounding second-stage cuticle, 278 ± 13 (247–293); greatest width of third-stage, 14 ± 1.6 (12–17).

Type specimens: Male (Holotype-T-597t) and female (Allotype-T-598t) deposited in the USDA Nematode Laboratory, Beltsville, MD. Paratypes in the senior author's collection.

Type host: *Odontotermes formosanus* Shiraki (Isoptera: Termitidae) collected from dead (unidentified) wood.

Type Locality: Dinghu Park, China; coordinates: $112^{\circ} 32.523'E$ and $23^{\circ} 9.522'N$.

Diagnosis and relationships

Chroniodiplogaster formosiana sp. n. can be separated from *C. aerivora* (Cobb) by its longer tail filament, and the presence of four micropapillae (three in *C. aerivora*) with the second and third macropapillae adjacent to each other rather than separated as in *C. aerivora* (Poinar, 1990).

While the gubernaculum of *Pristionchus uniformis* Fedorko & Stanuszek (1971) was drawn as being hooked at the apex (their Fig. 7d), the photograph in Plate 1B of the same paper shows a gubernaculum with lateral crurae enclosing the spicule tips, similar to the condition in *C. formosiana*. Since *P. uniformis* also has six pairs of megapapillae and three pairs of micropapillae, as well as other characters of *Chroniodiplogaster*, it is transferred to this genus. It can be distinguished from both *C. formosiana* n. sp. and *C. aervivora* by its anteriorly located excretory pore (anterior to the metacarpus). This species was described as a facultative parasite of adult Colorado potato beetles (*Leptinotarsa decemlineata* Say) in Poland (Fedorko and Stanuszek, 1971).

Whether the character state of the distal portion of the gubernaculum encircling the spicules indicates relatedness or arose independently (polyphyletic) in several lines is difficult to say. This condition was also depicted by Sachs (1950) for *Diplogastrellus* (= *Diplogaster*) *monhysteroides* Bütschli. However, this species possesses nine pairs of megapapillae, which separates it from members of *Chroniodiplogaster*.

The presence of four micropapillae at the base of the tail (quadriform condition) also occurs in the diplogasterid *Pristionchus longicaudatus* Kreis 1933, collected from leaves of lettuce (*Lactuca sativa* L.). However, this species has a straight gubernaculum that does not enclose the spicules, which separates it from *Chroniodiplogaster*.

Laboratory trials to evaluate the virulence of *Chroniodiplogaster formosiana*:

In the first trial, the average number of dead termites after 50 d was 3.4/plate (s.d. = 1.5) in the treated group and 1.4 (s.d. = 1.1) in the control group. Thirty of the 34 termite cadavers in the treated group were positive for nematodes, and none in the control group were. The survivorship of the grouped and treated termites was significantly lower than that of the control termites ($\chi^2 = 13.51$, d.f. = 1, prob. = 0.0002). However, the mean survivorship was 37.2 d (SE \pm 1.8) for treated termites compared to 45.3 d (SE \pm 1.1) for control termites; it is doubtful whether such a difference would have a practical application. Interestingly, the nematode treatment did not have a significant effect among termites kept alone (prob. = 0.39), and the mean survivorship was 32.5 d (SE \pm 3.2) for treated termites and 24.6 (SE \pm 4.8) for control termites. All eight of the treated termites kept alone died, and all were positive for nematodes.

In the second trial, the nematode treatment did not have a significant effect in either the grouped termites (prob. = 0.50) or the individually kept termites (prob. = 0.14). Survivorship among grouped termites was 48.2 d (SE \pm 0.5) for those treated and 46.4 d (SE \pm 1.1) for controls, and among termites kept alone was 35.1 d (SE \pm 4.6) for those treated and 40.1 d (SE \pm 3.6) for controls.

In neither of the remaining two trials did the nematode treatment have a significant effect on termite survivorship. In the third trial, among the grouped termites the average survivorship was 43.7 d (SE \pm 5.8) for those treated and 46.0 (SE \pm 1.3) for the controls, and among termites kept alone, the average survivorship was 31.7 d (SE \pm 5.6) for those treated compared to 35.0 (SE \pm 4.0) for the controls. Nine of the 14 treated termite cadavers were positive for nematodes, and none of the 12 untreated termite cadavers tested positive. In the fourth experiment, in spite of the much higher doses of nematodes, only two termites died among the grouped and treated termites after 50 d, and none among the grouped controls died. Among the termites kept alone in that experiment, the average survivorship was 32.0 d (SE \pm 4.0) among those treated and 41.3 d (SE \pm 5.7) among the controls.

