

***Heterodera thornei* n. sp. (Nematoda:Heteroderidae) and a Review of Related Species**

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Abstract: In a taxonomic review of the species of the *Heterodera* "cacti group," *H. thornei* n. sp. is described and illustrated from Miner's lettuce in California. This new species is distinguishable especially by having punctate egg shells and a larval stylet (27 μ m) and tail (56 μ m) longer than other related species. *Heterodera weissi* is redescribed, type specimens are designated, and new data added on the basis of original and topotype specimens. New morphometric data, along with illustrations, are given for *H. cacti*, *H. amaranthi*, and *H. estonica*, and certain details in the original descriptions are clarified on the latter two species. Diagnoses and a key for identification of these species are given. A common name for each species is proposed when one is lacking. Previously unrecognized tooth-like structures occurring in the vulval cone top of these species and in *H. schachtii* are characterized and named "vulval denticles." Because of its markedly different morphology, especially in cysts, *H. betulae* is removed from the *H. cacti* group and placed alone, since it is incompatible with any of the present *Heterodera* "groups." Known distribution of these species is given, with the result that many new areas and countries of occurrence for some of the species are listed. *Key Words:* Taxonomy, morphology, distribution, *Heterodera* species, cyst nematodes, new species, hosts.

In the genus *Heterodera*, cyst characteristics (particularly shape, cyst wall pattern, and fenestration) are of major importance in placing closely related species into common groups. These and other cyst characters and larval morphology are useful at the species level. In the present paper, five species are placed in the *Heterodera* "cacti group" on the basis of commonly shared cyst characters. One species is described as new, one is redescribed, and additional data are given for the remaining three species. Also, denticulate structures in the vulval cyst cone are named and discussed, and a key to the species is presented.

Procedures used in this study, including measuring, drawing, photomicrographing, and preparing specimens, were essentially

the same as those used by Golden and Birchfield (3). In making the SEM micrographs, the eggs which were previously fixed in 3% formaldehyde solution were placed on specimen stubs, sputter coated with gold-palladium, and examined with an Hitachi HHS-2R scanning electron microscope.

Heterodera thornei n. sp.

In April 1949, *Heterodera* cysts, larvae, and males were obtained from soil in a walnut orchard near Santa Clara, California by the second author and were later determined to be an undescribed species. Similar specimens from the same orchard were first noted in 1942 by Gerald Thorne (17) at the time of his discovery of *Cacopaurus pestis* Thorne, 1943 attacking the roots of the Mayette variety of Persian walnut, *Juglans regia* Linn., growing on original seedling rootstock. Further search of this field indicated that this cyst-forming species was feeding on the roots of Miner's lettuce, *Montia perfoliata* (Donn ex. Willd.) Howell. Subsequently, a heavy population of this nematode was found on the same host plant which was growing as a cover crop in a walnut orchard near San Jose, California.

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FEMALES (25): Length (including neck) 456-704 μm (mean 561 μm , standard deviation (SD) 67 μm); width 194-459 μm (326 μm , SD 74.2); L/W ratio = 1.3-2.2 (1.8, SD 0.3); stylet 28.4-30.7 μm (29.4 μm , SD 0.8); dorsal esophageal gland orifice 5.2-6.0 μm (5.6 μm , SD 0.3) from the base of stylet.

Holotype (female): Length (including neck) 635 μm ; width 330 μm ; L/W ratio = 1.9; stylet 29.0 μm ; dorsal esophageal gland orifice 5.8 μm from base of stylet.

Description: Body white to very light brown, basically lemon-shaped with protruding neck and vulva. Cuticle 12-15 μm thick with heavily punctate to granular surface, generally obscuring cuticular pattern. Head slightly set off, with two annules, the second being larger (Fig. 6). Stylet strong, slight dorsal curvature, and with well-developed stylet knobs. Esophageal region appearing about as illustrated (Fig. 6), with prominent excretory pore commonly at base of neck. Vulval slit small, averaging 17 μm (16-19). Anus small but distinct, located about 10% of body length from vulva.

CYSTS (40): Length (including neck) 485-806 μm (656, SD 83); width 286-581 μm (448, SD 81); L/W ratio = 1.2-1.9 (1.5, SD 0.18).

Description: Cysts light brown to brown in color, basically lemon-shaped, with protruding neck and vulva (Fig. 10); abullate, circumfenestrate (Fig. 7). Excretory pore near base of neck. Fenestra diameter averaging 34 μm (31-36). Vulval denticles (see discussion in later section and Fig. 43, 44, 46, 47, 48, 49, 50, 52) located about 20 μm below upper surface of fenestra and occurring singly, in small clusters, or as a partial ring. Vulval denticles measure approximately 5-10 μm in length and 3-6 μm in width. External cyst wall pattern at mid-body consisting of basically straight to wavy lines extending around cyst at right angles to long axis of cyst and frequently broken by short oblique or vertical lines (Fig. 9). Punctuation often present on cysts, randomly arranged, and sometimes heavy. Anus distinct, without surrounding pattern, and located about 10% of cyst length from posterior end.

MALES (20): Length 1315-1708 μm (1503, SD 125); a = 30-45 (37, SD 4.2); b = 7.3-9.8 (8.8, SD 0.7); c = 199-505 (321, SD 97);

stylet 27.8-31.0 μm (29.4, SD 1.4); dorsal esophageal gland orifice 5.5-8.0 μm (6.8, SD 1.1) from base of stylet; spicules 39-46 μm (43, SD 2); gubernaculum 10-15 μm (13, SD 2.2); tail length 2-8 μm (5.0, SD 1.7).

Allotype (male): Length 1436 μm ; a = 36; b = 6; c = 552; tail length 2.6 μm ; stylet 29.8 μm ; outlet of dorsal esophageal gland from base of stylet 6.4 μm ; spicules 42.5 μm ; gubernaculum 12.6 μm .

Description: Body slender, vermiform, tapering slightly at both extremities. Cuticular annulation prominent, subcuticular annulation less distinct but twice as numerous. Lateral field without areolation, with four incisures, and about 1/6 of mid-body width, the latter measuring 36-45 μm (40, SD 2.3). Head set off, generally with six annules. Cephalic framework heavily sclerotized. Stylet, knobs, and small cephalids (anterior and posterior) commonly appearing as illustrated (Fig. 2). Center of the ellipsoidal median bulb 101-144 μm (116, SD 11) from anterior end. Excretory pore located 2-5 annules posterior to distinct hemizonid. Testis one. Spicules arcuate, with bifid tips. Tail very short, shaped about as illustrated (Fig. 1).

SECOND-STAGE LARVAE (30): Length 446-620 μm (554, SD 38); a = 20-28 (24, SD 2.0); b = 2.4-4.7 (3.9, SD 0.7); c = 8.8-11.2 (9.8, SD 0.6); stylet 25-28 μm (27, SD 0.9); dorsal esophageal gland orifice 5-7 μm (6, SD 0.6) from base of stylet; tail 49-64 μm (56, SD 4.9); hyaline tail terminal 23-28 μm (25, SD 1.5); caudal ratio A = 2.5-3.3 (2.9, SD 0.2); caudal ratio B = 7-10 (8.7, SD 1.2). For details on caudal ratios, see Golden and Cobb (4).

Description: Body vermiform, tapering at both extremities, more so posteriorly. Distinct cuticular annulation; subcuticular markings less distinct and twice as frequent. Lateral field without areolation, consisting of four incisures, about 5-6 μm in width. Widest part of body measures 21-26 μm (23.5, SD 1.3). Head with cephalic sclerotization and slightly set off, bearing five annules. Stylet, knobs, cephalids, and anterior portion appearing about as illustrated (Fig. 4, 5). Median bulb center 69-90 μm (80, SD 6.3) from anterior end. Excretory pore posterior and adjacent to distinct hemizonid. Tail commonly appearing as illustrated (Fig. 3), with finely rounded

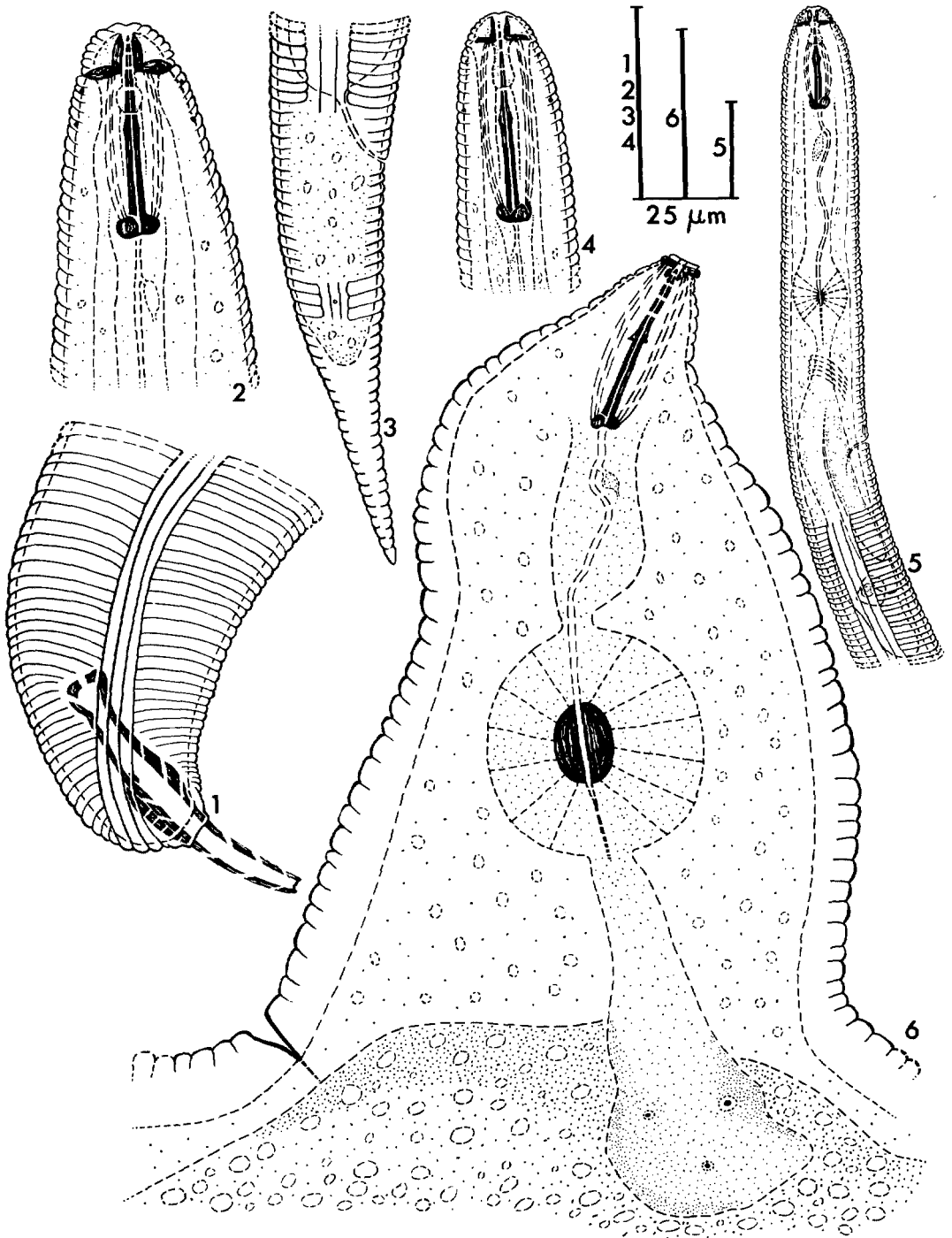


FIG. 1-6 Drawings of *Heterodera thornei* n. sp. 1-2) Male. 3-5) Larvae. 6) Anterior region of female.

terminus. Phasmids very small, located about middle of tail.

