

Descriptions and Comparative Morphology of *Cactodera milleri* n. sp. (Nematoda: Heteroderidae) and *Cactodera cacti* with a Review and Key to the Genus *Cactodera*¹

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Abstract: A new species, *Cactodera milleri* n. sp., is described and illustrated from specimens obtained from roots of common lambsquarter, *Chenopodium album* L., from Mattawan, Michigan. *Cactodera milleri* can be differentiated from other *Cactodera* species by the presence of punctated egg shells and a second-stage juvenile (J2) stylet length averaging 21.8 μ m as measured from freshly killed specimens in water mounts. Thirty-four plant species, including 11 weed species, 18 agronomic crop species, and 5 cactus species were tested as potential hosts of *C. milleri*. The new species reproduced only on *Chenopodium album*, *C. amaranticolor* Cofte. Reyn., and *C. quinoa* Willd. *Cactodera cacti* (Filipjev & Schuurmans Stekhoven, 1941) Krall & Krall, 1978, a morphologically similar species, is reexamined. A description of the female and additional morphometric and morphologic data of cysts, males, J2, and eggs are provided for several populations of *C. cacti*. A review of the morphometrics of all species of *Cactodera* and a taxonomic key to the seven species are presented.

Key words: *Cactodera cacti*, *Cactodera milleri* n. sp., cactus cyst nematode, *Chenopodium album*, *Chenopodium amaranticolor*, *Chenopodium quinoa*, common lambsquarter, comparative morphology, cyst nematode, host range, new species, taxonomy.

In the fall of 1982, a nematode population with lemon-shaped cysts was isolated from soil samples collected from a former asparagus field in Mattawan, Michigan (4). The host of the cysts could not be identified at the time of collection because the soil samples were taken when the field had just been cultivated and planted to rye. Preliminary morphological examination of the cysts, eggs, and second-stage juveniles (J2) indicated that the population represented a species of *Cactodera* Krall & Krall, 1978, morphologically distinct from all species of the genus except *C. cacti* (Filipjev & Schuurmans-Stekhoven, 1941) Krall & Krall, 1978. The range of measurements of *C. cacti* (1,2,6,7,9-12,16) overlapped with those of the unidentified *Cactodera* population. However, an intensive reexamination of the morphology and morphometrics of *C. cacti* revealed significant differences, and the *Cactodera* population

from Mattawan, Michigan, is described as *Cactodera milleri* n. sp. In addition, the reproductive ability of *C. milleri* was tested on 34 plant species, including 11 weed species, 18 agronomic crop species, and 5 cactus species.

A review of previously published morphometrics of cysts, males, J2, and eggs of other *Cactodera* species and additional morphometric and morphologic data of females, cysts, males, J2, and eggs of *C. cacti* are also presented.

A revised key to the genus *Cactodera* is provided.

MATERIALS AND METHODS

Field host identification and host range

The field host of *C. milleri* was determined in the greenhouse by placing infested field soil from the original site in flats and periodically observing the roots of the germinated plants for the presence of white females. In addition, 20-cm-d clay pots were filled with field soil and seeded with asparagus, *Asparagus officinalis* L. cv. Mary Washington. As weed seedlings emerged, they were removed. After 3 months, the roots of the asparagus plants were examined for females.

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TABLE 1. Plant species tested as hosts of *Cactodera milleri* n. sp.

Plant species	Common name	Nematode reproduction
Weeds		
<i>Digitaria sanguinalis</i> (L.) Scop.	Large crabgrass	—
<i>Amaranthus retroflexus</i> L.	Redroot pigweed	—
<i>Rumex crispus</i> L.	Curly dock	—
<i>Chenopodium album</i> L.	Lambsquarter	+
<i>Chenopodium amaranticolor</i> Cofte. Reyn.	Lambsquarter	+
<i>Chenopodium quinoa</i> Willd.	Quinoa	+
<i>Solanum dulcamara</i> L.†	Bitter nightshade	—
<i>Polygonum persicaria</i> L.	Ladysthumb	—
<i>Polygonum convolvulus</i> L.	Wild buckwheat	—
<i>Polygonum pensylvanicum</i> L.	Pennsylvania smartweed	—
<i>Stellaria media</i> (L.) Vill.‡	Common chickweed	—
Agronomic crops		
<i>Phaseolus vulgaris</i> L. cv. Seafarer	Dry bean	—
<i>Lycopersicon esculentum</i> Mill. cv. Rutgers	Tomato	—
<i>Glycine max</i> (L.) Merr. cv. Hark	Soybean	—
<i>Zea mays</i> L. cv. Mo17HT	Corn	—
<i>Apium graveolens</i> L. cv. F1683	Celery	—
<i>Mentha arvensis</i> (L.) Hill cv. Black Mitchum‡	Mint	—
<i>Brassica oleracea</i> L. cv. Golden Acre	Cabbage	—
<i>Asparagus officinalis</i> L. cv. Jersey Giant	Asparagus	—
<i>Beta vulgaris</i> L. cv. H20†	Sugarbeet	—
<i>Triticum aestivum</i> L. cv. Hyslop†	Wheat	—
<i>Daucus carota</i> L. cv. Gold Pak†	Carrot	—
<i>Allium cepa</i> L. cv. Krummery Special†	Onion	—
<i>Beta vulgaris</i> L. cv. Early Wonder Green Top†	Table beet	—
<i>Medicago sativum</i> L. cv. Vernal‡	Alfalfa	—
<i>Solanum tuberosum</i> L. cv. Superior§	Potato	—
<i>Trifolium pratense</i> L.‡	Red clover	—
<i>Lotus corniculatus</i> L.‡	Birdsfoot trefoil	—
<i>Vitis vinifera</i> L. cv. Baco Noir§	Grape	—
Cacti		
<i>Opuntia rufida</i> §	Cinnamon cactus	—
<i>Opuntia vulgaris</i> Miller§	Irish mittens	—
<i>Mammillaria elongata</i> DeCandolle§	Golden stars	—
<i>Lobivia silvestrii</i> (Spegazzini) Rowley§	Peanut cactus	—
<i>Schlumbergera truncata</i> (Hayworth) Moran§	Thanksgiving cactus	—

Seedlings transplanted except as otherwise noted.
† Seeded directly onto infested soil and thinned to one plant per pot.
‡ Seeded directly onto infested soil with no thinning.
§ Rooted cutting or tuber piece.

Thirty-four plant species (Table 1) to be evaluated as hosts of *C. milleri* were directly seeded or transplanted as seedlings, rooted cuttings, or tuber pieces. Nematode inoculum (brown cysts) was obtained from stock cultures established on *Chenopodium album* L., the field host, and maintained by periodic subculturing in the greenhouse at 25 ± 5 C. Four replications of each plant species were prepared as follows: 10-cm-d clay pots were filled with moistened pas-

teurized sandy loam soil and a hole, 2.5 cm d × 2.5 cm deep, was made in the center of each pot. Twenty-five brown cysts were placed in the hole with water, and a seedling, rooted cutting, or tuber piece was placed in the hole and secured with soil. When plant species were direct seeded, the hole containing the cysts was filled with soil and seeds were spread evenly over the surface and covered lightly with additional soil. After 3 months, the soil and root systems

were washed vigorously with water to remove newly formed females and cysts. The soil and root washings were poured onto a 600- μ m-pore sieve over a 250- μ m-pore sieve. The material from the 250- μ m-pore sieve was examined microscopically, and the cysts and females were counted. The presence of newly formed females, white to yellow in color, or more than 25 brown cysts indicated reproduction of the nematode. If 25 or fewer brown cysts were recovered, the plant was not considered to be a host.

Research populations

Nematode specimens of *C. milleri* were obtained from greenhouse stock cultures established and maintained by periodic subculturing on *Chenopodium album*.

Populations of *C. cacti* were obtained from the Department of Horticulture tropical greenhouse, Michigan State University (MSU); University of Florida at Gainesville, courtesy of Dr. R. P. Esser; and Lottum, The Netherlands, courtesy of Dr. P. Maas. Stock cultures of the Michigan and Lottum populations of *C. cacti* were maintained on *Cereus peruvianus* (L.) Miller and *Schlumbergera truncata* (Hayworth) Moran, but the Florida population did not reproduce in the MSU greenhouse. Viable specimens of eggs and J2 of the Florida population were examined before the rearing attempt and their data are included in the present study.

In addition to living specimens, permanent slides of eggs and J2 in glycerin of *C. cacti* from Italy (slides G-4637, G-4638) and Georgia, USA (slide G-4664) were obtained from the USDA Nematode Collection Nematology Lab, Beltsville, Maryland; and permanent slides of J2 and males in glycerin (slide 5429) were obtained from the Nematode Collection of the Landbouwhogeschool, Wageningen, The Netherlands.

Type material (cysts containing eggs and J2 of *H. schachtii* [*C. cacti*] from the roots of *Phyllocactus akkermanni* Hayworth) from Maartensdijk, The Netherlands, and pre-

served by Adam in 1932, was obtained from the Nematode Collection, Section of Recent Invertebrates, Institut Royal des Sciences, Naturelles de Belgique, Bruxelles, Belgium (I.G. 14.530).

The populations of *C. cacti* used in this study are designated as follows: MI (Michigan, USA); FL (Florida, USA); LO (Lottum, The Netherlands); GA (Georgia, USA); IT (Italy); WA (Wageningen, The Netherlands); and TY (type material, Maartensdijk, The Netherlands).

Specimen preparation

Light microscopy (LM): Holotype and paratype females of *C. milleri* and females of the MI population of *C. cacti* were mounted in water under a coverslip on a thin water agar plate for measurement of body dimensions. The anterior ends of the holotype and paratype females of *C. milleri* and females of the MI and LO populations of *C. cacti* were prepared by fixing intact white females in 3% HCHO for 5 minutes and then excising the head and mounting it in lactophenol. Cysts of *C. milleri* and the MI population of *C. cacti* were prepared for measurement of body dimensions as described for females. Cone tops of *C. milleri* (holotype female and paratype cysts) and *C. cacti* (females and cysts of MI and cysts of TY populations) were prepared by the methods of Mulvey (10). The female vulva-anus distance was measured from cone tops that had been cut to allow flattening of the vulval cone structure and mounted in lactophenol, except in the case of the holotype female which remained intact.

The allotype male of *C. milleri* was heat relaxed, mounted in water, measured, then carefully removed from the water mount, processed to glycerin with the Seinhorst method (15), and remeasured. All other male specimens of *C. milleri* and the LO population of *C. cacti* were heat relaxed and measured in water mounts. Paratype males of *C. milleri* were prepared with the Seinhorst method (15).

Second-stage juvenile paratypes of *C. milleri* were prepared with the same meth-

ods as for the allotype male. Specimens of the MI, FL, and LO populations of *C. cacti* were heat relaxed and measured in water mounts; only FL specimens were processed to glycerin and remeasured. The J2 specimens of the TY population of *C. cacti* were removed from preserved eggs by applying gentle pressure with a dental canal file to break the egg shell and release the J2. The folded J2 were mounted in preservative and measured.