DISCUSSION

Since we did not examine the stomal structure with the TEM, we have not employed the stomal framework nomenclature presented by De Ley et al. (1995) and instead use the classical terminology as presented by Weingärtner (1955), Goodey (1963), and others. Two stomal types (a wide stenostomatous and a narrow eury stomatous) have been described in some other adult diplogasterids (Hirshmann, 1961; Baldwin et al., 1997). Weingärtner (1955) placed *Mesodiplogaster* (= *Diplogaster*) *maupasi* Potts and *M. theritieri* into her *M. theritieri* group based on the presence of both stenostomatous and eury stomatous stomal types in these species. It is not stated if this condition was strongly correlated with the sex of the nematode, as is the case with *C. formosiana*, where most females have a stenostomatous stoma and most males a eury stomatous type.

Recent TEM studies have shown that the stomal apparatus of rhabditids is quite complicated (De Ley et al., 1995; Baldwin et al. 1997), which is certainly the case with *C. formosiana*. In the latter species, variation occurred between the stoma configuration of different juvenile stages and between juveniles and adults. The viewing position and the irregular shape of the teeth on the rhabdions make it difficult to generalize on the stomal structure of *C. formosiana*, other than stating that the tooth on the dorsal metarhabdion appears to be the most prominent.

Considering the difficulty interpreting the stomal structures of *C. formosiana*, the most practical characters for separating species in this group are the male sexual and accessory structures. These include the shape and size of the spicules and gubernaculi, the number and position of the micropapillae and megapapillae, and the number and lengths of the bursae. While tail length may also be useful, some variation does occur among different populations. The minute bursa associated with the micropapillae can be difficult to view; however,

the remaining male characters are fairly straightforward.

The determination of the effect of *C. formosiana* sp. n. on the Formosan termite and its possible use as a biological control agent was one of the goals of this project. Early studies with *C. aerivora* showed that the presence of dauer stages in the heads of *Leucotermes lucifugus* often resulted in termite mortality (Merrill and Ford, 1916). Similar observations were made with *C. aerivora* and *Reticulitermes flavipes*, with adult nematodes occurring in moribund individuals (Banks and Snyder, 1910). Studies with *C. uniformis* against wax moth larvae (*Galleria mellonella* L.) showed that nematode populations could build up in the insect gut and eventually break through the gut wall and enter the hemocoel, causing insect mortality (Poinar, 1969). This type of behavior was also typical of other facultative nematode parasites of insects (Poinar, 1972). In summarizing the effect of facultatively parasitic diplogasterid nematodes on insects, the general pattern was that mortality resulted when the dauer stages were able to enter natural opening of insects, mostly head glands or alimentary tract, and develop in these sites (Poinar, 1972). This same pattern of infectivity was noted in a study involving *C. aerivora* and corn earworm pupae (*Helicoverpa zea* (Boddie)) in a cornfield in Arkansas (Steinkraus et al., 1993). In a laboratory bioassay where *H. zea* larvae were exposed to 500 mixed nematode stages/insect larva, significantly more insects died than in the controls. Weakened or stressed *H. zea* appeared to be more susceptible than healthy insects. The nematodes entered the hemocoel through the hindgut, and host mortality (in both *G. mellonella* and *H. zea*) occurred seven or more d post-treatment.

Preliminary laboratory tests with *C. formosiana* sp. n. suggest that a similar type of association occurs between this nematode and *Reticulitermes banyulensis* Clément. However, the variability shown in the experimental infection trials suggests that some still unknown factor or factors (such as host stress, nematode stage, microbial associates, host nutrition, or temperature) may be important in altering the susceptibility of the termites for nematode infections. Further studies are being undertaken to better define these factors so that the nematode can be better evaluated as a potential biological control agent of the Formosan termite.