EGGS (20, nonsegmented or with only limited divisions): Length 123-134 μm (129, SD 2.6); width 50-57 μm (53, SD 2.1); L/W

ratio = 2.3-2.6 (2.4, SD 0.09). Egg shell as seen under optical microscope (oil immersion) covered with small but discrete punctations (Fig. 8); under SEM, these resemble microvilli (Fig. 38, 39). Within

developed egg, larvae are folded 4.5 to 5.0 times.

HOLOTYPE (female): Collected 3 February 1950 by D. J. Raski. Slide T-271t, United States Department of Agriculture Nematode Collection (USDANC), Beltsville, Maryland, USA.

ALLOTYPE (male): Slide T-272t. Same data as holotype. USDANC, Beltsville, Maryland, USA.

PARATYPES: Males, females, cysts, larvae, and eggs: USDA Nematode Collection, Beltsville, Maryland; and University of California Nematode Survey Collection (UCNSC), Davis, California, USA.

TYPE HOST AND LOCALITY: Roots of Miner's lettuce [*Montia perfoliata* (Donn ex. Willd.) Howell] growing in a Persian walnut orchard near San Jose, California.

DIAGNOSIS: *Heterodera thornei* n. sp. is readily distinguished from all other species of the *H. "cacti" group* by these larval characters: longer stylet, greater body length, and longer tail. The stylet length of males and females of *H. thornei* is also far greater than those of other species in this group, and in addition, egg shell punctation is present though somewhat finer than that in *H. cacti*, the only other described species with such markings on the egg shell.

DISTRIBUTION: For many years, known only from walnut orchards near San Jose and Santa Clara, California. Late in 1975, cysts collected from a cherry orchard at Linden, California by Dr. Adam Weiner, Division of Plant Industry, Sacramento, California were identified by the senior author as *H. thornei* n. sp. So far, Miner's lettuce is the only known host.

The species name is given in honor of the late eminent nematologist, Professor Gerald Thorne.

The common name, "Thorne's cyst nematode" is suggested for *H. thornei* n. sp.

Heterodera weissii Steiner, 1949

This species was briefly described by Steiner (14) in 1949 from specimens obtained from *Polygonum pensylvanicum* L. at the Plant Industry Station (now Beltsville Agricultural Research Center-West), Beltsville, Maryland. In 1931, Steiner (13) had reported *H. schachtii* Schmidt, 1871 on

P. pensylvanicum and *P. punctatum* Ell. growing near Broad Run between Tysons Corner and Leesburg, Virginia; but in the early 1950s, Steiner advised the senior author that this nematode, thought then to be *H. schachtii*, was actually *H. weissii*.

The present work with *H. weissii* was initiated to update the description and to establish types for this species. Steiner's original material, although in poor condition, was used for the selection of types, while the redescription and drawings were supplemented to some extent by new material collected from the type host and locality at Beltsville.

Our observations, in general, agree with those of Steiner on this species. However, he reported the male stylet to be about "28-29 μm "; in the present study the male stylet was found to average 24.3 μm , whereas Tarjan and Sasser (16) in 1953 reported its average length as 24.7 μm . This shorter length is, therefore, a more accurate measurement of the male stylet.

FEMALES (20): Length (including neck) 408-688 μm (503, SD 76); width 201-408 μm (278, SD 65); L/W ratio = 1.4-2.3 (1.4, SD 1.9); stylet 21.8-24.3 μm (22.8, SD 0.53); dorsal esophageal gland orifice 4.5-5.6 μm (5.2, SD 0.34) from base of stylet.

Holotype (female): Length 605 μm ; width 405 μm ; L/W ratio = 1.5; stylet 22.6 μm ; dorsal esophageal gland orifice 5.2 μm from base of stylet.

Description: Body pearly-white, basically lemon-shaped, with protruding neck and vulva. Cuticle about 12 μm thick; randomly arranged punctation on surface, often giving granular appearance and sometimes obscuring external cuticular pattern, which is essentially as described for the cysts. Head (bearing two annules, the second being larger) set off from body. Stylet rather delicate with small distinct knobs sloping posteriorly. Esophageal glands and excretory pore commonly located at base of neck as illustrated (Fig. 15). Vulva distinct, with slit measuring 13-20 μm (15, SD 1.9). Anus small, inconspicuous, located about 10% of body length from posterior end.

CYSTS (20): Length (including neck) 385-750 μm (598, SD 87); width 230-460 μm (350, SD 68); L/W ratio = 1.2-2.3 (1.7, SD 0.3); diameter of fenestra (on longest axis) 29-38 μm (34, SD 2.8).

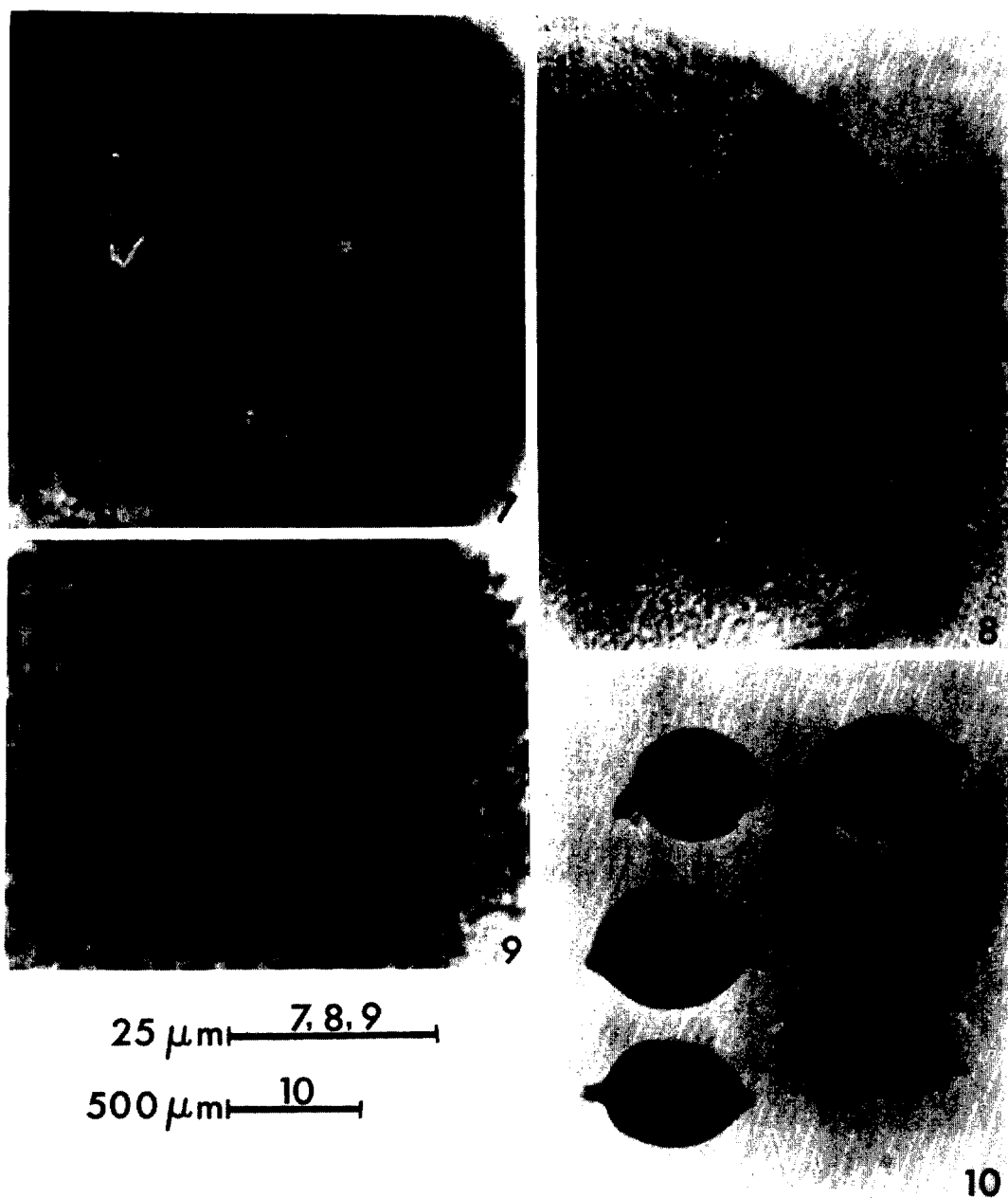


FIG. 7-10. Photomicrographs of *Heterodera thornei* n. sp. 7) Fenestra of a cyst. 8) Portion of egg showing punctation of egg shell. 9) External cyst wall pattern. 10) Whole cysts.

Description: Cysts abullate, circumfenestrate, light brown to brown in color, basically lemon-shaped, and with protruding neck and vulva (Fig. 16, 19). Excretory pore situated near base of neck. Vulval denticles about 16-20 μm below fenestral surface and measure approximately 6-11 μm in length and 3-5 μm in width at their base. Vulval denticles might occur singly at

random, in small clusters, as a partial ring, or occasionally as a complete ring (Fig. 48, 49, 50). External cyst wall pattern at mid-body consists of basically straight to wavy lines extending around the cysts at right angles to the long axis of the cyst and commonly broken by short oblique or vertical lines (Fig. 18). Rather fine punctation, arranged randomly, often present on cyst

wall. Anus distinct though small, without a surrounding pattern; located about 10% of cyst length from posterior end.

MALES (20): Length 943-1240 μm (1034, SD 69); a = 27-33 (31, SD 2.1); b = 5.1-6.7 (6.0, SD 0.9); c = 346-991 (631, SD 112); stylet 22.5-25.2 μm (24.2, SD 0.9); dorsal esophageal gland orifice 4.5-5.6 μm (4.8, SD 0.4) from base of stylet; spicules 30.8-33.6 μm (32.4, SD 0.99); gubernaculum 9.5-11 (10, SD 0.5); tail length 1.1-2.8 μm (1.6, SD 0.5).