Eggs of *C. milleri* and the MI population of *C. cacti* were removed from cysts and mounted in water, and the embryonated eggs were measured. Eggs of the FL, LO, and TY populations were examined for the presence of punctations on the eggshell surface, but no measurements were made.

Scanning electron microscopy (SEM): Cysts of *C. milleri* and the MI, LO, and TY populations of *C. cacti* were fixed in 3% formalin for 12 hours and cut in half, and the cone top was excised, cleaned, trimmed, transferred to 95% ethanol for 1 minute, and mounted on SEM stubs. The anterior half of the cyst was transferred to stubs, and the eggs were removed with a dental canal file and distributed across the sticky surface. The cone tops and eggs were air dried for at least 48 hours.

Viable J2 of *C. milleri* and the MI and LO populations of *C. cacti* were heat relaxed, fixed in 3% formalin for 12 hours, transferred to a BPI dish containing 0.5 ml of 0.1 M phosphate buffer (pH 7.2), and then chilled to 5 °C. Cold 4% glutaraldehyde (5 °C) in phosphate buffer (pH 7.2) was gradually added over a 2-hour period to reach a final concentration of 2%, and fixation continued in 2% for 20 hours at 5 °C. The J2 specimens were transferred to a processing chamber and washed with 0.1 M phosphate buffer at 5 °C for 30 minutes, postfixed with 2% osmium tetroxide buffered with 0.1 M phosphate buffer (pH 7.2) for 20 hours at 5 °C, and washed in 0.1 M phosphate buffer at 5 °C for 30 minutes. Specimens were dehydrated at room temperature in a six-step graded ethanol series over 2 hours. The J2 were critical-point

dried with CO₂ and mounted on stubs. All specimens were sputter coated with 30 nm gold palladium and examined with a JEOL JSM-35C scanning electron microscope operating at 15 kV.

Statistics

Morphometrics of J2 of *C. milleri* were compared with *C. cacti* by analysis of variance (ANOVA) and Duncan's multiple-range test. All analyses were performed using the SAS (13).

All measurements are in micrometers (µm) unless otherwise specified.

SYSTEMATICS

Genus *Cactodera* Krall & Krall, 1978

Type species: *Cactodera cacti* (Filipjev & Schuurmans-Stekhoven, 1941)

Other species: *Cactodera acnidae* (Schuster & Brezina, 1979) Wouts, 1985; *C. amaranthi* (Stoyanov, 1972) Krall & Krall, 1978; *C. eremica* Baldwin & Bell, 1985; *C. estonica* (Kir'janova & Krall, 1963) Krall & Krall, 1978; *C. thornei* (Golden & Raski, 1977) Mulvey & Golden, 1983; and *C. weissi* (Steiner, 1949) Krall & Krall, 1978

Cactodera milleri n. sp. (Figs. 1–9)

Holotype (female): Length with neck 658; length without neck 598; width 466; stylet 23.9; DGO 5.4; anterior end to excretory pore 138.0; vulval slit length 16.1.

Paratype females (n = 50): Length with neck 538–885 (mean 718, standard deviation ± 88.2); length without neck 436–789 (625 ± 84.5); width 335–640 (491 ± 83.7); length/width ratio with neck 1.2–1.9 (1.5 ± 0.2); L/W without neck 1.1–1.5 (1.3 ± 0.1). Paratype females (n = 25): Stylet 22.9–25.6 (24.1 ± 0.6); DGO 4.4–9.3 (5.7 ± 1.2); anterior end to excretory pore 100.0–180.5 (124.8 ± 16.8); vulval slit length 14.3–17.8 (16.2 ± 0.8); distance from vulval slit to anus 36.6–62.9 (47.4 ± 6.2).

Body shape variable, from lemon shaped to nearly spherical. Newly formed females pearly white, then yellow or golden, becoming light brown. Neck usually distinct-

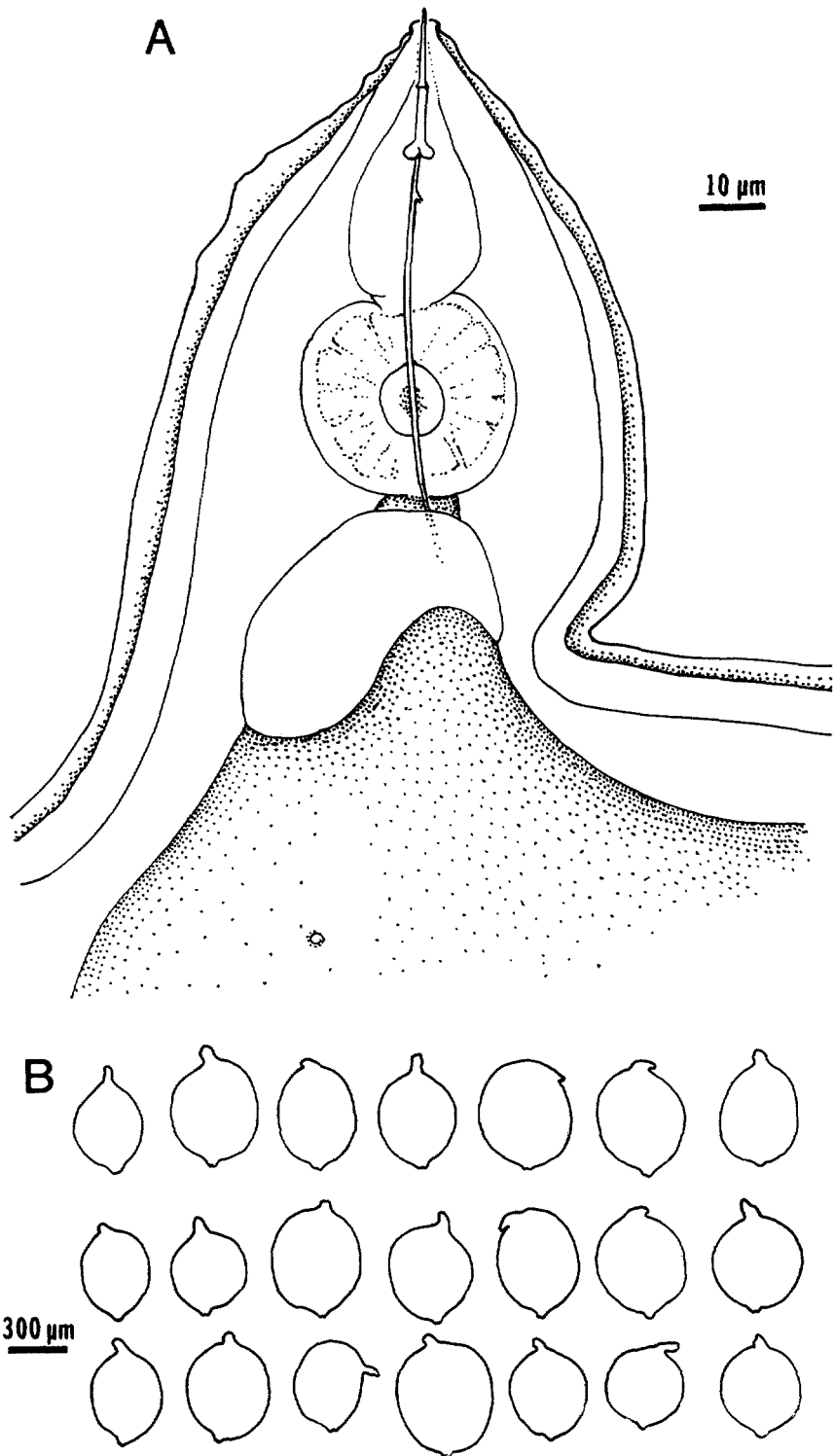


FIG. 1. Female and cysts of *Cactodera milleri* n. sp. A) Anterior end of female (latero-ventral). B) Outlines of cysts.

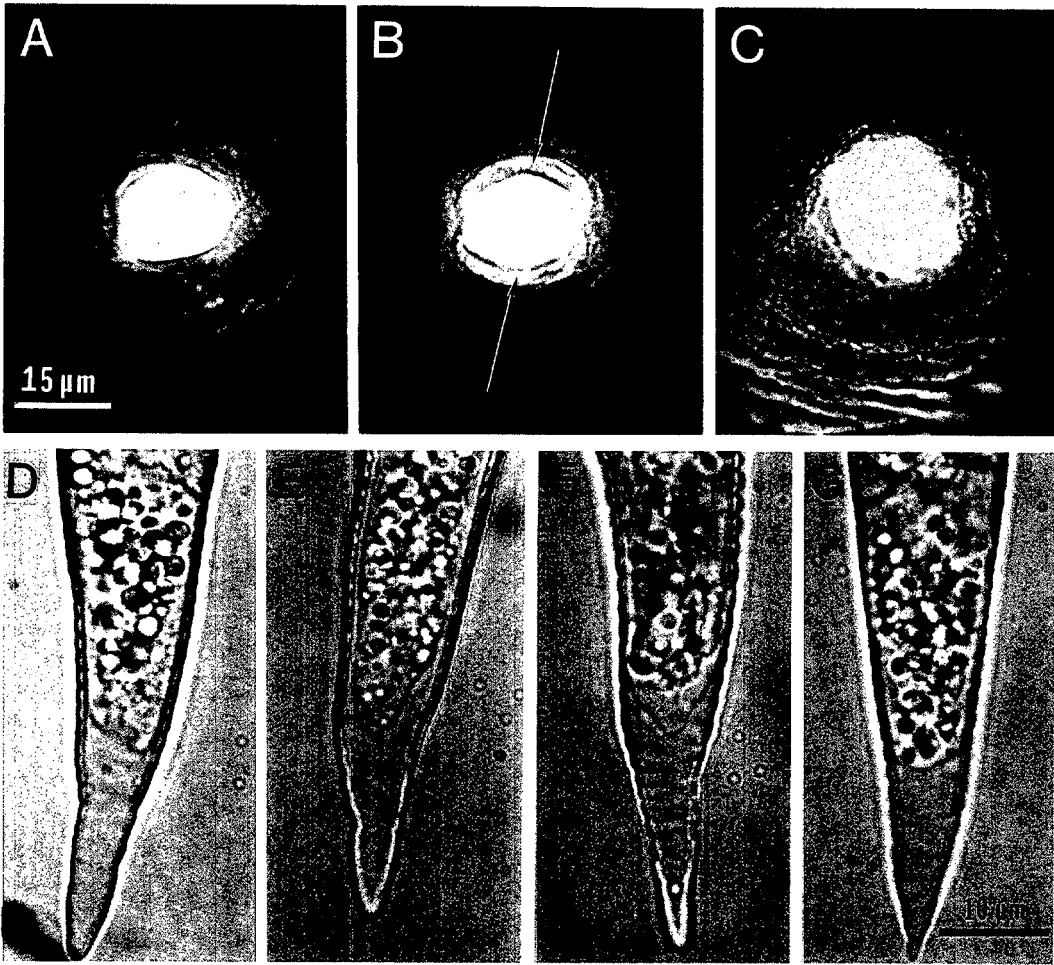


FIG. 2. LM photographs of cyst cone tops and J2 tails. A, B, D) *Cactodera milleri* n. sp. A) Cyst fenestra. B) Cyst fenestra, membrane-like material (arrows). D) J2 tail hypodermis ventrally sloped. C, E–G) *Cactodera cacti*. C) Cyst fenestra, MI population. E) J2 tail hypodermis V-shaped, MI population. F) J2 tail hypodermis V-shaped, FL population. G) J2 tail hypodermis ventrally sloped, LO population.

ly offset. Some specimens with prominent vulval cone reduced on larger spherical females. Subcrystalline layer and gelatinous egg sac not observed. Labial disc slightly elevated. Stylet and knobs well developed. Stylet knob width 4.4–5.0, average 4.8 (10 specimens in lateral view). Excretory pore posterior to median bulb.

