JOURNAL OF NEMATOLOGY

VOLUME 15 JANUARY 1983 NUMBER 1

An Illustrated Key to the Cyst-forming Genera and Species of Heteroderidae in the Western Hemisphere with Species Morphometrics and Distribution[1]

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Abstract: Diagnoses of the cyst-forming genera of Heteroderidae (viz., *Heterodera, Sarisodera, Globodera, Punctodera, Cactodera,* and *Dolichodera*) and distribution and morphometrics of the 34 known cyst species in the Western Hemisphere are presented along with an illustrated key for the identification of these genera and species. The key is based mainly on cysts and larvae, and important morphological and diagnostic features are extensively shown by LM and SEM illustrations. The genus *Bidera* is placed as a new synonym under the genus *Heterodera*.
Key words: cyst nematodes, taxonomy, identification.

Journal of Nematology 15(1):1-59. 1983.

Early in 1981 the corn cyst nematode (*H. zeae* Koshy, Swarup & Sethi, 1971 [30]) was found in three corn fields in Kent County, Maryland, the first known occurrence of this cyst species in the United States (47). Subsequent limited surveys showed the nematode to be on several nearby farms, and preliminary tests indicated field corn, sweet corn, and barley to be hosts. Because of the potential threat to corn production in Maryland and in the United States posed by this cyst nematode, extensive research—including surveys, host range and pathogenicity studies, and possible control measures—was planned and initiated.

As part of this overall research effort, our report here gives an illustrated key to the 6 genera and 34 cyst-forming species known to occur in the Western Hemisphere. The key is based on both cysts and larval characters and provides diagnostic details essential in surveys and related work. Included also are generic diagnoses and distribution and morphometric data for all of the known species in the Western Hemisphere. The genus *Bidera* is synonymized with *Heterodera*.

MATERIALS AND METHODS

Living specimens of several species, including *Heterodera glycines* and *H. trifolii*, were obtained from isolated cultures in the greenhouse or growth chambers at Beltsville, Maryland, while fresh specimens of *H. zeae* were provided by Dr. L. Krusberg, University of Maryland, College Park. The procedures used for preparing these specimens were essentially the same as those used by Golden and Birchfield (16). Fixed specimens of the various other species were obtained from the USDA Nematode Collection at Beltsville. Photomicrographs of cysts, vulva cones, females, and larvae were made with an automatic 35 mm camera attached to a compound microscope having an interference contrast system; those of infected roots, whole females, and cysts were made with a 8.3 × 10.8 cm sheet-film camera attached to a dissecting microscope. In making the scanning electron micrographs, living specimens were fixed in 3% glutaraldehyde solution 0.05 M phosphate buffer (pH 6.8), dehydrated in a graded series of ethanol, critical-point dried from liquid CO^2, sputter coated with a 20–30 μm layer of gold-palladium, and examined with a scanning electron microscope (SEM). Some specimens were prepared previously

Received for publication 19 April 1982.

[1]Scientific article number A-3308, contribution number 6380 of the Maryland Agricultural Experiment Station. This research was done in the laboratory of the second author and supported in part through a USDA Cooperative Agreement with the University of Maryland, College Park. Thanks are given especially to Dr. Lorin Krusberg, Department of Botany, for his assistance and cooperation.

Appreciation for technical assistance is extended to Donna M. S. Ellington, Support Scientist, and Paula Crowley, Laboratory Technician (in laboratory of second author), and to Bruce Ingber, Laboratory Technician, Electron Microscopy Laboratory, USDA ARS, Beltsville, MD 20705, for SEM technical assistance. We also thank Dr. Roger V. Anderson, Biosystematics Research Institute, Canada Agriculture, for some of the photomicrographs and SEM micrographs used in this paper.

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in Canada by the senior author using the same methods as Mulvey (39,40). Some distribution data were supplied by the USDA Nematode Collection at Beltsville, Maryland, while much of the data on distribution were based on published reports (5, 18, 35, 39).

SYSTEMATICS
(Figs. 1–164)

Family: Heteroderidae (Filipjev & Schuurmans Stekhoven, 1941) Skarbilovich, 1947.

Subfamily: Heteroderinae Skarbilovich, 1947.

Diagnosis: After Mulvey & Stone, 1976 (42).

Female: Cyst formed after death. Cuticle non-annulated. Anus dorsal or on the inside of the dorsal vulval lip. Vulva terminal.

Second-stage juvenile: Labial disc present but with low profile and only seen clearly under scanning electron microscope. Cuticle of labial region of even thickness. Esophageal glands fill body width.

Male: Length up to 1.7 mm. Labial disc present but with low profile, or apparently so. Tail present or absent.