Allolectotype (male): Length 1040 μm ; a = 32; b = 5.6; c = 928; stylet = 24.6 μm ; body width 31 μm .

Description: Body cylindrical, elongate, and tapering gradually at each end. Head offset, bearing 5-6 annules. Cuticular annulation distinct, annules approximately 1.8 μm wide; subcuticle with annules about one-half this size but twice as numerous. Lateral field 5.6-6.2 μm (5.7) in width, consisting of 4 incisures forming 3 bands of equal width on most of body, and not areolated except in extreme anterior portion. Mid-body width measures 29-36 μm (33, SD 2.1). Cephalic framework heavily sclerotized; stylet strong with rather rounded, prominent knobs. Center of median bulb 45-60 μm (51, SD 3.4) from anterior end. Hemizonid small but distinct, usually located 5-6 annules anterior to excretory pore; hemizonion smaller, about 10 annules posterior to excretory pore. Esophageal region appearing about as illustrated (Fig. 11). Testis one. Spicules arcuate, singly notched at tips. Tail extremely short (Fig. 12), somewhat variable in shape. Small phasmids near tail terminus.

SECOND-STAGE LARVAE (20): Length 372-420 μm (407, SD 12); a = 18-22 (20, SD 0.9); b = 2.3-3.5 (2.6, SD 0.1); c = 8.4-9.5 (8.9, SD 0.3); stylet 19.6-21.8 μm (20.4, SD 0.5); dorsal esophageal gland orifice 4.5-5.6 μm (5.3, SD 0.3) from base of stylet; tail 43-50 μm (45.9, SD 1.9); hyaline tail terminal 17-24 μm (20.2, SD 1.9); caudal ratio A = 3.0-3.9 (3.5, SD 0.3); caudal ratio B = 6.6-10.5 (8.4, SD 1.2).

Description: Body cylindrical, elongate, tapering especially to posterior end. Head, bearing 5 indistinct annules, offset from body. Cuticular annulation of body distinct, annules measuring about 1.4 μm at mid-body; subcuticular annules less distinct and

twice as numerous. Lateral field without areolation except anteriorly; composed of 4 incisures and averages 3.5 μm in width at mid-body. Cephalic framework heavily sclerotized. Stylet strong, with prominent knobs concave on anterior surface. Center of median bulb 35-42 μm (38, SD 1.6) from anterior end. Hemizonid prominent, located anterior and adjacent to excretory pore; hemizonion usually about 8-10 annules posterior to the latter. General esophageal region commonly appearing as illustrated (Fig. 14). Tail tapering to a fine, rounded terminus, with annulation continuing to terminus, sometimes giving a bead-like effect (Fig. 13). Phasmids small, indistinct; located in center of lateral field about mid-way on tail.

EGGS (20) (Larvae within): Length 96-106 μm (101, SD 2.9); width 40-44 μm (42, SD 0.8); L/W ratio = 2.3-2.6 (2.4, SD 0.09). Egg shells hyaline, without visible markings, as seen with both an optical microscope (Fig. 17) and a scanning electron microscope (Fig. 41).

HOLELECTOTYPE (female): Collected by Dr. G. Steiner and Dr. F. Weiss on 8 June 1943 at Plant Industry Station (now Beltsville Agricultural Research Center-West), Beltsville, Maryland. Slide T-50t, United States Department of Agriculture, Beltsville, Maryland, USA.

ALLOLECTOTYPE (male): Same data as hololectotype. Slide T-51t. USDANC, Beltsville, Maryland, USA.

PARALECTOTYPES: Females, males, cysts, larvae, and eggs; same data and collection as hololectotype.

Females, males, cysts, larvae, and eggs from the type host and locality (topotype) are deposited with: USDANC, Beltsville, Maryland; UCNSC, Davis; Canadian National Collection of Nematodes, Ottawa; Rothamsted Experimental Station Nematology Collection, Harpenden, Herts., England; National Nematode Collection, Indian Agricultural Research Institute, New Delhi; Collection of the Nematology Department, Landbouwhogeschool, Wageningen, The Netherlands; Nematology Collection, Instituut voor Dierkunde, Rijksuniversiteit, Gent, Belgium.

TYPE HOST AND LOCALITY (designated by original author): Roots of knot-weed, *Polygonum pensylvanicum* L., growing

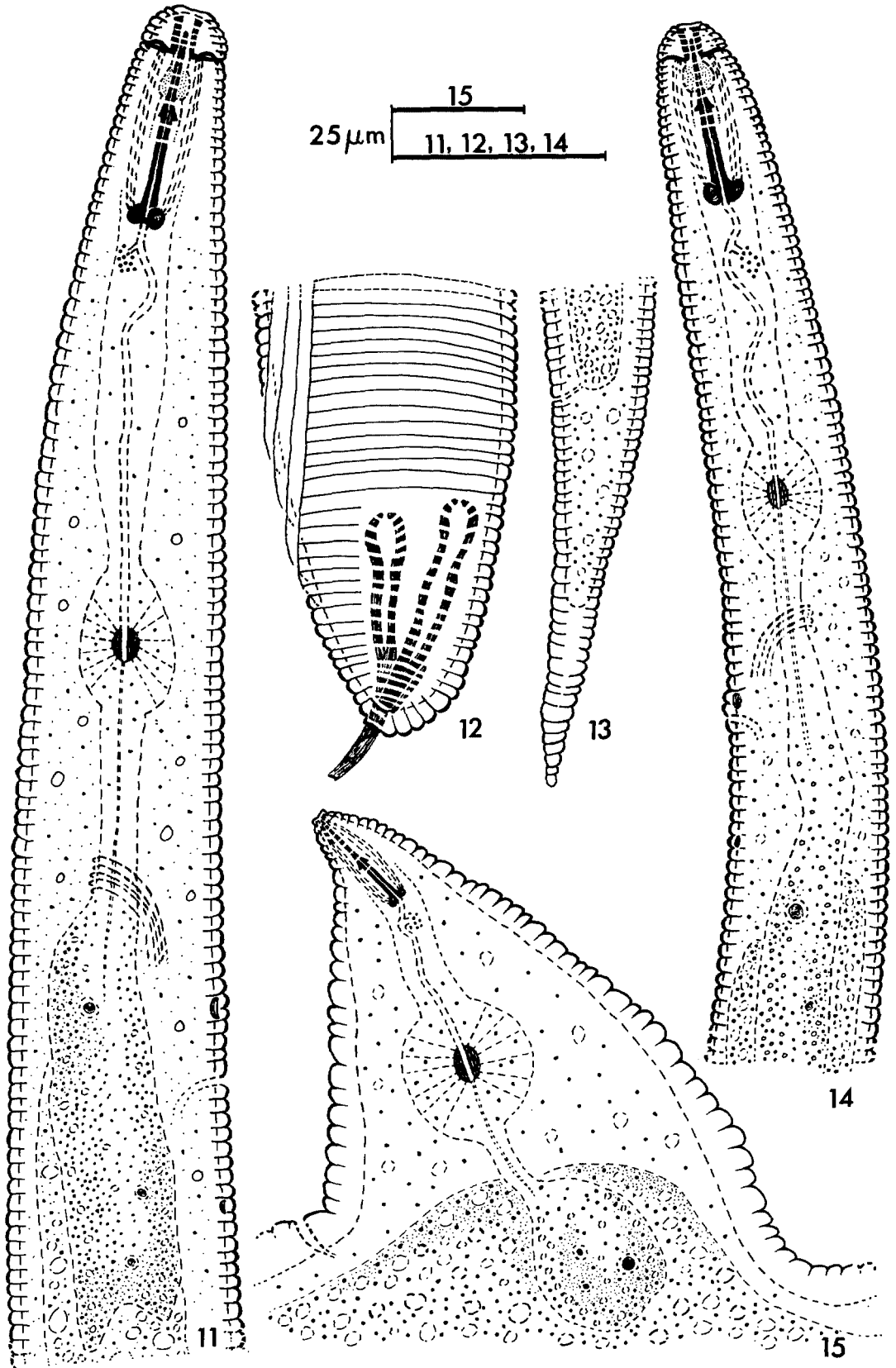


FIG. 11-15. Drawings of *Heterodera weissi*. 11-12) Male. 13-14) Larva. 15) Anterior portion of female.