Paratype cysts ($n = 50$): Length with neck 550–849 (700 ± 59); length without neck 514–730 (632 ± 55); width 419–598 (506 ± 48); L/W with neck 1.2–1.6 (1.4 ± 0.1); L/W without neck 1.1–1.4 (1.2 ± 0.1). *Paratype cysts* ($n = 35$): Fenestra diameter (dorsal–ventral) 7.1–21.4 (13.3 ± 3.2); fe-

nestra diameter (lateral) 14.3–22.0 (18.7 ± 2.2).

Cysts usually lemon shaped, some rounded. Color variable, dark brown to almost black. Cone top abullate, circumfenestrate. Some fenestra surrounded with thin, semitransparent, cuticle-like material (Fig. 2B). Vulval denticles present at times. Anus usually distinct. Midcyst pattern consists of straight to wavy striae encircling body.

Allotype (measurements in water): Length 1,368; width 31.2; anterior end to stylet knob base 27.3; stylet 25.3; stylet knob width (lateral) 4.9; DGO 4.4; esophagus 164.7; tail 5.8; spicule 35.1; gubernaculum

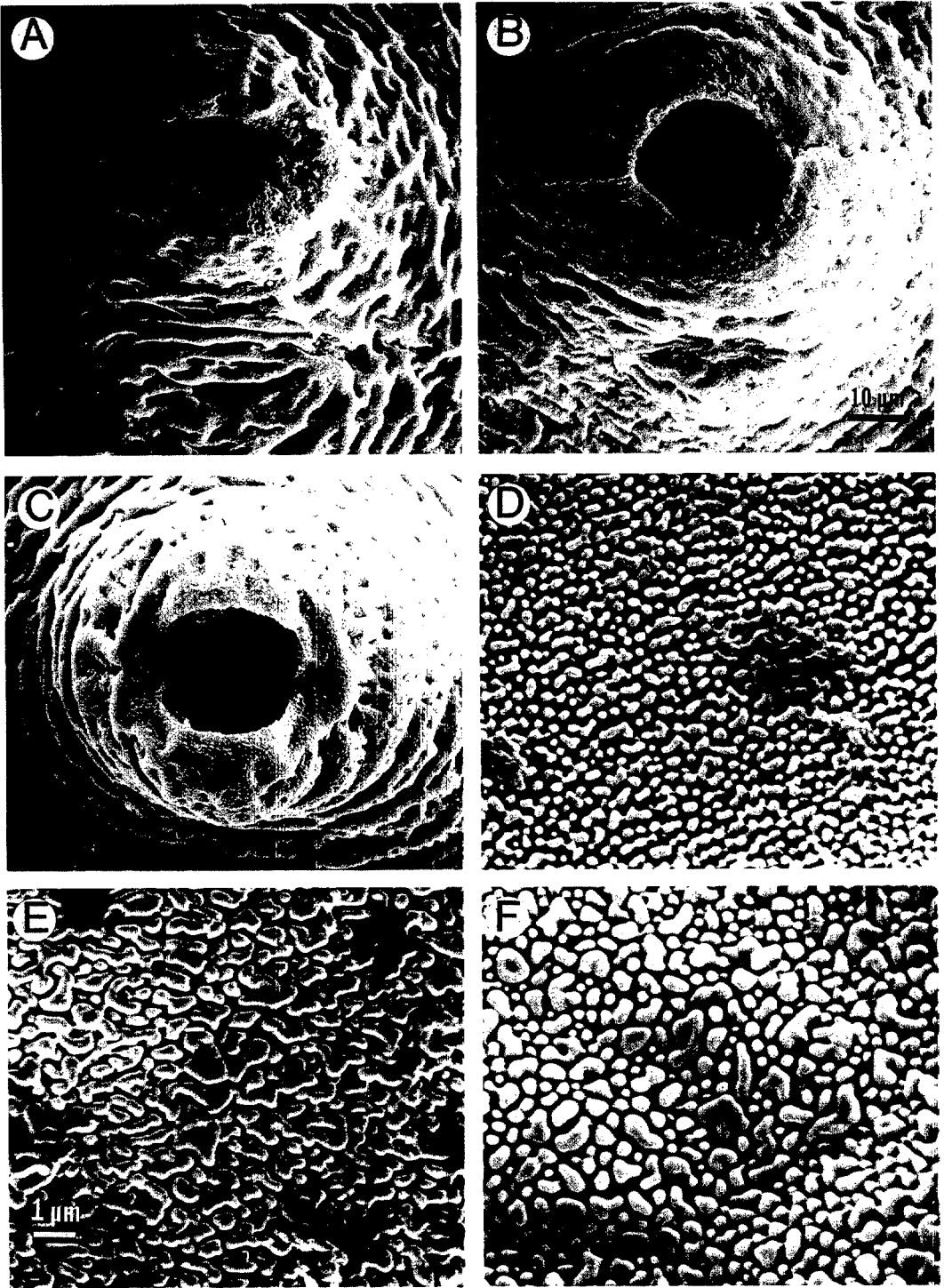


FIG. 3. SEM photographs of cyst cone tops and egg shells. A, D) *Cactodera milleri* n. sp. A) Cyst fenestra. D) Egg shell punctations. B, C, E, F) *Cactodera cacti*. B) Cyst fenestra, MI population. C) Cyst fenestra, TY population. E) Egg shell punctations, MI population. F) Egg shell punctations, TY population. A-C) Same magnification. D-F) Same magnification.

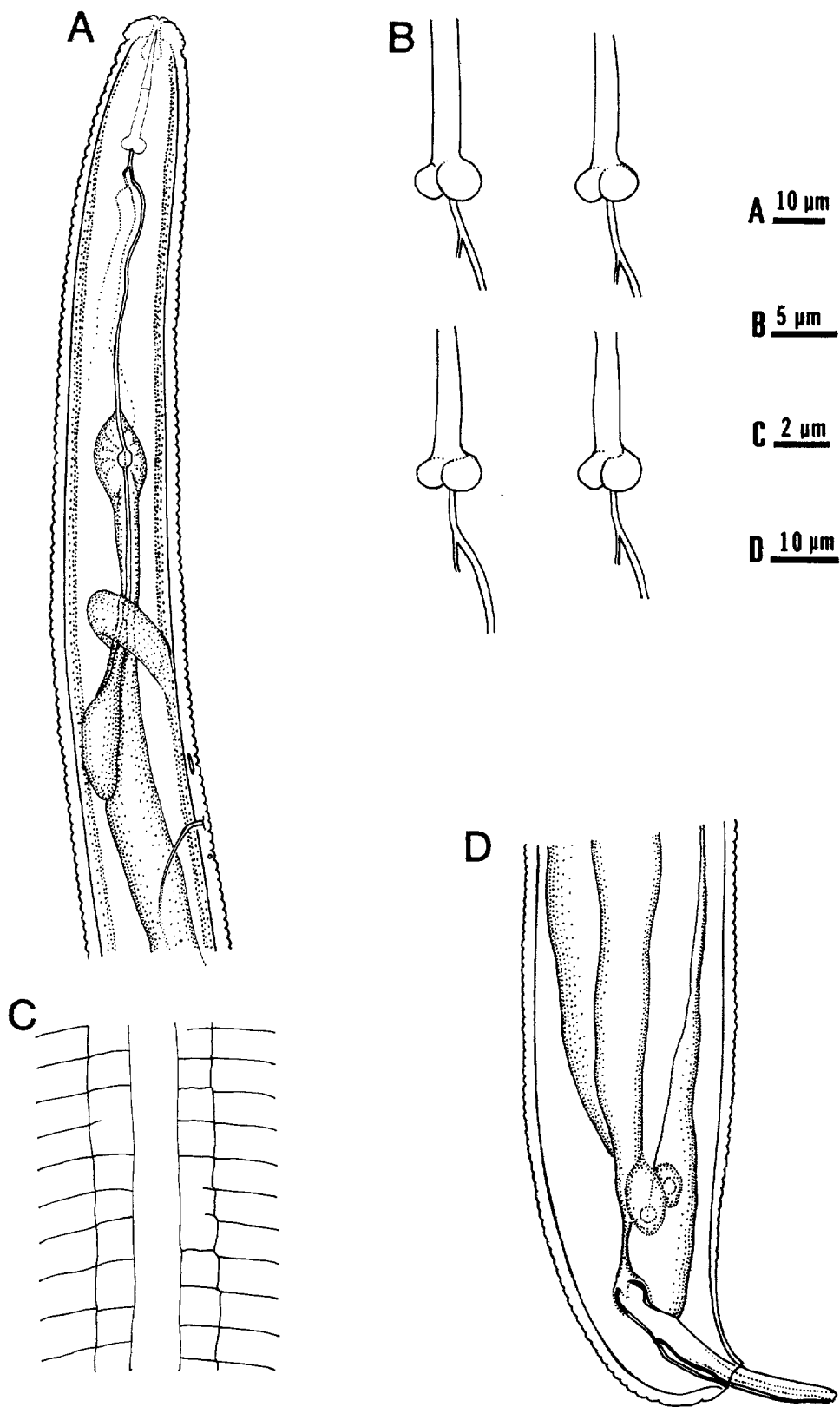


FIG. 4. Males of *Cactodera milleri* n. sp. (lateral). A) Anterior body region. B) Stylet knobs. C) Lateral field. D) Tail.