LITERATURE CITED

Baldwin, J. G., Giblin-Davis, R. M., Eddleman, C. D., Williams, D. S., Vida, J. T., and Thomas, W. K. 1997. The buccal capsule of *Aduco-*

spiculum halicti (Nemata: Diplogasterina): An ultrastructural and molecular phylogeny study. *Canadian Journal of Zoology* 75:407–423.

Banks, N., and Snyder, T. E. 1920. A revision of the Nearctic termites with notes on biology and geographic distribution. *Bulletin of the U. S. National Museum* 108:1–288.

De Ley, P., Van de Velde, M. C., Mounport, D., Baujard, P., and Coomans, A. 1995. Ultrastructure of the stoma in Cephalobidae, Panagrolaimidae and Rhabditidae, with a proposal for a revised stoma terminology in Rhabditida (Nematoda). *Nematologica* 41:153–182.

Fedorko, A., and Stanuszek, S. 1971. *Pristionchus uniformis* sp. n. (Nematoda, Rhabditida, Diplogasteridae), a facultative parasite of *Leptinotarsa decemlineata* Say and *Melolontha melolontha* L. in Poland. Morphology and biology. *Acta Parasitologica* 19:95–112.

Hirschmann, H. 1951. Über das Vorkommen zweier Mundhöhlentypen bei *Diplogaster lheritieri* Maupas und *Diplogaster bififormis* n. sp. und die Entstehung dieser hermaphroditischen Art aus *Diplogaster lheritieri*. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 80:132–170.

Kreis, H. A. 1933. Beiträge zur Kenntnis Pflanzenparasitischer Nematoden. *Zeitschrift für Parasitenkunde* 5:184–194.

Lax, A. R., and Osbrink, W. L. A. 2003. United States Department of Agriculture - Agricultural Research Service research on targeted management of the Formosan subterranean termite *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). *Pest Management Science* 59:788–800.

Loof, P. A. A. 1976. The author of the genus-group name *Mesodiplogaster* (Diplogasteridae). *Nematologica* 22:122–123.

Meikle, W. G., Mercadier, G., Kirk, A., Bon, M., Sawicki, L., Derouane, F., Peppuy, A., He, Y., Reid, A., and Quimby, P. C. 2003. Nematodes and entomopathogenic fungi associated with termites. Society of Invertebrate Pathology, Program and Abstracts for the 36th Annual Meeting, 26–30 July 2003, Burlington, VT.

Merrill, J. H., and Ford, A. L. 1916. Life history and habits of two new nematodes parasitic on insects. *Journal of Agriculture Research* 6:115–127.

Poinar, Jr., G. O. 1969. Diplogasterid nematodes (Diplogasteridae: Rhabditidae) and their relationship to insect disease. *Journal of Invertebrate Pathology* 13:447–454.

Poinar, Jr., G. O. 1972. Nematodes as facultative parasites of insects. *Annual Review of Entomology* 17:103–122.

Poinar, Jr., G. O. 1990. Redescription of *Chroniodiplogaster aerivora* (Cobb) gen. n., comb. n. (Rhabditida: Diplogasteridae) from Termites. *Journal of the Helminthological Society of Washington* 57:26–30.

Sachs, H. 1950. Die Nematodenfauna der Rinderexkreme. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 79:209–320.

Singer, J. D., and Willett, J. B. 2003. *Applied longitudinal data analysis*. Oxford: Oxford University Press.

Steinkraus, D. C., Boys, G. O., Kring, T. J., and Ruberson, J. R. 1993. Pathogenicity of the facultative parasite, *Chroniodiplogaster aerivora* (Cobb) (Rhabditida: Diplogasteridae) to corn earworm (*Helicoverpa zea* (Boddie)) (Lepidoptera: Noctuidae). *Journal of Invertebrate Pathology* 61:308–312.

Sudhaus, W., and Von Lieven, A. F. 2003. A phylogenetic classification and catalogue of the Diplogasteridae (Secernentea, Nematoda). *Journal of Nematode Morphology and Systematics* 6:43–90.

Weingärtner, I. 1955. Versuch einer Neuordnung der Gattung *Diplogaster* Schulze 1857 (Nematoda). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 84:248–317.