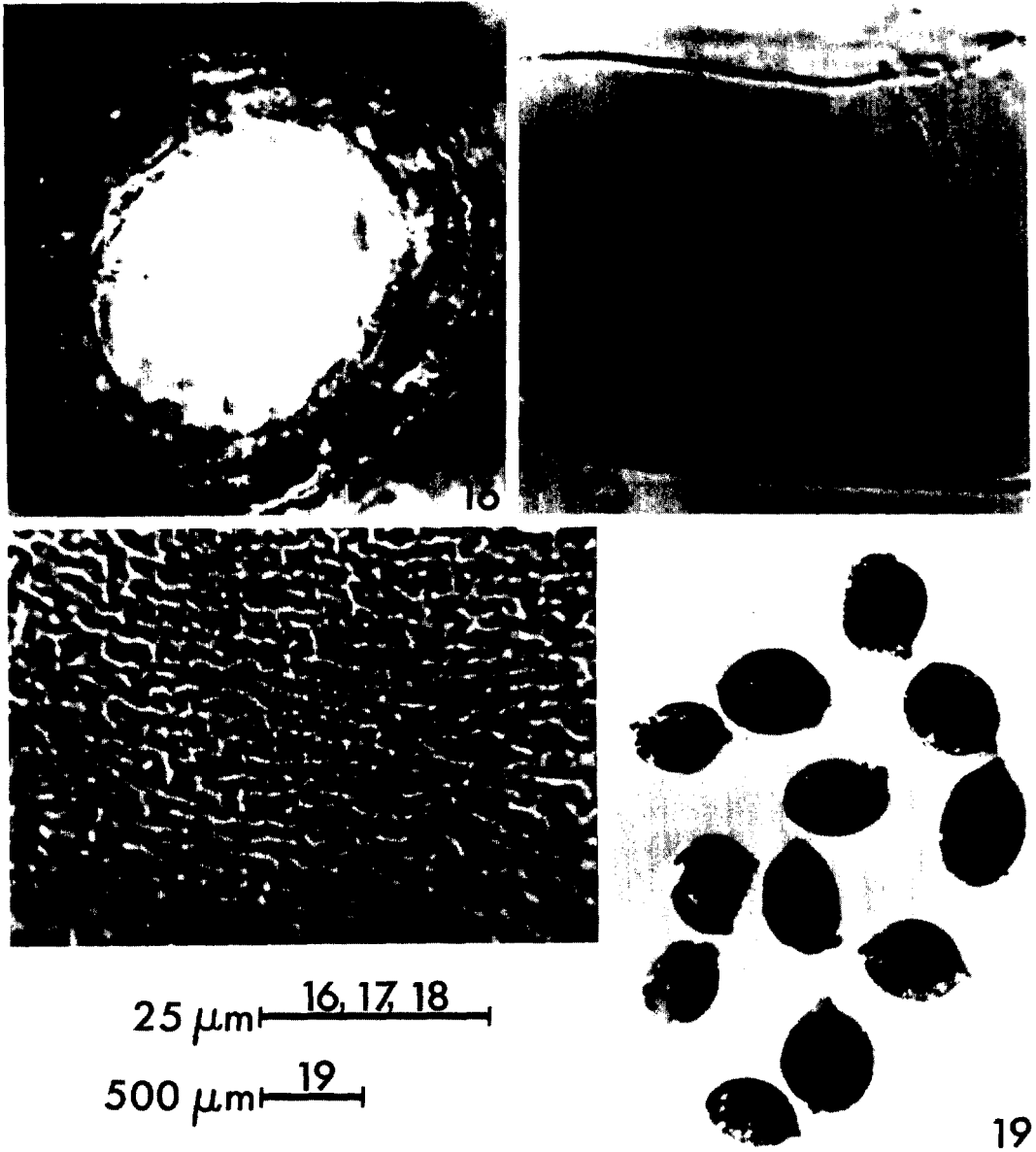


FIG. 16-19. Photomicrographs of *Heterodera weissi*. 16) Fenestra of a cyst. 17) Portion of egg showing clear egg shell. 18) Cyst wall pattern near mid-body. 19) Whole cysts.

near the steam plant at Plant Industry Station (now Beltsville Agricultural Research Center-West), Beltsville, Maryland.

DIAGNOSIS: *Heterodera weissi* is most closely related to *H. amaranthi* but differs mainly in having a longer larval tail and tail terminal ($46\ \mu\text{m}$ and $20\ \mu\text{m}$ vs $35\ \mu\text{m}$ and $15\ \mu\text{m}$, respectively, for *H. amaranthi*). Though of an indefinite nature, the cysts of *H. weissi* are lighter in color than those of *H. amaranthi* which are commonly dark

brown to almost black. Hyaline egg shells without punctation and larval stylet knobs with concave anterior surface distinguish *H. weissi* from *H. cacti* which have heavily punctate egg shells and convex stylet knobs in larvae. (See key to the species also for further diagnostic details.)

DISTRIBUTION: Ontario and Quebec, Canada [Mulvey (10)]. In USA: New Jersey [Hutchinson et al. (6)]; Beltsville, Maryland [Steiner, (14)]; and from the

Sample Records Division of the USDA Nematode Collection these additional locations, based on one to many samples: Arkansas, Florida, Illinois, Iowa, Maryland, Michigan, Missouri, New York, North Carolina, and Virginia.

H. weissi is so far known only from various species of *Polygonum* as hosts.

The common name "knotweed cyst nematode," as used to some extent already, seems appropriate for *H. weissi*.

Heterodera amaranthi Stoyanov, 1972

This species was described in 1972 by D. Stoyanov of the Plant Protection Institute, Sofia, Bulgaria, while he was working as a collaborator in the Instituto de Mejoramiento de Plantas de la Academia de Ciencias de Cuba, Santiago de las Vegas, Havana, Cuba (15). He designated *Amaranthus viridis* L. as the type host and Terrenos del Instituto de Investigaciones Tropicales, Santiago de las Vegas, Havana, Cuba as the type locality. His description (in Spanish) included drawings and photomicrographs of various stages of the nematode.

Although described only four years ago, *H. amaranthi* has an interesting history going back about 20 years. In 1957, the late George J. Rau, then with Nematology Section, ARS, U.S. Department of Agriculture, Sanford, Florida, wrote in his annual report (unpublished) the following statement about nematodes in the area of Zellwood, Florida near Sanford: "The predominating nematode on the virgin muck which is covered with the sawgrass is a new species of cyst nematode of the genus *Heterodera* belonging to the *cacti* group." He found cysts of this species associated with various vegetables grown in the Zellwood area but the actual host eluded him for some time. About 1960, Rau determined the host of this new cyst species to be spiny amaranth, *Amaranthus spinosus* L., but he did not describe this form before his untimely death in 1970. In 1971, G. Fassuliotis, formerly in Sanford, Florida and now at Nematology Investigations, U.S. Vegetable Breeding Laboratory, Charleston, South Carolina, kindly sent to the senior author for description Rau's specimens of this *Heterodera* (and the annual report referred

to earlier). Later, in April 1974, through the efforts and cooperation of H. Rhoades, Agricultural Research and Education Center, Sanford, Florida, additional specimens (from *A. spinosus* and *A. retroflexus* L.) in better condition for species description were obtained. About the same time, the senior author received from A. C. Tarjan, University of Florida, AREC, Lake Alfred, Florida, the publication by Stoyanov describing *H. amaranthi*. It was then evident that the *Heterodera* species found by Rau in 1957 in Florida was the same as that described in Cuba as *H. amaranthi* in 1972. However, through the assistance of Tarjan again and the cooperation of Stoyanov who was then back in Sofia, Bulgaria, some type specimens of *H. amaranthi* were obtained and examined as a further check.

The measurements of various stages and brief description presented below are based mainly on specimens collected by H. Rhoades near Zellwood, Florida and on those grown on *Amaranthus retroflexus* in the greenhouse at Sanford, Florida. In addition, measurements of some paratype larvae are included.

FEMALES (12): Length (including neck) 404-688 μm (563, SD 98); width 181-464 μm (366, SD 87); L/W ratio = 1.1-2.2 (1.6, SD 0.3); stylet 24.9-26.6 μm (25.3, SD 1.5); dorsal esophageal gland orifice 4.3-5.2 μm (4.8, SD 0.5) from base of stylet; vulval slit length 14-16 μm (15, SD 1.2).

In gross shape and morphology, the females resemble those of *H. weissi*. However, in our specimens, the stylet length averages 25.3 μm , whereas in *H. weissi* it averages 22.8, an important difference of 2.5 μm . In some cases, protruded stylets were found and measured to verify these measurements because such a difference would be of value as a character in distinguishing these two species. Unfortunately, there is a discrepancy of 1.9 μm in our female stylet length measurements and those given in the original description of *H. amaranthi*. Stoyanov (15) gave the stylet length as 23.4 μm , based on four specimens, but type or other female specimens of *H. amaranthi* from Cuba have not been available for further examination of this point.

CYSTS (25): Length (including neck) 525-774 μm (642, SD 62); width 370-550 μm

(472, SD 54); L/W ratio = 1.1-1.7 (1.4, SD 0.12); diameter of fenestra (on longest axis of fully fenestrated cysts) 25-38 μm (31, SD 3.6).

Cysts are abullate, circumfenestrate, and basically lemon-shaped with protruding neck and vulva (Fig. 20, 23). Color of cysts ranges from light to dark brown, sometimes appearing almost black. Cyst wall pattern in middle half of body consists of essentially straight to wavy lines extending around the

cysts at right angles to the long axis of the cyst and generally broken by short oblique or vertical lines (Fig. 22) typical of the "*H. cacti* group" species. Vulval denticles about 20 μm below upper surface of fenestra, about 5-10 μm in length, approximately 3-5 μm wide at their base. The denticles occur singly in a random way, in small groups, as a partial ring, or occasionally as a complete ring (Fig. 45 at fenestra surface; Fig. 46 shows denticles below surface). Anus dis-

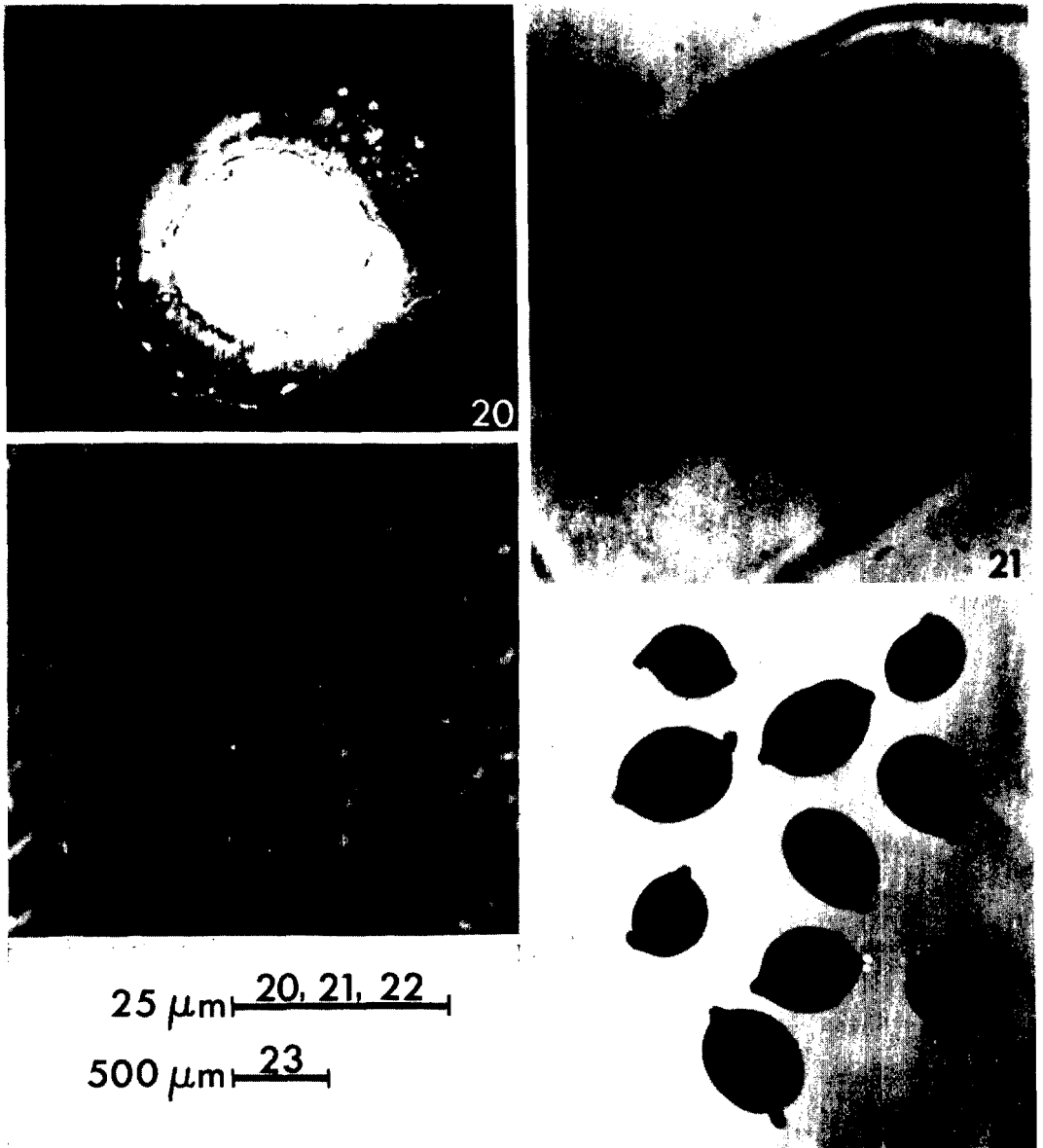


FIG. 20-23. Photomicrographs of *Heterodera amaranthi*. 20) Fenestra of a cyst. 21) Portion of egg showing clear egg shell. 22) Cyst wall pattern near mid-body. 23) Whole cysts.

tinct, without surrounding pattern, located about 10% of body length from posterior end.