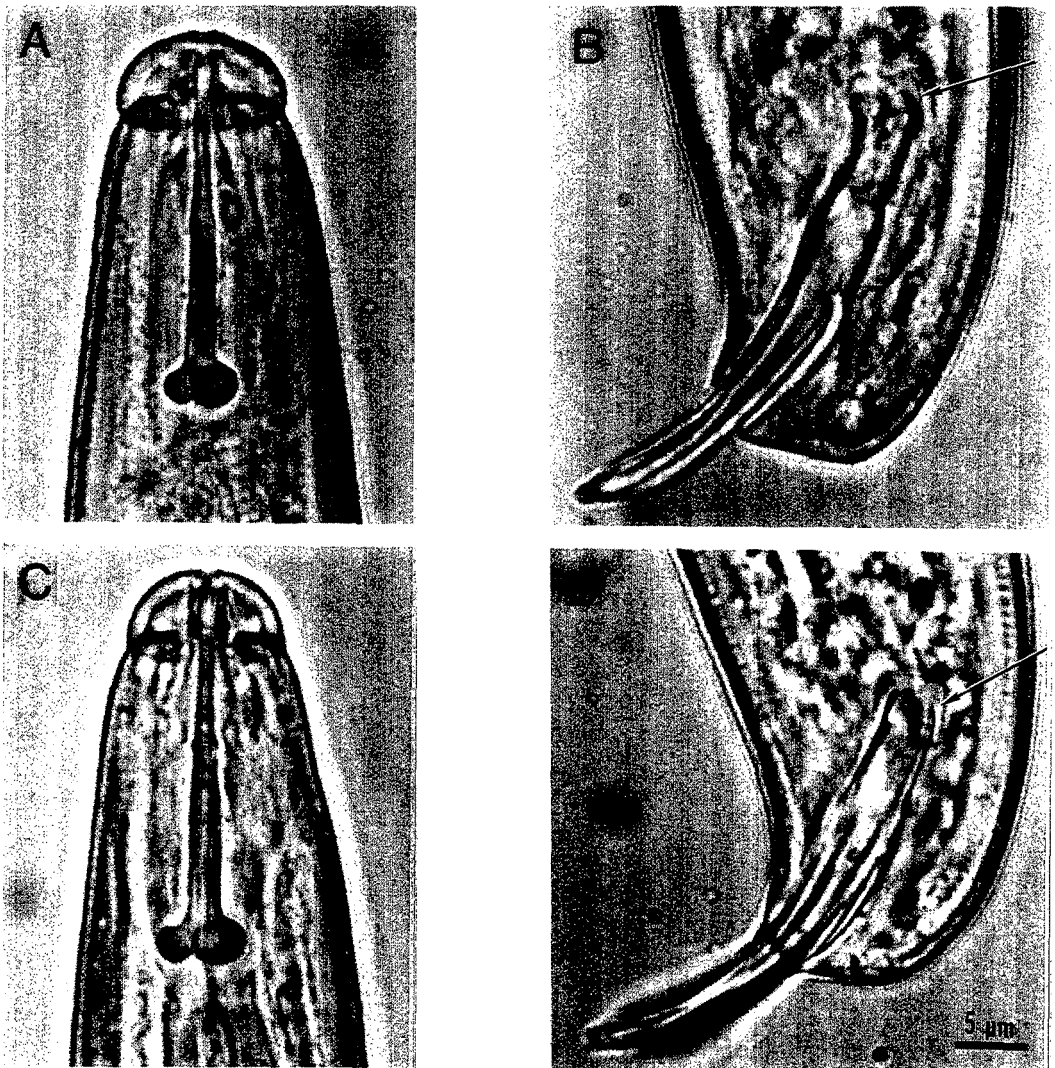


FIG. 5. LM photographs of males. A, B) *Cactodera milleri* n. sp. A) Head region (lateral). B) Spicule head curved (arrow). C, D) *Cactodera cacti*, LO population. C) Head region (lateral). D) Spicule head straight (arrow).

11.7; lip height 5.8; lip width 11.7; a 43.8; b 8.3; b' 7.1; c 235.9; o 17.4. Measurements in glycerin: Length 1,202; width 24.9; anterior end to stylet knob base 26.3; stylet 24.4; stylet knob width (lateral) 4.4; DGO 2.4; esophagus 120.0; tail 5.4; spicule 34.6; gubernaculum 11.7; lip height 5.1; lip width 10.2; a 48.3; b 10.0; b' 8.2; c 222.6; o 9.8.

Males ($n = 30$): Length 1,190–1,499 ($1,316 \pm 71.4$); width 27.1–33.6 (31.1 ± 1.7); anterior end to stylet knob base 26.1–29.3 (27.5 ± 0.8); stylet 23.4–26.1 (25.0 ± 0.6); stylet knob width (lateral) 4.6–5.1

(4.9 ± 0.1); DGO 2.0–5.1 (3.6 ± 0.9); tail 4.6–8.0 (6.2 ± 1.0); spicule 34.6–37.6 (36.2 ± 1.0); lip height 5.1–6.4 (5.9 ± 0.3); lip width 11.5–13.1 (12.0 ± 0.4); a 37.8–48.7 (42.5 ± 2.7); c 156.1–291.1 (219.9 ± 39.6); o 8.0–20.9 (14.3 ± 3.4). Males ($n = 10$): Gubernaculum 11.7–13.7 (12.7 ± 0.7); esophagus 144.7–178.2 (163.3 ± 10.7); b 8.0–9.1 (8.3 ± 0.4); b' 6.9–7.7 (7.1 ± 0.3).

Body vermiform, tapering at extremities, greater anteriorly. Lateral field with four incisures, outer two bands areolated. Head region slightly set off, six or seven

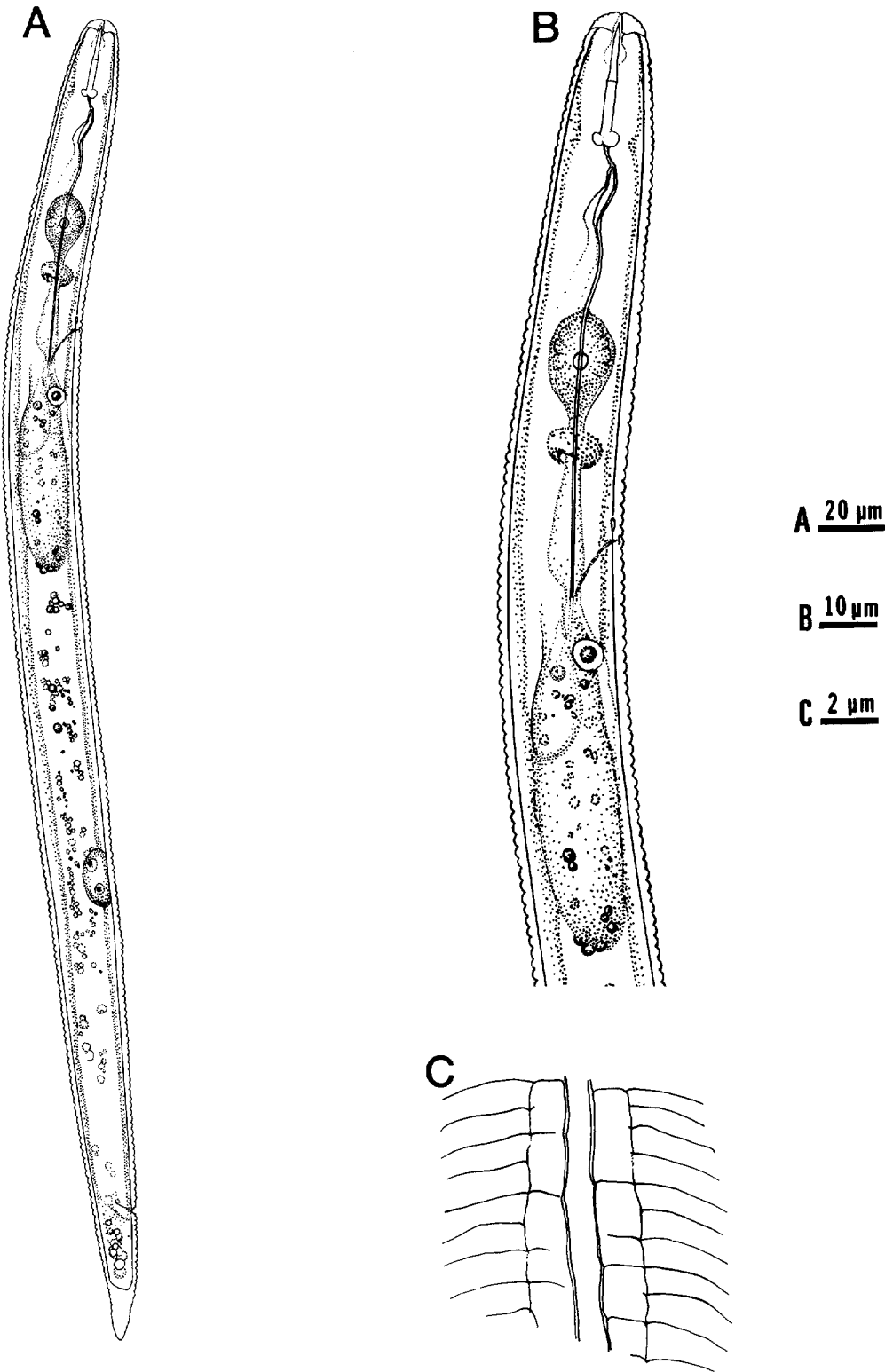


FIG. 6. Second-stage juveniles of *Cactodera milleri* n. sp. (lateral). A) Total specimen. B) Anterior end. C) Lateral field.

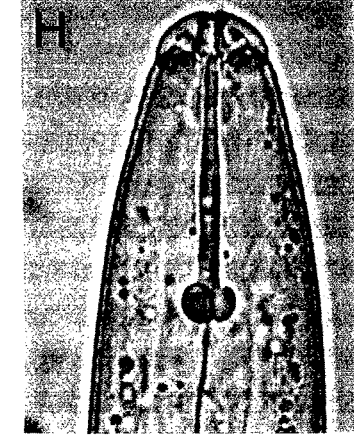
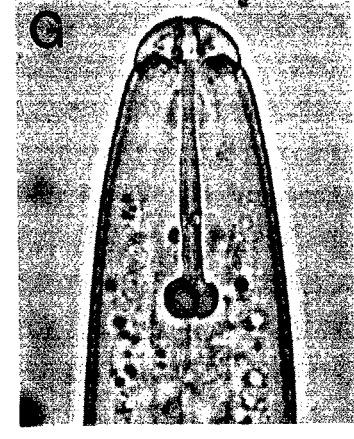
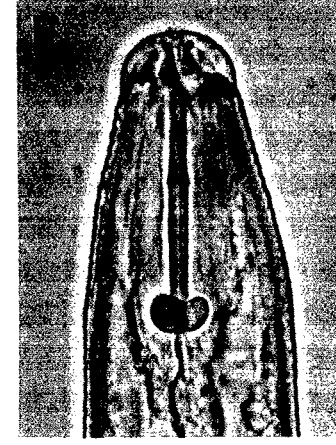
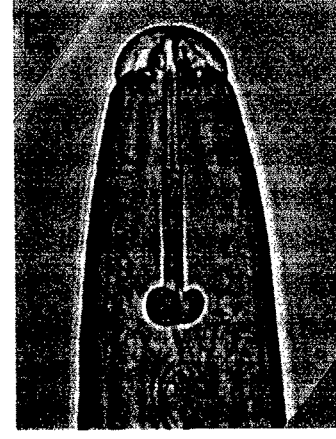
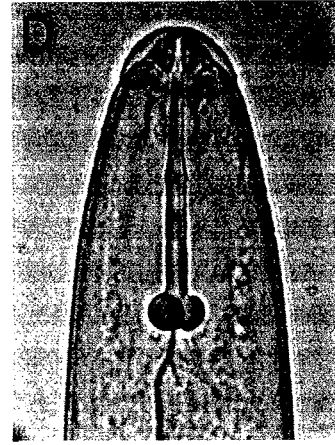
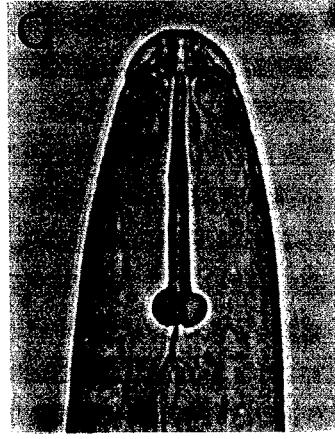
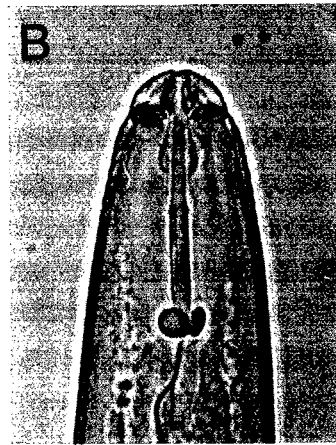
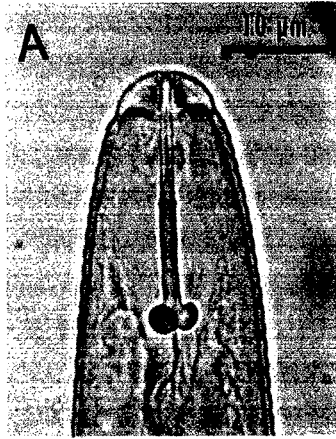


FIG. 7. LM photographs of head regions of J2 (lateral). A, B) *Cactodera milleri* n. sp. C–H) *Cactodera cacti*. C, D) MI population. E, F) FL population. G, H) LO population.