MALES (25): Length 792-1195 μm (974, SD 85); a = 31-47 (38, SD 5); b = 5.4-6.8 (6.2, SD 0.1); c = 302-1244 (558, SD 274); stylet 24.7-26.4 μm (25.6, SD 0.5); dorsal esophageal gland orifice 2.6-4.3 μm (3.7, SD 0.6) from the base of stylet; spicules 27-33 μm (30.5, SD 1.4); gubernaculum 8-12 μm (10, SD 1.4).

These measurements of our Florida specimens in general correspond well with those in the original description. However, the gubernaculum length here is larger than that given by Stoyanov (15) as "5-7 μm ." As indicated by our "c" value, the tail, measuring 0.9-3.4 μm (1.8, SD 0.6), is extremely short. Spicules, forming bifid tips, were seen to be singly notched.

SECOND-STAGE LARVAE from Florida (25, hatched from cysts): Length 340-406 μm (374, SD 15); a = 16-20 (18, SD 1); b = 2.5-3.0 μm (2.8, SD 0.2); c = 9.7-11.8 (10.6, SD 0.6); stylet 20.2-21.3 μm (20.7, SD 0.4); dorsal esophageal gland orifice 3.9-5.1 μm (4.5, SD 0.4) from base of stylet; tail 32-40 μm (35, SD 2.2); hyaline tail terminal 11-18 μm (15, SD 1.9); caudal ratio A = 1.6-2.6 (2.1, SD 0.3); caudal ratio B = 3.3-6.9 (4.9, SD 1); width of head 8.5-9.4 μm (8.7, SD 0.4); height of head 3.4-4.3 μm (3.6, SD 0.4); w/h ratio of head = 2-2.8 (2.5, SD 0.3); center of median bulb from anterior end 52-64 μm (58, SD 3).

Paratype second-stage larvae from Cuba (17, cracked from eggs of two cysts): Length 343-402 μm (368, SD 18); a = 15-23 (18, SD 2.4); b = 2.5-2.9 (2.7, SD 0.1); c = 9.1-12.4 (10.5, SD 1.0); stylet 20.4-21.3 μm (20.7, SD 0.4); outlet of dorsal esophageal gland from base of stylet 4.0-5.2 μm (4.6, SD 0.4); tail 31-40 μm (35, SD 2.5); hyaline tail terminal 12-16 μm (14, SD 1.0); caudal ratio A = 1.9-2.4 (2.0, SD 0.2); caudal ratio B = 3.5-4.6 (4.2, SD 0.3); width of head 8.5 μm ; height of head 3.4 μm ; w/h ratio of head 2.5; center of median bulb from anterior end 54-60 μm (56, SD 1.9).

Our measurements of Florida specimens and paratypes from Cuba are essentially identical in most respects. However, in both of these larval populations, our measurements of two characters differ considerably from those given in the original description.

The total body length and stylet length as given by Stoyanov are 372-447 μm (409) and 21.6-24 μm (23), respectively. The difference in body length might be due in part at least to fixation or perhaps time of collection of specimens. However, these factors would not account for the relatively large difference of 2.3 μm in stylet length between our specimens and those of Stoyanov. In trying to resolve this difference, we examined Florida and paratype specimens under three different, accurately calibrated microscopes. In all cases, the length of the stylet was found to be as we gave previously (20.7 μm , average). Consequently, we feel that our measurements are more accurate representations of the actual stylet length in *H. amaranthi*.

EGGS (25, larvae within): Length 88-108 μm (96, SD 5); width 43-52 μm (48, SD 2.7); L/W ratio = 1.8-2.3 (2.0, SD 0.2). Egg shells hyaline although often appearing somewhat yellowish, without visible markings as seen with both an optical microscope (Fig. 21) and a scanning electron microscope (Fig. 40). Larvae commonly folded 4.25 times within the egg.

TYPE HOST AND LOCALITY (designation by original author): *Amaranthus viridis* L. at Terrenos del Instituto de Investigaciones Tropicales, Santiago de las Vegas, Havana, Cuba.

DIAGNOSIS: *Heterodera amaranthi* is most closely related to *H. weissi* but differs primarily in having a shorter larval tail and hyaline tail terminal (35 μm and 15 μm vs 46 μm and 20 μm , respectively, for *H. weissi*). The cysts of *H. amaranthi* are generally darker in color than those of *H. weissi*, the former being rather dark brown with some appearing almost black, although this is an indefinite character. The basically hyaline egg shells without markings and larval stylet knobs with concave anterior surface separate *H. amaranthi* from *H. cacti* which has heavily punctate egg shells and convex stylet knobs in larvae. (See key to the species for further diagnostic details also.)

DISTRIBUTION: Havana, Cuba [Stoyanov (15)]. In USA: (From Sample Records Division, USDA Nematode Collection): Florida (near Zellwood and Sanford); Illinois (in Union County); Missouri (near

St. Charles); and Tennessee (near Nashville).

H. amaranthi is known only from *Amaranthus viridis*, *A. spinosus*, and *A. retroflexus*. We propose the common name, "amaranth cyst nematode" for *H. amaranthi*.

Heterodera cacti Filipjev &

Schuermans Stekhoven, 1941

syn: *Heterodera schachtii* of Adam, 1932

This well known species of cyst nematodes is widely distributed, and like *Heterodera weissi*, has been recognized for well over 40 years. *Heterodera cacti* was proposed as a new species by Filipjev and Schuurmans Stekhoven (2) on the basis of data and description by Adam (1) of a cyst nematode which he had called *H. schachtii* Schmidt, 1871. This nematode was collected by Adam on cactus plants identified as *Phyllocactus akkermannii* and *Cereus speciosus* from Maartensdijk, near Utrecht, The Netherlands.

In the present study, an ample supply of good male and female specimens of *H. cacti* was not available for extensive examination. Consequently, our data are based on various populations of cysts, eggs, and larvae, the latter two stages being of most importance in identification of this species.

cysts (15, from Yugoslavia): Length (including neck) 498-662 μm (587, SD 48); width 387-550 μm (475, SD 57); L/W ratio = 1.1-1.4 (1.3, SD 0.13); diameter of fenestra (on longest axis) 29-48 μm (38, SD 5.5).

Cysts are abullate, circumfenestrate, light to dark or reddish brown in color, basically lemon-shaped, and with protruding neck and vulva (Fig. 29). External cyst wall pattern consists of essentially straight to wavy lines encircling the cysts at right angles to the long axis of the cyst and generally broken or interrupted by short oblique or vertical lines (Fig. 27). Outer cyst surface often granular, with heavy, random punctation. Vulval denticles generally present, about 20 μm below fenestra surface; often obscure, occurring singly at random or sometimes in small clusters (Fig. 44). Fenestra (Fig. 24) of variable size and shape. Anus distinct, without a surrounding pattern, and about 10% of cyst length from posterior end.

SECOND-STAGE LARVAE (50, from Italy): Length 364-453 μm (409, SD 18); a = 15-20 (18, SD 1.5); b = 2.1-3.1 (2.6, SD 0.3); c = 7.8-10.1 (8.9, SD 0.6); stylet 22.4-24.6 μm (23.5, SD 0.6); dorsal esophageal gland orifice 3.4-4.6 μm (3.8, SD 0.3) from base of stylet; tail 36-52 μm (46, SD 3.6); hyaline tail terminal 12-19 μm (15.7, SD 1.8); caudal ratio A = 1.5-3.0 (2.3, SD 0.3); caudal ratio B = 2.7-6.6 (4.5, SD 0.8); width of head 6.2-8.4 μm (6.9, SD 0.5); height of head 2.8-4.5 μm (3.5, SD 0.4); w/h ratio of head averaging 1.9; center of median bulb 26-38 μm (33, SD 2.8) from anterior end.

Specimens from Mexico (25): Length 376-451 μm (418, SD 38); a = 17-21 (19, SD 2.2); b = 2.7; c = 9.5-10.7 (9.9, SD 0.4); stylet 22.4-24.0 μm (23.4, SD 0.4); dorsal esophageal gland orifice 4.5-6.1 μm (5.0, SD 0.5) from base of stylet; tail 34-48 μm (43, SD 3.6); hyaline tail terminal 14-21 μm (19, SD 2.2); caudal ratio A = 2-3 (2.4, SD 0.3); caudal ratio B = 3.4-7.6 (5.2, SD 1.3); width of head 6.2-8.4 μm (7.0, SD 0.5); height of head 2.8-4.5 μm (3.5, SD 0.5); w/h ratio of head averaging 2.0; center of median bulb 35-42 μm (39, SD 1.9) from anterior end.

Specimens from Georgia, USA (23): Length 412-451 (432, SD 17); a = 18-21 (19.4, SD 1.0); b = 2.8; c = 9.5-10.7 (9.9, SD 0.4); stylet 22.4-24.0 μm (22.9, SD 0.5); dorsal esophageal gland orifice 3.4-4.5 μm (3.8, SD 0.3) from base of stylet; tail 39-48 μm (44, SD 2.2); hyaline tail terminal 14.5-19.6 μm (17.2, SD 1.2); caudal ratio A = 2-3 (2.4, SD 0.2); caudal ratio B = 4.3-8.8 (6.8, SD 1.4); width of head 6.2-7.8 μm (7.2, SD 0.5); height of head 2.2-3.4 μm (2.6, SD 0.4); w/h ratio of head averaging 2.7; center of median bulb 38-44 μm (40, SD 1.7) from anterior end.

These populations, although from diverse areas, measure essentially the same in all respects. Measurements of a population of nine larvae in fern soil from Cali, Colombia were the same as those described previously, but they are not included because of the limited number of specimens involved.