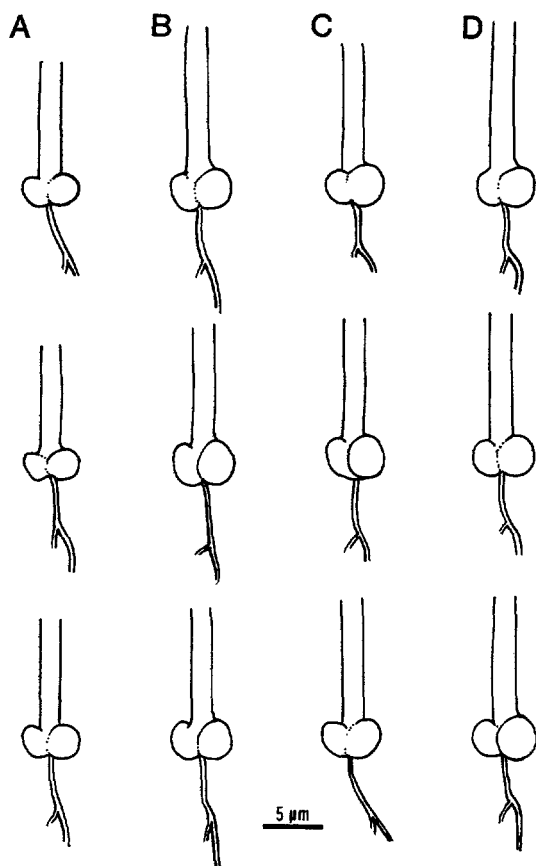


FIG. 8. Styllet knobs of J2 (lateral). A) *Cactodera milleri* n. sp. B–D) *Cactodera cacti*. B) MI population. C) FL population. D) LO population.

lip annuli. Styllet and knobs distinct. Styllet shaft curvature slightly dorsal. Dorsal styllet knob slopes posteriorly. Cephalids not observed. Hemizonid distinct, five annuli anterior to excretory pore. Hemizonin small, not distinct, nine annuli posterior to excretory pore. Testis, one, usually filled with sperm. Spicules curved, tips slightly notched. Tail short, phasmids not observed.

Second-stage juveniles: Morphometrics of J2 in water mounts ($n = 30$), and paratypes in glycerin ($n = 6$ – 16) in Tables 2, 3. Body vermiform, tapering at extremities, greater posteriorly. Lateral field with four incisures, outer two bands areolated. Head region set off, five or six lip annuli. En face pattern consistent, labial disc elongated, four submedial and two lateral lips. Lateral lips greatly reduced. Styllet and knobs well developed. Anterior surface of dorsal sty-

let knob usually concave, varies from slight to deeply concave, a few without concavity. Cephalids not observed. Hemizonid about one body annulus anterior to excretory pore. Esophageal glands overlap ventrally. Tail hypodermis outline slants ventrally (Fig. 2D).

Embryonated eggs ($n = 50$): Length 93.4–113.7 (102.1 ± 4.8); width 38.1–51.2 (43.6 ± 2.7); L/W 1.9–2.8 (2.4 ± 0.2).

Exterior shell with small, distinct punctations, visible with the light microscope and scanning electron microscope (Fig. 3). Punctations forming a distinct pattern.

Type specimens

Holotype (female), slide numbers T-436t and T-437t; allotype (male), slide number T-438t; and paratypes (20 females, 20 cysts, 10 males, 20 J2) deposited in the U.S. Department of Agriculture Nematode Collection, Beltsville, MD 20705.

Additional paratypes (20 females, 20 cysts, 10 males, 20 J2) deposited in each of the following nematode collections: University of California, Riverside Nematode Collection, Department of Nematology, University of California, Riverside, CA 92521; and Nematode Collection Section of Recent Invertebrates, Institut Royal des Sciences, Naturelles de Belgique, Rue Vautier, 29, B-1040, Bruxelles, Belgium. Paratype slides of 200 females, 85 cysts, 18 males, and 20 J2 and preserved specimens in vials of 100 females and several cysts, males, and J2 deposited in the Michigan State University Nematode Collection, Department of Entomology, Michigan State University, East Lansing, MI 48824.

Type host and locality

Chenopodium album, common lambs-quarter, in a former vineyard of the Francis Ryan farm adjacent to Country Road 652 and the Francis Ryan residence in Section 13 of Antwerp Township in Van Buren County near Mattawan, Michigan.

Diagnosis and relationships

Cactodera milleri n. sp. is morphologically distinct from all other species of the genus by one or more of the following diagnostic

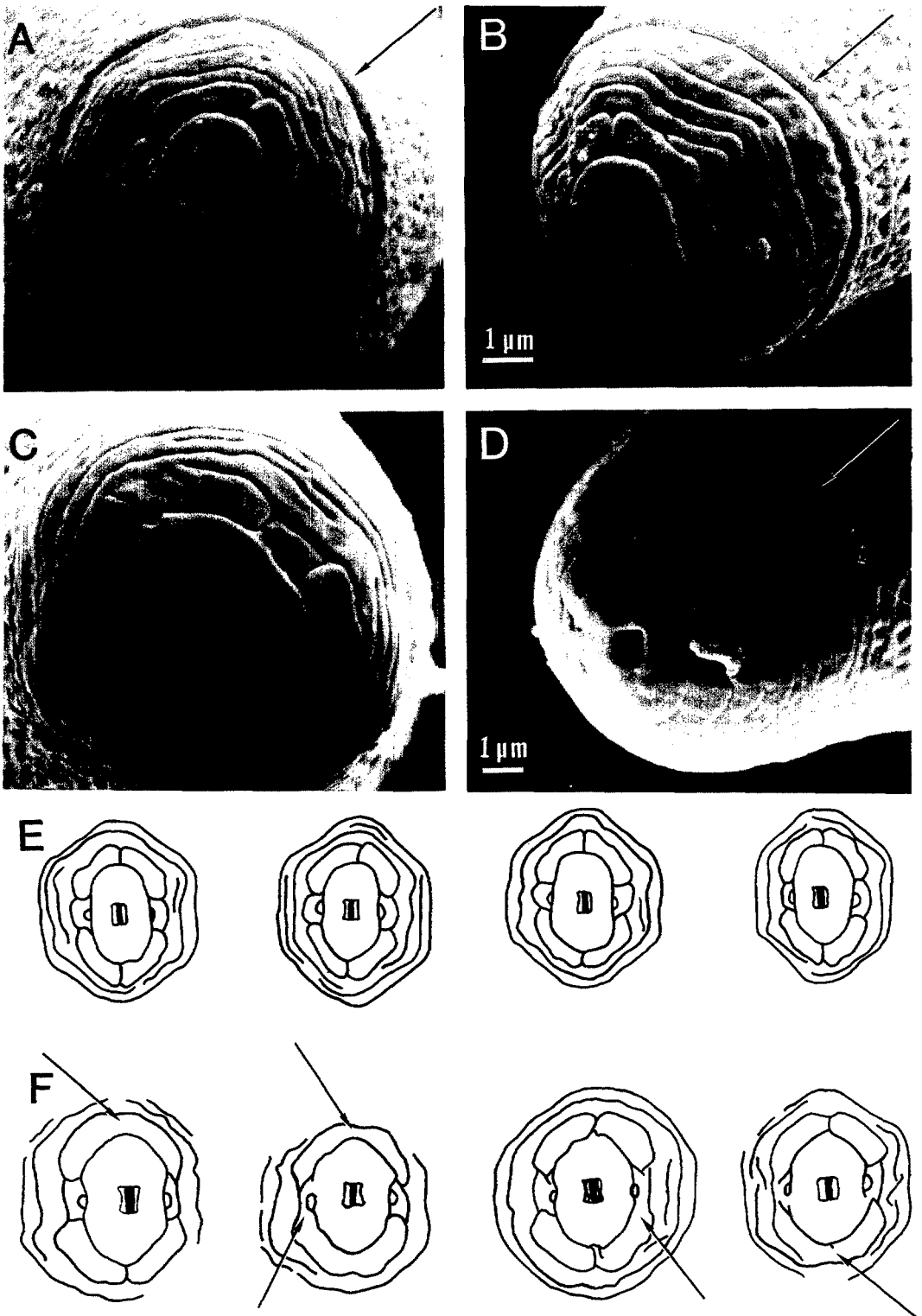


FIG. 9. SEM photographs and line drawings of en face views of J2. A, B, E) *Cactodera milleri* n. sp. A, B) Head region set off (arrows). E) Lip region with six distinct lips and oral disc. C, D, F) *Cactodera cacti*. C, D) Head region nearly continuous (arrow). F) Fusion of lips (arrows).

TABLE 2. Measurements of 30 second-stage juveniles of *Cactodera milleri* n. sp. in water mounts.

Characteristic	Range	Mean	Standard deviation
Body length	370–479	426.0	24.4
Body width	19.5–25.4	22.4	1.5
Anterior end to stylet knob base	22.7–25.4	24.3	0.6
Stylet length	21.0–22.9	21.8	0.5
Stylet knob width (lateral)	3.9–4.9	4.6	0.2
DGO	3.2–5.1	4.2	0.4
Anterior end to center of median bulb valve	62.9–70.1	66.4	1.9
Center of median bulb valve to excretory pore	26.6–42.7	33.7	4.5
Anterior end to excretory pore	89.7–110.7	100.1	5.3
Esophagus length	137.6–166.6	146.8	6.8
Tail length	36.6–48.8	42.7	2.6
Tail hyaline terminus length	14.6–21.2	18.2	1.7
Width at anus	12.2–15.4	13.3	0.6
Lip height	3.6–4.4	4.0	0.3
Lip width	8.8–9.7	9.2	0.2
a	17.0–21.2	19.0	0.8
b	2.6–3.1	2.9	0.1
b'	2.3–2.6	2.5	0.1
c	9.0–10.8	10.0	0.4
c'	2.8–3.6	3.2	0.2
Caudal ratio A†	2.1–3.0	2.5	0.3
Percentages			
o	15.1–23.5	19.4	2.0

† Caudal ratio A = tail hyaline terminus ÷ body width at anterior end of tail hyaline terminus.

features: female stylet length; cyst fenestra dimensions and length/width ratio; male stylet, DGO, tail, spicule, and gubernaculum lengths, and ratios a, b, and c; J2 stylet, DGO, tail, and tail hyaline terminus lengths, lip width, caudal ratio A, and ratios a, and b'; and egg length and surface (smooth versus punctate) (Table 4).

Cactodera milleri differs distinctly from *C. cacti*, the most closely related species, in the following morphometric characters: female stylet length (range 22.9–25.6, *C. cacti* 29.3–35.6) and vulval slit length (range 14.3–17.8, mean 16.2, *C. cacti* 9.5–15.1, 12.6); male body length (range 1,190–1,499; *C. cacti* 869–1,166) stylet length (range 23.4–26.1, *C. cacti* 26.1–28.3), spicule (range 34.6–37.6, *C. cacti* 31.7–34.6), gubernaculum (range 11.7–13.7, *C. cacti* 8.8–11.2), and lip width (range 11.5–13.1, *C. cacti* 10.2–11.2); and J2 stylet length (range 21.0–22.9, *C. cacti* 24.4–26.7) and anterior end to stylet knob base (range 22.7–25.4, *C. cacti* 25.8–30.2). In addition, cyst fenestra diameter measured dorsal-ventrally and laterally may also be useful, although the ranges of the measurements

of the two species overlap (mean dorsal-ventral 13.3, *C. cacti* MI 26.2, TY 18.9; mean lateral 18.7, *C. cacti* MI 26.2, TY 25.7). Other useful J2 morphometric characters showing significant ($P = 0.01$) differences between the species are body length, stylet knob width, anterior end to center of median bulb valve, anterior end to excretory pore, tail length, and lip height (Tables 3, 5). Distinguishing morphologic features are the more anterior position of the female median bulb of *C. milleri* (Figs. 1, 10), the dorsal stylet knob of males of *C. milleri* sloping posteriorly versus concave anteriorly (Fig. 5), the head of the spicule of *C. milleri* curving in contrast to *C. cacti* (Fig. 5), SEM en face views of J2 of *C. milleri* consisting of six distinctly separated lips, whereas *C. cacti* lips are often fused (Fig. 9), and the finer egg shell punctations of *C. milleri* as viewed with SEM (Fig. 3).

Remarks

The species name is in honor of Dr. Lawrence I. Miller for his extensive contributions to cyst nematode taxonomy.

TABLE 3. Morphometrics of second-stage juveniles of *Cactodera milleri* n. sp. and five populations of *C. cacti*.

Character	<i>C. milleri</i>	<i>C. cacti</i>				
		Florida, USA	Georgia, USA	Italy	Wageningen, The Netherlands	Type Maartensdijk, The Netherlands
Body length	379 a 16 (348–415)	447 b 16 (418–475)			430 5 (418–446)	
Stylet length	21.3 a 14 (20.0–22.0)	24.7 b 16 (23.9–25.8)	22.8 d 15 (22.4–23.4)	23.6 c 25 (22.4–24.4)	24.8 5 (24.4–25.1)	24.7 b 25 (22.9–25.9)
Stylet knob width (lateral)	4.0 a 6 (3.9–4.3)	4.4 b 13 (3.9–4.9)		4.5 b 7 (4.1–4.9)		4.7 b 25 (4.4–4.9)
Anterior end to stylet knob base	23.0 a 14 (22.4–23.9)	26.4 b 16 (25.4–27.3)	25.1 c 14 (24.4–26.8)	26.0 b 25 (24.4–26.8)	27.3 5 (26.8–27.8)	26.5 b 25 (24.9–27.3)
Tail hyaline terminus	17.1 ab 14 (14.1–19.5)	19.5 c 11 (15.8–22.0)	17.3 ab 8 (14.6–19.9)	15.3 b 25 (12.7–18.5)	20.6 4 (18.5–22.9)	19.0 bc 25 (15.1–23.9)
Lip height	3.8 a 14 (3.4–4.1)	4.7 c 16 (4.3–5.4)	4.4 b 13 (3.9–4.6)	4.0 a 15 (3.4–4.4)	4.3 5 (4.1–4.4)	4.3 b 20 (3.9–4.9)
Lip width	8.4 a 14 (8.0–9.0)	9.8 c 16 (9.3–10.2)			9.3 5 (9.3–9.5)	9.5 b 20 (9.3–10.2)

Mean measurement (μm) over number of specimens and (range).

Character means followed by a letter in common are not significantly ($P = 0.01$) different according to Duncan's multiple-range test. The Wageningen population was not included in the statistical analysis.

All specimens were measured in glycerin mounts except for type population which were measured in fixative mounts.

TABLE 4. Morphometrics of five life stages of selected *Cactodera* spp.

Characteristic	<i>C. thornei</i> (6)	<i>C. weissii</i> (6)	<i>C. amaranthi</i> (6, 18)	<i>C. estonica</i> (6, 8)	<i>C. eremica</i> (3)	<i>C. acnidae</i> (14)	<i>C. milleri</i> n. sp.
Female							
Length w/neck	561 (456–704)	503 (408–688)	563 (404–688)	Females	546.3 (373–676)	744 (633–874)	718 (538–885)
Width	326 (194–459)	278 (201–408)	366 (181–464)	not described	352 (233–495)	413 (358–498)	491 (335–640)
L/W	1.8 (1.3–2.2)	1.4 (1.4–2.3)	1.6 (1.1–2.2)		1.6 (1.2–2.8)	1.8 (1.4–2.6)	1.5 (1.2–1.9)
Stylet	<u>29.4 (28.4–30.7)</u>	22.8 (21.8–24.3)	25.3 (24.9–26.6)		25.5 (23.7–27.4)	23.3 (19.5–25)	24.1 (22.9–25.6)
DGO	5.6 (5.2–6)	5.2 (4.5–5.6)	4.8 (4.3–5.2)		3.9 (3–4.8)		5.7 (4.4–9.3)
Vulval slit	17 (16–19)	15 (13–20)	15 (14–16)		15.8 (14–19)	17 (12–20)	16.2 (14.3–17.8)
Cyst							
Length w/neck	656 (485–806)	598 (385–750)	642 (525–774)	922 (536–1,178)	620 (530–810)	698 (504–857)	700 (550–849)
Width	448 (286–581)	350 (230–460)	472 (370–550)	391 (207–535)	434 (290–590)	417 (319–493)	506 (419–598)
L/W	1.5 (1.2–1.9)	1.7 (1.2–2.3)	1.4 (1.1–1.7)	<u>2.3 (2–2.4)</u>	1.5 (1.2–1.9)	1.8 (1.2–2.4)	1.4 (1.2–1.6)
Fenestra	<u>34 (31–36)</u>	<u>34 (29–38)</u>	<u>31 (25–38)</u>	(35)	20.6 (14.4–25.2)	<u>33 × 30</u>	18.8 (14.3–22)
Male							
Length	1,503 (1,315–1,708)	1,034 (943–1,240)	974 (792–1,195)	Males not	1,170 (950–1,320)	1,127 (1,120–1,148)	1,316 (1,190–1,499)
Stylet	<u>29.4 (27.8–31)</u>	24.2 (22.5–25.2)	25.5 (21–27)	reported	28.5 (25.5–30.5)	<u>21.7 (19.5–23.4)</u>	25 (23.4–26.1)
DGO	<u>6.8 (5.5–8)</u>	4.8 (4.5–5.6)	3.7 (2.6–4.3)		3.4 (3–4.5)		3.6 (2–5.1)
Tail	5 (2–8)	1.6 (1.1–2.8)	<u>1.8 (0.9–3.4)</u>				6.2 (4.6–8)
Spicule	<u>43 (39–46)</u>	<u>32.4 (30.8–33.6)</u>	<u>30.5 (27–33)</u>		38.2 (33–42)	<u>25.7 (24.7–27.8)</u>	36.2 (34.6–37.6)
Gubernaculum	13 (10–15)	10 (9.5–11)	10 (8–12)		10.6 (9.5–13.5)	<u>9–11</u>	12.7 (11.7–13.7)
a	37 (30–45)	<u>31 (27–33)</u>	38.8 (36–44.5)		43.4 (39.3–48.9)	39–45	42.5 (37.8–48.7)
b	8.8 (7.3–9.8)	<u>6.0 (5.1–6.7)</u>	6.2 (5.4–6.8)		7.6 (6.4–9.8)	<u>13.3–13.7</u>	8.3 (8.0–9.1)
c	321 (199–505)	<u>631 (346–991)</u>	<u>588 (302–1,244)</u>			187–228	219.9 (156.1–291.1)

TABLE 4. Continued.

Characteristic	<i>C. thornei</i> (6)	<i>C. weissi</i> (6)	<i>C. amaranthi</i> (6, 18)	<i>C. estonica</i> (6, 8)	<i>C. eremica</i> (3)	<i>C. acnidae</i> (14)	<i>C. milleri</i> n. sp.
Second-stage juvenile							
Length	554 (446-620)	407 (372-420)	374 (340-406)	440 (426-465)	480 (440-510)	411 (361-448)	426 (370-479)
Stylet	<u>27 (25-28)</u>	20.4 (19.6-21.8)	20.7 (20.2-21.3)	22.8 (21-25)	<u>26.5 (25-28)</u>	21.2 (18.9-24.7)	21.8 (21-22.9)
DGO	<u>6 (5-7)</u>	5.3 (4.5-5.6)	4.9 (4.8-5.2)	3.6 (3.4-4.3)	<u>4.4 (3.5-6)</u>	<u>2.5-3.0</u>	4.2 (3.2-5.1)
Tail	<u>56 (49-64)</u>	45.9 (43-50)	39 (34-47)	40 (36-44)	40.4 (36.5-47.5)	44 (43-48)	42.7 (36.6-48.8)
Tail hyaline terminus	<u>25 (23-28)</u>	20.2 (17-24)	15 (11-18)	17 (14-21)	18.1 (17-23.5)	21.6 (17.5-26)	18.2 (14.6-21.2)
Lip height			3.6 (3.4-4.3)	3.7 (3.4-4.3)		3.3 (2.8-5.6)	4 (3.6-4.4)
Lip width			8.7 (8.5-9.4)	<u>8.3 (7.7-8.5)</u>		10.7 (8.3-12.2)	9.2 (8.8-9.7)
Caudal ratio A†	2.9 (2.5-3.3)	<u>3.5 (3.0-3.9)</u>	2.1 (1.6-2.6)	<u>2.8 (2.3-3.6)</u>			2.5 (2.1-3.0)
a	24 (20-28)	20 (18-22)	18 (16-20)	<u>22.8 (22-25)</u>	23 (20.9-23.8)	20.3-29.9	19 (17-21.2)
b	3.9 (2.4-4.7)	2.6 (2.3-3.5)	2.8 (2.5-3.0)	<u>2.8 (2.7-2.9)</u>	2.7 (2.5-3.1)	4.2-6.9	2.9 (2.6-3.1)
b'					<u>3.2 (2.6-3.7)</u>		2.5 (2.3-2.6)
c	9.8 (8.8-11.2)	8.9 (8.4-9.5)	10.6 (9.7-11.8)	11.2 (10.5-11.9)	11.9 (10.1-12.5)	8.9-9.9	10 (9-10.8)
Egg							
Length	<u>129 (123-134)</u>	101 (96-106)	96 (88-108)	124.9 (108.5-133)	104.5 (99-115)	99 (88-112)	102.1 (93.4-113.7)
Width	53 (50-57)	42 (40-44)	48 (43-52)	48.2 (42-52)	50.3 (48-54)	48 (34-52)	43.6 (38.1-51.2)
L/W	2.4 (2.3-2.6)	2.4 (2.3-2.6)	2.0 (1.8-2.3)	(2.6)	2.1 (1.9-2.4)		2.4 (1.9-2.8)
Surface	Punctate	<u>Smooth</u>	<u>Smooth</u>	<u>Smooth</u>	Punctate	<u>Smooth</u>	Punctate

Mean measurement (μm) is followed by range in parentheses.