Description: Larval body of *H. cacti* is cylindrical, elongate, and tapers more posteriorly. Slightly offset head (Fig. 25), bearing 5 annules, the 2 anterior ones often

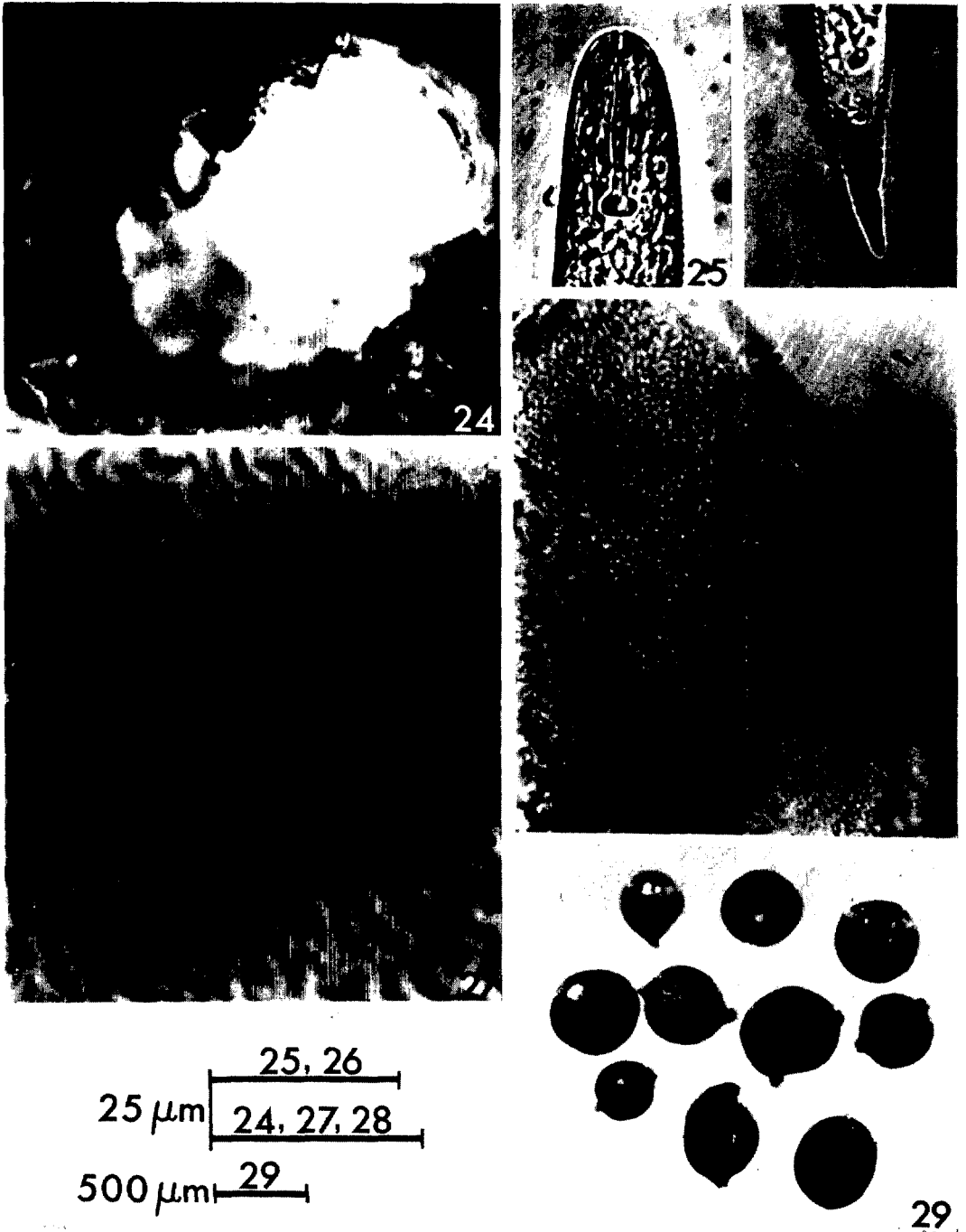


FIG. 24-29. Photomicrographs of *Heterodera cacti*. 24) Fenestra of a cyst. 25) Stylet and head of larva. 26) Tail portion of larva. 27) Cyst wall pattern near mid-body. 28) Portion of egg showing heavy punctation on egg shell. 29) Whole cysts.

indistinct. Lateral field is without areolation except far anteriorly, composed of 4 incisures, and measures about 1/5 body width. Tail tapering, appearing about as illustrated (Fig. 26), with hyaline tail

terminal generally being shorter than stylet length. Phasmids small, located about mid-way on tail.

EGGS (25, larvae within, from Italy): Length 102-112 μm (107, SD 2.5); width

46-53 μm (49, SD 1.9); L/W ratio = 1.9-2.3 (2.2, SD 0.08). Egg shells as seen under optical microscope (oil immersion) heavily punctate (Fig. 28); under scanning electron microscope, the punctations resemble microvilli (Fig. 36, 37). Larvae generally folded 5 times within the egg.

Type specimens, host, and locality have not been specifically designated previously and we feel it would be inappropriate to do

so at this time in the absence of original or valid topotype specimens.

DIAGNOSIS: *Heterodera cacti* is most closely related to *H. weissi* and *H. amaranthi* but differs primarily in having (1) egg shells heavily punctate vs. shells without visible markings in the latter two species; and (2) longer larval stylet (averaging 23.0 μm) with stylet knobs convex anteriorly vs. larval stylet averaging 20.4 μm

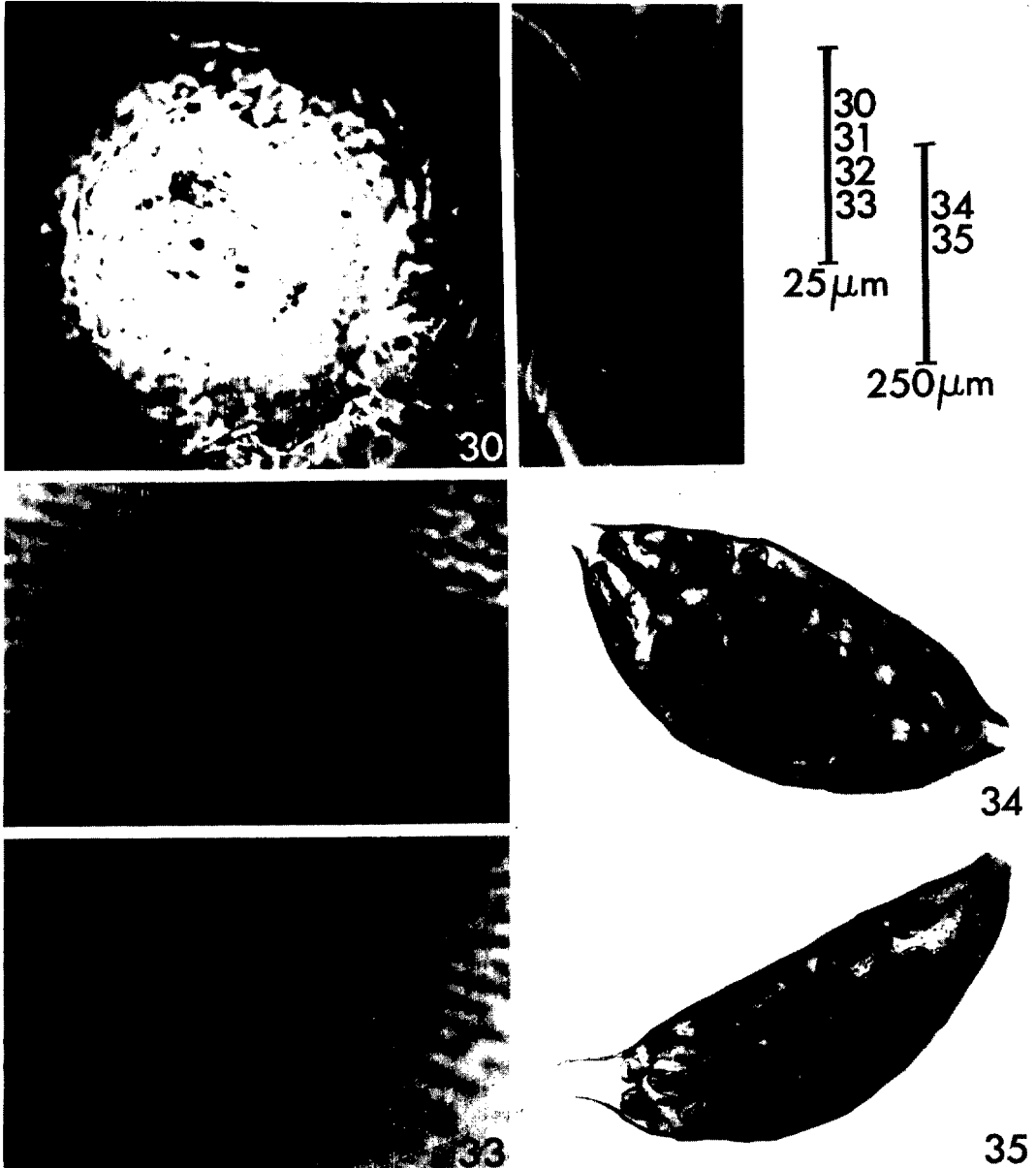


FIG. 30-35. Photomicrographs of *Heterodera estonica*. 30) Fenestra of a cyst. 31) Tails of two larvae. 32-33) Cyst wall pattern near mid-body. 34-35) Two whole cysts.

for *H. weissi* and 20.7 for *H. amaranthi*, with stylet knobs in both of the latter two species being concave anteriorly. Also, *H. cacti* differs further from *H. weissi* in having a hyaline tail terminal shorter (averaging 17.0 μm) than the stylet length (23.0 μm), whereas in *H. weissi* the hyaline tail terminal is about the same length (20 μm) as the stylet. (See key to the species for further diagnostic details also.)

DISTRIBUTION: In reporting his finding of *H. cacti* in Georgia, USA, and in reviewing the distribution of this species up to that time, Johnson (7) in 1968 listed 10 countries known through published reports to have this species. At the same time, through the cooperation of the senior author, Johnson included from the Sample Records Division of the USDA Nematode Collection a list of 15 additional countries from which *H. cacti* specimens had been received, and 11 of these were new records of occurrence for this nematode to that time. Mulvey (10) gave a list of 16 countries having *H. cacti* and all of these except one (Australia) had been included in Johnson's 1968 report which presumably had escaped Mulvey's attention.