Useful diagnostic characters of *Cactodera* spp. whose ranges do not overlap with *C. milleri* are underlined.

† Caudal ratio A = tail hyaline terminus \div body width at anterior end of tail hyaline terminus.

TABLE 5. Morphometrics of second-stage juveniles of *Cactodera milleri* n. sp. and three populations of *C. cacti* in water mounts.

Character	<i>C. cacti</i>			
	<i>C. milleri</i>	Michigan, USA	Florida, USA	Lotum, The Netherlands
Body length	426 a (370-479)	504 b (456-540)	515 b (451-568)	478 c (418-562)
Stylet length	21.8 a (21.0-22.9)	25.1 b (24.4-26.3)	25.7 c (24.4-26.7)	25.0 b (24.4-26.3)
DGO	4.2 a (3.2-5.1)	3.8 b (2.9-4.4)	4.1 ab (3.4-4.9)	5.2 c (3.4-6.3)
Stylet knob width (lateral)	4.6 a (3.9-4.9)	5.3 b (5.0-5.8)	5.2 b (4.9-5.5)	5.0 c (4.7-5.4)
Anterior end to stylet knob base	24.3 a (22.7-25.4)	27.6 b (26.8-28.8)	27.8 b (25.8-30.2)	27.6 b (26.3-29.3)
Anterior end to center of median bulb valve	66.4 a (62.9-70.1)	77.6 b (73.6-82.0)	79.8 c (71.2-87.7)	77.2 b (69.3-82.9)
Center of median bulb valve to excretory pore	33.7 a (26.6-42.7)	35.3 a (29.3-43.9)	39.4 b (34.6-46.8)	36.1 a (28.8-42.9)
Anterior end to excretory pore	100.1 a (89.7-110.7)	112.9 b (103.9-121.5)	119.2 c (109.2-128.7)	113.3 b (98.1-125.2)
Tail length	42.7 a (36.6-48.8)	55.0 b (49.3-59.5)	52.2 c (46.3-60.5)	48.8 d (43.2-56.8)
Tail hyaline terminus length	18.2 a (14.6-21.2)	17.6 a (13.7-20.5)	21.5 b (16.6-25.6)	21.9 b (18.0-25.4)
Lip height	4.0 a (3.6-4.4)	4.6 b (3.9-4.9)		4.4 b (3.9-4.9)
Lip width	9.2 a (8.8-9.7)	10.5 b (10.0-11.0)		9.9 c (9.3-10.2)

Mean measurement (μm) over (range).

n = 30, except stylet knob width of the Florida population, n = 24.

Character means followed by a letter in common are not significantly ($P = 0.01$) different according to Duncan's multiple-range test.

The field host of *C. milleri*, determined in the greenhouse, is *Chenopodium album* (common lambsquarter). Other weed species present in the field soil but not hosts of *C. milleri* were *Stellaria media* L., *Amaranthus retroflexus* L., *Sesbania* sp., and *Digitaria sanguinalis* (L.) Scop. Asparagus did not support reproduction of *C. milleri*. Results of the host range study indicated a narrow host preference with reproduction on only three *Chenopodium* species (Table 1). *Cactodera milleri* did not reproduce on the 18 agronomic crops, 5 cactus species, and the remaining 8 weed species (Table 1).

Cactodera cacti
(Figs. 2, 3, 5, 7-10)

Females, MI population (n = 30): Length with neck 532-765 (646 ± 56); length

without neck 401-652 (550 ± 59); width 323-574 (450 ± 62); length/width ratio with neck 1.2-1.7 (1.5 ± 0.1); L/W ratio without neck 1.0-1.4 (1.2 ± 0.1). Females (n = 25): Stylet length 30.2-35.6 (33.2 ± 1.2); DGO 5.4-9.8 (6.9 ± 1.2); vulval slit length 9.5-15.1 (12.6 ± 1.4); distance from vulval slit to anus 34.5-50.0 (40.6 ± 4.2). Females (n = 20): Anterior end to excretory pore 90.2-159.0 (124.9 ± 21.2).

Females, LO population (n = 7): Stylet length 29.3-32.2 (30.4 ± 1.1).

Body lemon shaped to almost spherical. Color pearly white, yellow, or golden, becoming light brown. Neck offset, vulval cone prominent. Subcrystalline layer or gelatinous egg sac not observed. Labial disc elevated. Stylet and knobs well developed. Excretory pore near median bulb.

Cysts, MI population (n = 30): Length with neck 472-730 (629 ± 64); length without

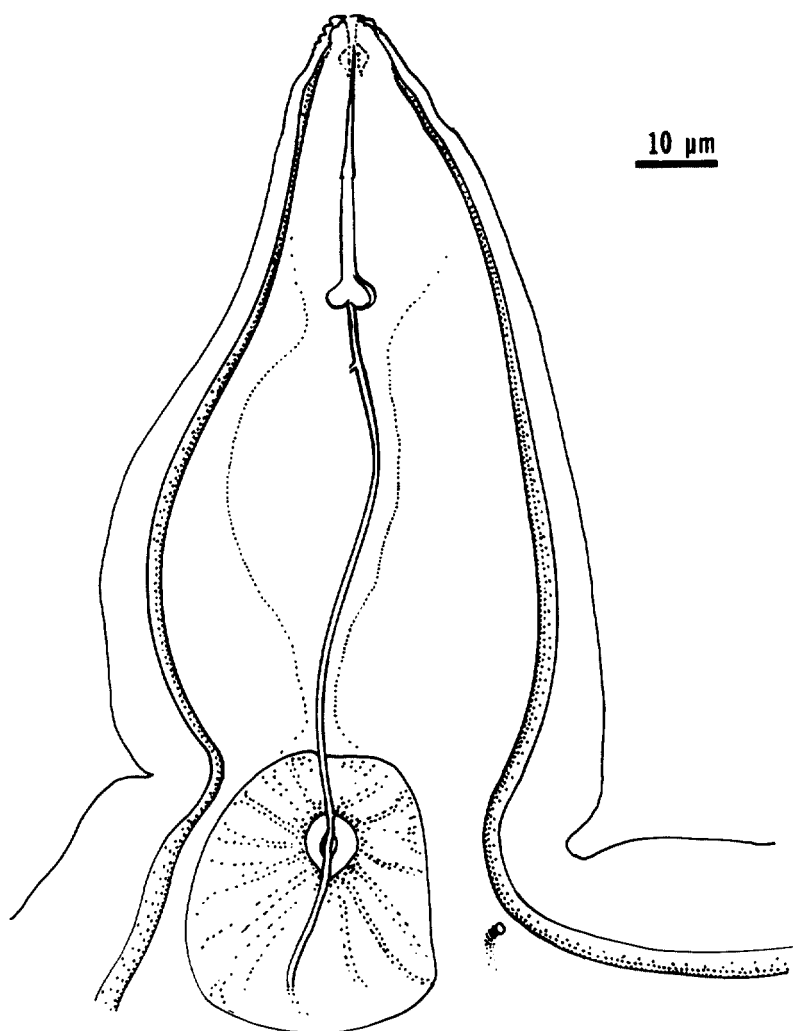


FIG. 10. Female anterior body region of the MI population of *Cactodera cacti* (latero-ventral).

neck 389–658 (558 ± 66); width 323–598 (470 ± 72); L/W ratio with neck 1.1–1.6 (1.4 ± 0.1); L/W without neck 1.0–1.4 (1.2 ± 0.1); fenestra diameter (dorsal–ventral) 16.1–34.5 (26.2 ± 4.4); fenestra diameter (lateral) 15.5–29.8 (26.2 ± 3.6).

Cysts, TY population ($n = 8$): Fenestra diameter (dorsal–ventral) 15.5–22.6 (18.9 ± 2.7); fenestra diameter (lateral) 22.6–28.6 (25.7 ± 2.1).

Cysts usually lemon shaped, but may be rounded. Color light brown, brown to reddish brown. Vulval denticles rarely observed. Cone tops abullate, circumfenestrate.

Males, LO population ($n = 18$): Length 869–1,166 ($1,011 \pm 94.4$). Males ($n = 17$):

Anterior end to stylet knob base 28.0–29.8 (28.9 ± 0.6); stylet length 26.1–28.3 (27.1 ± 0.7). Males ($n = 8$): Stylet knob width (lateral) 4.9–6.3 (5.7 ± 0.4); lip height 4.9–6.3 (5.5 ± 0.4); lip width 10.2–11.2 (10.7 ± 0.3). Males ($n = 10$): DGO 2.4–5.4 (3.6 ± 1.1); tail 3.9–6.3 (4.8 ± 0.9). Males ($n = 11$): Spicule 31.7–34.6 (33.5 ± 1.0). Males ($n = 9$): Gubernaculum 8.8–11.2 (9.9 ± 0.6).

Males, WA population ($n = 2$): Stylet length average 27.3; anterior end to stylet knob base 28.8–29.0 (28.9 ± 0.1).

Head region nearly continuous with body, usually six lip annuli. Dorsal stylet knob anterior surface concave. Hemizonid 1–3 annuli anterior to excretory pore.

TABLE 6. Selected morphometrics of cysts and eggs of 10 populations of *Cactodera cacti* (with reference numbers in parentheses).

Character	Netherlands† (1) (n = 50)	Netherlands‡ (1) (n = 100)	Yugoslavia (6) (n = 15)	Belgium (10) (n = 15)	USSR (7)	USSR (16)	USSR (12)	Italy (2) (n = 25)	Italy (6) (n = 25)	India (9) (n = 20)
Cyst										
Length w/neck	475 (232–656)	497 (328–617)	587 (498–662)	(430–450)	(464–750)	(270–753)	(465–747)	535.7 (384–780)		
Width	424 (270–617)	447 (309–598)	475 (387–550)	(400–420)	(420–600)	(254–737)	(425–685)	377.8 (240–588)		(360–590)
L/W	1.12	1.12	1.3 (1.1–1.4)					1.4 (1.1–2.0)		
Fenestra length			38 (29–48)	(20–40)				26		(25–38)
Fenestra width				(18–30)				28		(20–26)
Vulval slit§				(15–19)	(25–28)					
Egg										
Length	110 (97–120)	114 (92–132)				(86–120)		114.8 (107.5–122.5)	107 (102–112)	(90–112)
Width	46 (38–48)	43 (40–48)				(38–52)		52.4 (50.0–62.5)	49 (46–53)	(39–44)
L/W	2.36	2.6						2.1 (1.9–2.3)	2.2 (1.9–2.3)	

Mean measurement (μm) is over (range).† Measurements of specimens from *Cereus speciosus* (Cactaceae).‡ Measurements of specimens from *Phyllocactus akhermanni* (Cactaceae).

§ Measured from newly formed cysts.

Spicules with bifid tips. Testis one, sperm present.

Second-stage juveniles: Morphometrics of the MI, FL, IT, GA, LO, WA, and TY populations in Tables 3, 5. Body vermiform, both extremities tapering. Lateral field with four incisures, outer field areolated. Head region nearly continuous with body, usually five lip annuli. Lip region with dorso-ventrally elongated labial disc, two small lateral and four large submedial lips. Frequent fusion between submedial lip pairs, lateral lips and oral disc, and lateral lips and submedial lips. Dorsal stylet knob anterior surface slopes posteriorly to slightly concave. Cephalids not observed. Hemizonid just anterior or superimposed by excretory pore. Posterior tail hypodermis outline usually V-shaped and U-shaped, rarely slopes ventrally (Fig. 2E–G).

Embryonated eggs, MI population (n = 30): Length 101.1–113.1 (107.2 ± 3.2); width 44.0–54.7 (49.1 ± 2.4); L/W ratio 1.9–2.4 (2.2 ± 0.1).

Eggshells usually covered with large, irregular-shaped punctations. Punctations form distinct pattern easily observed with LM and SEM.

Relationships of populations

A review of previously published morphometrics of cysts, males, J2, and eggs of *C. cacti* is presented in Tables 6–8. Substantial morphometric variability exists among the different populations; e.g., vulval slit length, male gubernaculum and b ratio, and J2 stylet length, distance between the anterior end and median bulb, b ratio, and lip region dimensions (Tables 6–8).

In general, the morphology and morphometrics of cysts, males, and eggs of the *C. cacti* populations examined in the present study correspond with previously published literature. However, the average cyst length including neck is longer than any other previously recorded average (629 vs. 587). In addition, fenestra diameter as reported by Golden and Raski (6) is larger than that of the MI or TY populations (38 vs. 26.2 for MI and 25.7 for TY). Vulval slit length of newly formed cysts reported

TABLE 7. Selected morphometrics of males of *Cactodera cacti* from The Netherlands (1) and India (9).

Characteristic	The Netherlands† (n = 6)	India (n = 5)
Body length	1,010 (972–1,048)	(910–1,130)
Stylet length		(22–28)
DGO		(3–4)
Anterior end to stylet knob base	28 (26–29)	
Anterior end to excretory pore	146.3 (139.4–156)	(120–150)
Spicule	33.5 (32.3–36)	(30–37)
Gubernaculum	11.4 (10.2–12)	(13–15)
a	34.8 (33.5–37.1)	(33–42)
b	9.7 (9.3–9.8)	(5–5.7)
c	<200	(113.7–146.4)
Lip height		(5–6)
Lip width		(10–11)

Mean measurement (μm) over (range).

† Measurements of specimens from *Phyllocactus akkermanni* (Cactaceae).

by Mulvey (10) and Kir'yanova and Terent'eva (7), 15–19 and 25–28, respectively, may not be comparable to vulval slit length of the female. Female slit length of the MI population averaged 12.6 and ranged from 9.5 to 15.1. Gubernaculum length of LO males averaged 9.9, shorter than that reported by Adam (1) and Mulk (9), 11.4 and 12.7, respectively.

In general, J2 dimensions, such as body length, stylet length, anterior end to excretory pore, tail length, and lip width of specimens measured in water mounts of the MI, FL, and LO populations, were larger than previously reported (Tables 5–8). However, dimensions of the FL, GA, IT, WA, and TY populations measured in glycerin or fixative were similar to earlier reports (Tables 3, 6–8). Average stylet length reported by Ambrogioni (2) is 27.9, considerably longer than the stylet of any other population but it was similar as a measurement of the distance from anterior end to stylet knob base. Lip heights of the two Netherlands populations reported by Adam (1) average 5.7 and 5.2 and are consider-

TABLE 8. Selected morphometrics of second-stage juveniles of seven populations of *Cactodera cacti* with reference numbers in parentheses.

Character	Netherlands† (1) (n = 11)	Netherlands‡ (1) (n = 15)	Italy (6) (n = 50)	Italy (2) (n = 10)	Mexico (6) (n = 25)	Georgia, USA (6) (n = 23)	India (9) (n = 20)
Body length	473.6 (436–630)	485.8 (428–584)	409 (364–453)	470.8 (446.3–512.5)	418 (376–451)	432 (412–451)	(393–440)
Stylet length			23.5 (22.4–24.6)	27.9 (26.3–28.7)	23.4 (22.4–24.0)	22.9 (22.4–24.0)	(23–25)
DGO			3.8 (3.4–4.6)	3.7 (3.8–4.4)	5.0 (4.5–6.1)	3.8 (3.4–4.5)	
Anterior end to stylet knob base	27.1 (24.0–29.0)	25.2 (22.0–28.2)					
Anterior end to center of median bulb	81.2 (74–88)	80.0 (64–92)	33 (26–38)		39 (35–42)	40 (38–44)	
Anterior end to excretory pore	109.7 (100–139)	103.4 (96–128)	(101–108)				
Tail	50.6	51.4	46 (36–52)		43 (34–48)	44 (39–48)	(43–50)
Tail hyaline terminus			15.7 (12–19)	(18.8–26.5)	19 (14–21)	17.2 (14.5–19.6)	(18–25)
a	22.6 (20.6–23.8)	22.0 (19.2–29.4)	18 (15–20)	22.0 (21.0–22.7)	19 (17–21)	19.4 (18–21)	(21–23)
b	5.8 (5.4–7.1)	6.0 (5.6–6.8)	2.6 (2.1–3.1)	5.7 (5.2–5.8)	2.7 (3.5–3.7)	2.8	
c	9.3 (8.8–10.3)	9.4 (8.4–10.5)	8.9 (7.8–10.1)	9.0 (8.0–10.0)	9.9 (9.5–10.7)	9.9 (9.5–10.7)	(8.7–9.3)
Lip height	5.7	5.2	3.5 (2.8–4.5)		3.5 (2.8–4.5)	2.6 (2.2–3.4)	(4–5)
Lip width			6.9 (6.2–8.4)		7.0 (6.2–8.4)	7.2 (6.2–7.8)	(9–10)

Mean measurement (μm) over (range).† Measurements of specimens from *Cereus speciosus* (Cactaceae).‡ Measurements of specimens from *Phyllocactus akkermanni* (Cactaceae).

ably larger than lip heights observed in the present study (averages range from 4.0 to 4.7) and in other previously published reports (averages range from 2.6 to 3.5). Golden and Raski (6) describe the shape of the J2 stylet knobs of *C. cacti* as being "convex" anteriorly, whereas the J2 drawings of Mulk (9) and Adam (1) show stylet knobs as concave anteriorly or sloping posteriorly, respectively. In the present study, the anterior surface of the dorsal stylet knob ranges from sloping posteriorly to concave (Figs. 7, 8), with the majority of specimens predominantly concave. The tail hypodermis outline depicted by Golden and Raski (6) and Mulk (9) is U-shaped. Observations of the MI, FL, IT, GA, LO, WA, and TY populations indicate a high degree of variability in this characteristic. Outlines were U-shaped, V-shaped, or sloped ventrally.

Remarks

The MI population of *C. cacti* was first discovered by Dr. Natalie Knobloch in 1972 from soil samples taken from *Cereus peruvianus* (Cactaceae) plants growing in the tropical greenhouse at MSU.

KEY TO SPECIES OF *CACTODERA* KRALL & KRALL, 1978

- 1a. Cyst length usually 2× width, L/W ratio averaging 2.3; egg shells smooth *C. estonica*
- 1b. Cyst length less than 2× width, average L/W ratio 1.1–1.7; egg shells smooth or punctate 2
- 2a. J2 stylet length averages 26 or greater; egg shells distinctly punctate 3
- 2b. J2 stylet averages less than 26; egg shells smooth or punctate 4
- 3a. J2 tail length = 49–64; J2 tail hyaline terminus = 23–28; cyst fenestra diameter = 31–36 *C. thornei*
- 3b. J2 tail length = 36–48; tail hyaline terminus = 17–24; cyst fenestra diameter = 14–25 *C. eremica*
- 4a. Egg shells distinctly punctate; J2 stylet length averages 21 or more 5
- 4b. Egg shells smooth; J2 stylet length averages less than 22 6
- 5a. J2 stylet length = 21–23; anterior end to stylet knob base = 23–25; cyst fenestra diameter averages 19 or less *C. milleri* n. sp.
- 5b. J2 stylet length = 24–27; anterior end to stylet knob base = 26–30; cyst fenestra diameter averages greater than 19 *C. cacti*
- 6a. J2 tail hyaline terminus = 17–26; tail length = 43–50 7

- 6b. J2 tail hyaline terminus = 11–18; tail length = 34–47 *C. amaranthi*
- 7a. J2 stylet knobs anterior surface concave; DGO = 4.5–5.6 *C. weissi*
- 7b. J2 stylet knobs anterior surface convex; DGO = 2.5–3.0 *C. acnidae*

DISCUSSION

The results of the host range study indicate that *C. milleri* n. sp. probably does not pose any economic threat in this country. It could be of concern, however, to countries where *Chenopodium* is cultured as a food source. *Heterodera schachtii* Schmidt, 1871 reproduces on *C. album* (5,17,19) and is economically significant in sugar beet and cabbage production. Because both *Cactodera milleri* and *H. schachtii* reproduce on *Chenopodium album*, it should no longer be assumed that a lemon-shaped cyst on *C. album* is *H. schachtii*.

Morphometric variability among populations of *Cactodera cacti* was greatest for measurements of J2. Some of this variability may be attributed to different specimen preparations, i.e., water mounts vs. glycerin mounts. Comparison of measurements of FL J2 in water vs. measurements of the same J2 in glycerin shows shrinkage of body length, stylet length, stylet knob width, anterior end to stylet knob base, and tail hyaline terminus in the glycerin mounted specimens (Tables 3, 5). In addition to the morphometric variability reported in this study, variability in the mode of reproduction is also possible because males of the MI population were never recovered from greenhouse cultures, whereas males of the LO population were; also, male morphometrics were reported by Adam (1) and Mulk (9).

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