The following distribution list, now encompassing 26 countries and seven states in the USA, is compiled from the Sample Records Division of the USDA Nematode Collection and certain publications as indicated. An asterisk (*) denotes a new record of distribution based on USDANC records. The 20 countries (including Canada) and one state (USA) listed which do not have an asterisk or literature reference were included in the updated report on *H. cacti* distribution by Johnson (7) in 1968. Appreciation for several of the foreign records in USDANC is extended to Mr. W. Friedman, Plant Protection and Quarantine, APHIS, USDA, Beltsville, Maryland.

Algeria, Austria, Australia [Mulvey (10)], Argentina, Belgium, Brazil*, Canada, Colombia, Czechoslovakia, England, France, Germany, Hungary*, India, Israel, Italy, Japan, Korea*, Malta, Mexico, Netherlands, Russia (USSR), Switzerland, Vietnam*, Yugoslavia*, and these states within the USA: Arkansas*, California [Siddiqui et al. (12)]; Colorado, Florida [Langdon and Esser

(9)], Georgia [Johnson (7)], Minnesota*, and New York*.

The known hosts of *H. cacti* are various kinds of cacti. However, Langdon and Esser (9) listed *Euphorbia canariensis* and *E. enigata* as hosts on the basis of a 1959 Russian report.

The generally used common name, "cactus cyst nematode," seems quite appropriate for this *Heterodera* species.

Heterodera estonica Kirjanova & Krall, 1963

This interesting species was described on the basis of 12 cysts (with eggs and larvae) collected from soil around several different plants in Estonian S.S.R. Through the courtesy of R. H. Mulvey, (Canada Department of Agriculture, Ottawa) some cysts, larvae, and cone mounts were made available to us for examination.

CYSTS (8, from Poland): Length (including neck) 686-1014 μm (852, SD 130); width 312-468 μm (383, SD 57); L/W ratio = 2.0-2.4 (2.3).

Original authors' measurements of "12 cysts" (one of which was evidently a female): Length 536-1178 μm (922); width 207-535 μm (391); L/W ratio = 2.34. The female stylet is given as 21 μm .

Description: Cysts abullate, circumfenestrate, light to dark brown in color, basically lemon-shaped although some are elongated, and with protruding neck and vulva (Fig. 34, 35). Cyst wall rather thin (6-10 μm) with eggs generally visible within. Cyst wall pattern consists of basically straight to wavy lines encircling the cyst at right angles to its long axis and commonly broken by short oblique or vertical lines (Fig. 32, 33). Diameter of fenestra (Fig. 30, 42) averaging about 35 μm but highly variable, apparently in relation to size, age, and condition of cysts. Vulval denticles (Fig. 43) generally present, located about 20-24 μm below upper surface of fenestra, approximately 6-12 μm in length and 3-6 μm wide at base. Denticles may occur singly at random, in small clusters, or as a partial or complete ring. Anus distinct, located about 10% of cyst length from posterior end.

Males are not known.

SECOND-STAGE LARVAE (8, from type locality in Estonian S.S.R.): Length 426-465 μm (440, SD 12); a = 22-25 (22.8, SD 1.0);

b = 2.7-2.9 (2.8, SD 0.1); c = 10.5-11.9 (11.2, SD 0.7); stylet 22.1-23.6 μm (22.8, SD 0.4); dorsal esophageal gland orifice 3.4-4.3 μm (3.6, SD 0.4) from base of stylet; tail 36-44 μm (40, SD 2.8); hyaline tail terminal 14-21 (17, SD 2.5); caudal ratio A = 2.3-3.6 (2.8, SD 0.5); caudal ratio B = 4.3-6.5 (5.4, SD 0.9); width of head 7.7-8.5 μm (8.3, SD 0.4); height of head 3.4-4.3 μm (3.7, SD 0.5); w/h ratio of head = 2.0-2.5 (2.3, SD 0.2); center of median bulb from anterior end 62-72 μm (67, SD 3.4).

Measurements of larvae (unknown numbers) from original authors: Length 392-456 μm (427.7); stylet 21-25 μm (22.8); head with 3-4 annules; tail 31.5-36 μm (33.5); hyaline tail terminal 18-21 μm (19.2).

Drawings of larvae in the original description and our own observations of only a limited number of specimens indicate that the general shape and gross morphology of these larvae are similar to other species in the *H. cacti* group. The tail and hyaline tail terminal in particular are rather short and

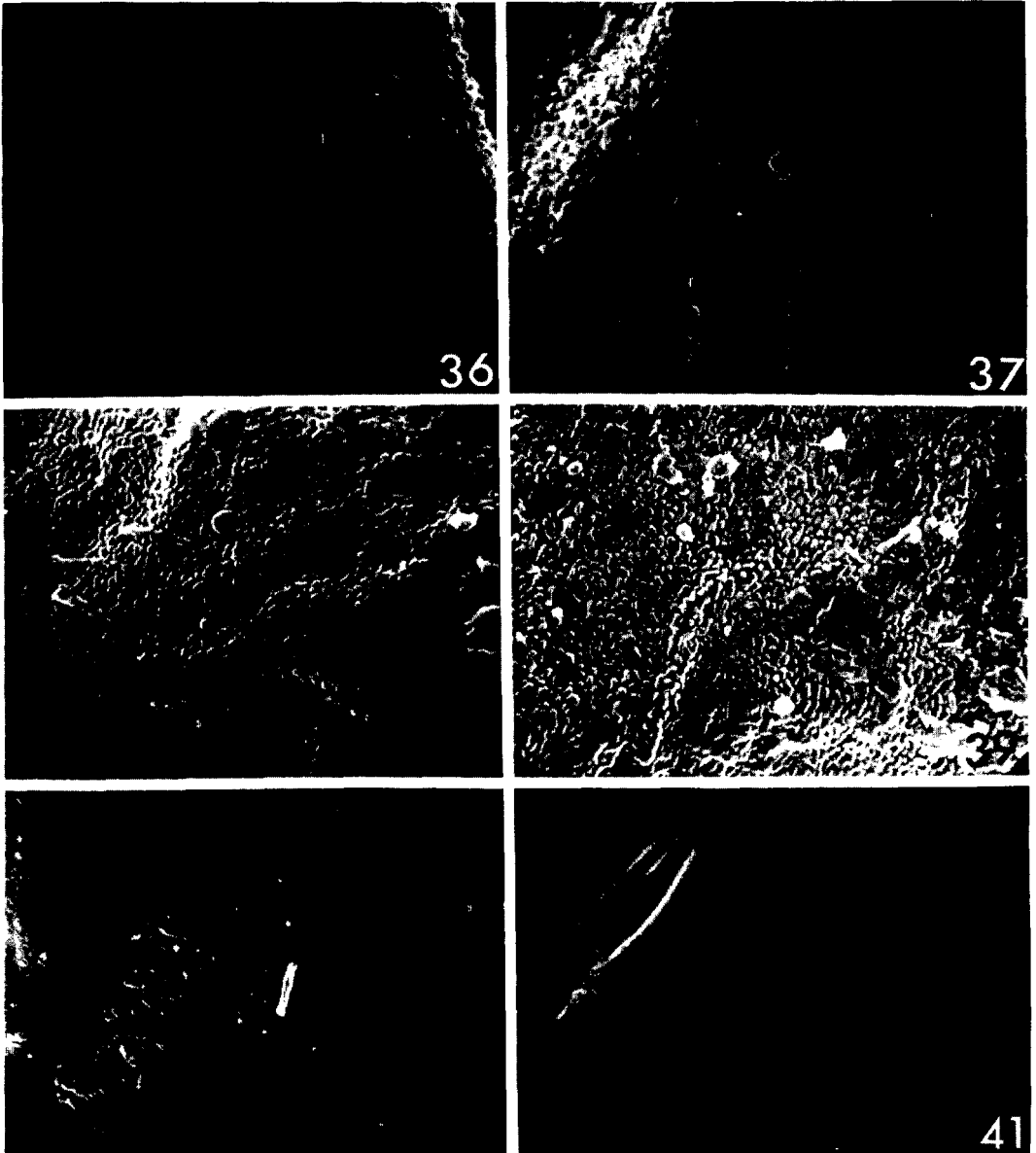


FIG. 36-41. Scanning electron micrographs of egg shell surface of four *Heterodera* species. 36-37) *H. cacti*. 38-39) *H. thornei*. 40) *H. amaranthi*. 41) *H. weissii* (all at 5,000 x).

blunt (Fig. 31). The original authors reported that the head had 3-4 annules, an observation with which we agree. They also reported that the lateral field was composed of 5 incisures. The lateral field on the specimens we examined was obscure and 5 incisures are unusual for this group but must be accepted for now as originally described.

EGGS (measurements on unknown number from original authors): Length 108.5-133 μm (124.9); width 42-52 μm (48.2); L/W ratio = 2.58 (average). Although type was not specified in the original description, our observations found the egg shells to be hyaline, and without visible markings as seen under oil immersion of a light microscope. Drawings of eggs in original description show larvae folded 4.5 times within the egg.

The type specimen (female) and paratypes (cysts with eggs and larvae) are at the Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad, and some paratype cysts are at the Institute of Zoology and Botany, Academy of Sciences of the Estonian S.S.R.

TYPE HOST: Unknown. Original specimens were collected from soil in which were growing *Polygonum aviculare*, *Poa pratensis* (Kentucky bluegrass), *Trifolium repens* (white clover), and *Agrostis capillaris* (creeping bentgrass).

TYPE LOCALITY: (Designated by original authors.) Village of Makas, Tartu district, Estonian S.S.R.

DIAGNOSIS: *Heterodera estonica* can be distinguished from other species of the *H. cacti* group by the nature of the cysts (as described) which have an L/W ratio averaging 2.3. Also, this is the only species in this group having larvae with 5 lines in the lateral field; the others have only 4.

DISTRIBUTION: Estonia [Kirjanova and Krall (8)]; and Poland, Yugoslavia, and Turkey [Mulvey (10)].

A specific host for this species is not definitely known, although probably one or more of the plants named previously are hosts.

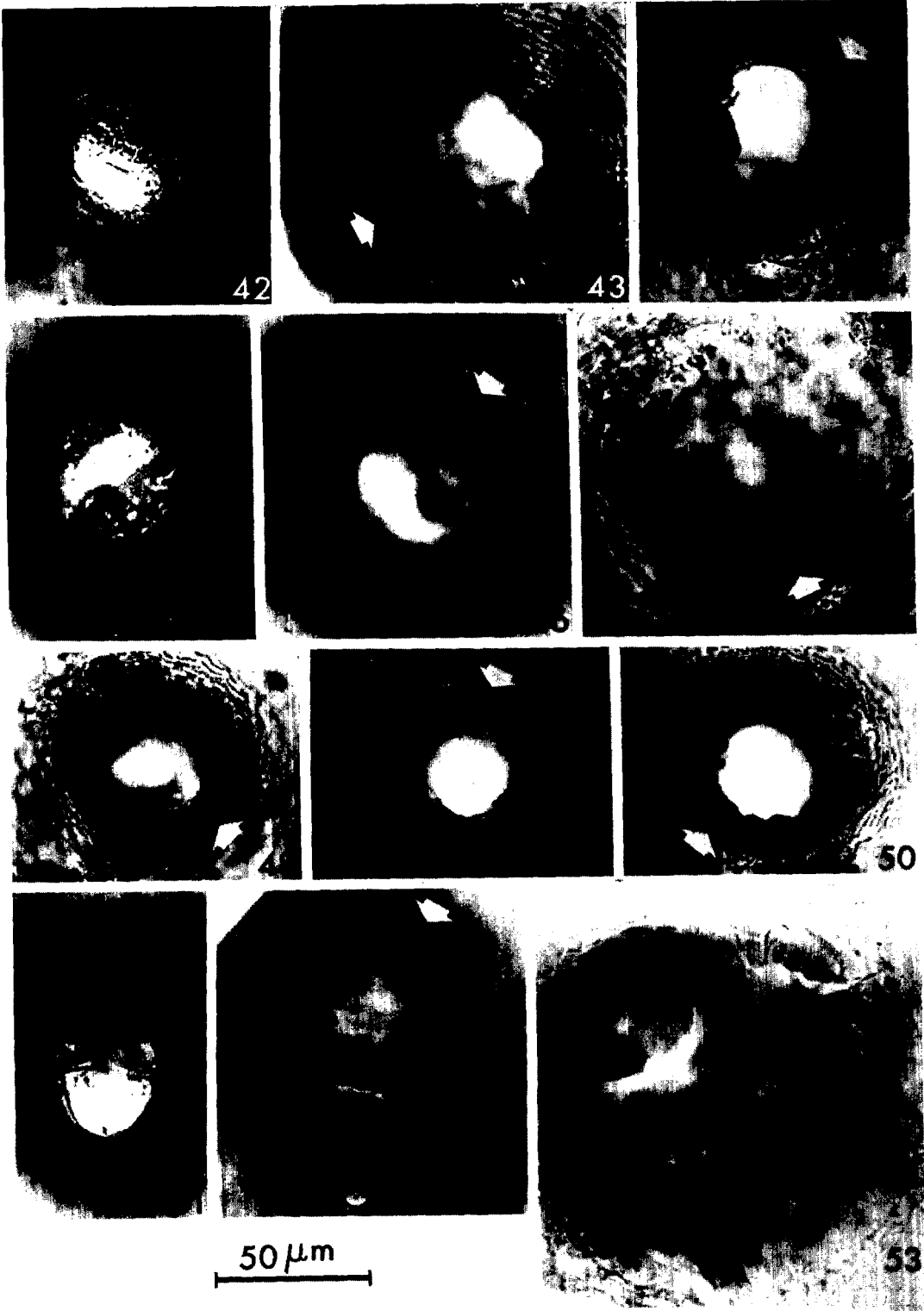
In the English abstract title by Kirjanova and Krall (8), the name "Estonian cyst-forming nematode" appears. Being in agreement, we suggest the common name "Estonian cyst nematode" for *H. estonica*.

In further comments on the original description of *H. estonica*, particularly the English abstract, Kirjanova and Krall (8) refer to the cyst "cuticle" as having "finest zig-zag lines on its surface," and also state, "Bullae situated as a compact circle around vulva and fenestra." Their drawing (Fig. 2, page 220) was supposed to illustrate these two points, but we interpret it differently. The cyst wall pattern, as illustrated on the vulval cone in Fig. 2, is quite characteristic of other *H. cacti* group species and is unlike the typical zig-zag pattern found on the cyst wall of *H. schachtlii* and the many other species in that group characterized by a zig-zag pattern. The "Bullae" in Fig. 2 are not bullae, in our opinion, but instead are vulval denticles referred to elsewhere in this paper. In fact, the vulval denticles (as illustrated) form a complete ring in this and some other species.

It is of interest to note that Mulvey (10) also showed a complete ring of vulval denticles, in our opinion, in his photomicrograph of a cone top of *H. estonica* (his Fig. 51). This picture was taken at the "lower level" of the cone top (see page 1291) and possibly could have been about 20 μm below the fenestral surface where we have observed vulval denticles in this and other *Heterodera* species. Mulvey (10) apparently did not consider the structures shown in his Fig. 51 to be "true" bullae since he referred to them as "bullae-like structures" (page 1291); however, in his key and brief diagnosis of this species, he used the term "bullae" (page 1281).

Heterodera betulae Hirschmann & Riggs, 1969

An excellent description of this unusual species was presented by Hirschmann and Riggs (5) in 1969 on the basis of specimens from birch in Washington County, Arkansas. Some of the striking features of the cysts and females are their shape, which is pear-shaped to mainly spheroidal and essentially rounded posteriorly with only a small button-like protrusion, and a cuticular pattern on most of the body which is zig-zag, wavy, or network-like. Bullae or "bullae-like" structures are also present in cysts, but the frequency of occurrence is undetermined. These characters are unlike any in



the species of the *H. cacti* group. Especially because of the circumfenestrate cysts, the original authors at the time compared *H. betulae* with *H. weissi* and *H. cacti* but pointed out major differences of important characters in the species. Mulvey (10) included *H. betulae* in his "Group 2" which also contained *H. weissi*, *H. cacti*, and *H. estonica*.

The markedly different morphology of *H. betulae* is incompatible in the *H. cacti* group of species as presented herein. The only major character common to both *H. betulae* and the other species of the *H. cacti* group is the circumfenestrate nature of the cysts. If this cyst character should be used as an overriding factor to put *H. betulae* with all of the species of the *H. cacti* group, then it would seem necessary to apply the same criterion and logic to all the other circumfenestrate species. Such an action would result in the many species in the "*H. rostochiensis* group" (or "round cyst" forms) being lumped with the previously mentioned species and increase the incompatibility and difficulty in making identifications. We therefore propose to have *H. betulae* separate and perhaps it will be the basis for the "*H. betulae* group" when another related species is described. Consequently, we exclude *H. betulae* from the key to the species of the *H. cacti* group presented hereafter. It is not likely that *H. betulae* would be mistaken for any of the *cacti* group species.

DISTRIBUTION: Washington County, Arkansas [Hirschmann and Riggs, (5)]; Northwest Arkansas [Riggs et al. (11)]. Following are new records of occurrence from the Sample Records Division, USDA Nematode Collection: Mississippi County, Arkansas (samples in 1963); Lawrence County, Arkansas (in 1966); Mississippi County, Missouri (in 1963); and near Mason City, Iowa (in 1964).

According to Riggs et al. (11), *H. betulae* reproduced well on several *Betula* species and *Cleome spinosa* L. Limited reproduction occurred on *Alnus glutinosa* (L.) Gaertn., and only occasional females developed on orchard grass, *Dactylis glomerata* L.; sweet alyssum, *Lobulana maritima* Desv.; and "butternut" squash, *Cucurbita moschata* Duch. ex Poir.

The currently used common name "birch cyst nematode" seems very appropriate for *H. betulae*.

FURTHER COMMENTS ON VULVAL DENTICLES: In this paper, we propose the name "vulval denticles" for the small, tooth-like structures seen below the fenestral surface and within the vulval cone. The denticles were seen in specimens of all five species of the *H. cacti* group and generally seemed to be more prominent in *H. weissi* and *H. amaranthi*. Vulval denticles are not restricted to species of the *H. cacti* group although we have not made a specific survey of various cyst forms for this purpose. However, *H. schachtii*, as a representative of the "schachtii group," was examined and a small cluster of denticles was seen (Fig. 52). In this particular cyst cone, the denticles were located 20 μm below the fenestral surface (Fig. 51). In the same cone, the prominent bullae (Fig. 53) were situated 26 μm below the denticles; thus these bullae were 46 μm below the fenestral surface in this particular cyst cone. On the other hand, several topotype cysts of *H. rostochiensis* were examined and no denticles were seen. It may well be though, that in certain species where bullae have been reported as scattered and are not always evident (as in *H. fici* Kirjanova, 1954), vulval denticles could have been seen and misinterpreted as being true bullae. A case in point, at least in our opinion, is the reference by Kirjanova and Krall (8) to the presence of bullae in *H. estonica* as discussed earlier.



FIG. 42-53. Photomicrographs of cyst cone fenestrae and structures. 42) View at fenestra surface of *Heterodera estonica*. 43) View of 42 at 20 μm below surface; shows vulval denticles. 44) Scattered vulval denticles in *H. cacti*. 45) Surface view of fenestra of *H. amaranthi*. 46) View of 45 at 20 μm below fenestra surface; shows vulval denticles. 47) Scattered vulval denticles in *H. thornei*. 48-50) Views showing vulval denticles in *H. weissi* about 20 μm below fenestra surface. 51) Fenestra surface view of *H. schachtii*. 52) View of 51 about 20 μm below fenestra surface; shows a small cluster of vulval denticles. 53) View of 51 at 46 μm below fenestra surface; shows true bullae typical of *H. schachtii*. (Arrows point to vulval denticles.)

The nature, origin, and function of vulval denticles are not known.

KEY TO THE *HETERODERA* SPECIES OF THE *H. CACTI* GROUP

(Cyst abullate, circumfenestrate, basically lemon-shaped, with protruding neck and vulva, and may or may not have vulval denticles within the cone. Cyst wall pattern, especially in middle half of cyst, consists of essentially straight to wavy lines extending around the cysts at right angles to the long axis and commonly broken by short oblique or vertical lines.)

1. Cysts generally twice or more as long as wide, L/W ratio averaging 2.3; larvae with 5 lines in lateral field *H. estonica*
 Cysts commonly less than twice as wide, the average L/W ratio for the various species ranging from 1.3 to 1.7; larvae with 4 lines in lateral field 2
2. Egg shells distinctly punctate; stylets of larvae averaging about 23 μm or more 3
 Egg shells hyaline, without visible markings; stylets of larvae averaging approximately 20 μm 4
3. Larval stylet averaging 23.5 μm ; tail or larvae averaging 46 μm ; hyaline tail terminal short, blunt, and usually measuring 12-20 μm *H. cacti*
 Larval stylet averaging 27 μm ; tail of larvae averaging 56 μm ; hyaline tail terminal relatively long, tapering to finely rounded terminus, and generally measuring 23-28 μm *H. thornei* n. sp.
4. Tail of larvae averaging about 46 μm ; hyaline tail terminal about same length as stylet and averages 20.2 μm *H. weissi*
 Tail of larvae averaging 35 μm ; hyaline tail terminal shorter than stylet and averages 15 μm *H. amaranthi*

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