Type genus: Heterodera Schmidt, 1871. (See page 50 for generic diagnosis.)

Punctodera Mulvey & Stone 1976
(Tables 1–4)

Diagnosis: After Mulvey & Stone (42).

Mature female and cyst: Without posterior protuberance; spherical, ovoid, or pear shaped. Cuticle with lacelike pattern of ridges and subsurface pattern of punctations. Vulval slit very short, underbridge absent. Bullae present or absent. Perineal tubercles absent. Circumfenestrate fenestra surrounding vulva and circumfenestrate fenestra of similar size surrounding anus. Anus offset toward ventral margin of anal fenestra.

Second-stage juveniles: Stylet less than 30 μm. Esophageal glands fill body cavity. Phasmids without lenslike structure in muscle layer.

Male: To 1.5 mm long. Labial disc present but with low profile. Tail present, less than half body width.

Type species: Punctodera punctata (Thorne, 1928) Mulvey & Stone, 1976.

Punctodera chalcoensis Stone, Sosa Moss & Mulvey, 1976
(Fig. 22)

Described and illustrated by Stone et al. (55).

Type host and locality: Maize (*Zea mays* L.). Chalco area, Valley of Mexico, Mexico State, Mexico.

Distribution: Only Tlaxcala and Mexico States, Mexico.

Punctodera matadorensis Mulvey & Stone, 1976
(Figs. 23–27)

Described and illustrated by Mulvey & Stone (42).

Type host and locality: Permanent grass. Matador Ranch, Matador, Saskatchewan, Canada.

Distribution: Only Saskatchewan, Canada.

Punctodera punctata (Thorne, 1928) Mulvey & Stone, 1976
(Figs. 19–21)

Described by Thorne (59).

Type host and locality: Wheat (*Triticum aestivum* L.) and grasses. Humboldt area, Saskatchewan, Canada.

Distribution: Western Hemisphere—Saskatchewan, Labrador, Newfoundland, Sable Island (off Nova Scotia), Manitoba, Ontario, Quebec, and British Columbia in Canada; Michigan, South Dakota, Texas, and Arkansas in USA. *World*—Austria, Belgium, England, Holland, Ireland, Norway, Poland, USSR, West Germany.

Discussion: Thorne's *P. punctata* specimens (slide 3A) in the USDA Nematode Collection at Beltsville, Maryland, of white females and cysts provided new information on vulva and anal fenestra, length of vulva slit, and position of anus. Other information concerning larvae (from Thorne's slide 3B) was taken from Mulvey and Stone (42).

Genus *Dolichodera* Mulvey & Ebsary, 1980

Diagnosis: After Mulvey & Ebsary (44).

Mature female and cyst: Stylet well developed. Body elongate-ovoid, without posterior protuberance. Cuticle thin with interrupted, irregular striae, and no regular

annules. Crystalline layer absent. Vulva slit not observed. Underbridge absent, bullae present. Perineal tubercles absent. Vulva circumfenestrate, anus lacking fenestra.

Second-stage larvae: Stylet 22–24 μm. Esophageal glands occupying entire body cavity. Phasmids small. Tail 95–120 μm long, hyaline area 30% of tail length.

Type species: Dolichodera fluvialis Mulvey & Ebsary, 1980.

Dolichodera fluvialis Mulvey & Ebsary, 1980
(Figs. 28–35; Tables 5–8)

Described and illustrated by Mulvey and Ebsary (44).

Type host and locality: Aquatic grass, (*Spartina pectinata*) growing on the bottom of the Ottawa River (females and cysts found on the roots by B. A. Ebsary in 1981) near Deschenes, Quebec, Canada.

Distribution: Quebec, Canada.

Genus *Sarisodera* Wouts & Sher, 1971

Diagnosis: Emended from Mulvey & Stone (42).

Mature female and cyst: Cuticle with lacelike pattern of ridges. Vulva sunken into terminal cone, anus on upper inside of dorsal vulva lip, vulva without fenestration.

Second-stage larva: Esophageal glands fill body width, phasmids with lenslike structure in muscle layer. Stylet greater than 38 μm in length.

Male: To 1.5 mm in length, labial disc apparently absent, tail absent.

Type species: Sarisodera hydrophila Wouts & Sher, 1971.

Sarisodera hydrophila Wouts & Sher, 1971
(Figs. 56–64; Tables 5–8)

Described and illustrated by Wouts and Sher (64).

Type host and locality: Willow (*Salix lasiolepis* Benth.). Arroyo River, 12 miles east of Temecula, Riverside County, California, USA.

Distribution: California, USA; unidentified species of *Sarisodera* from Idaho, USA, reported by Wouts and Sher (64). Wouts and Sher (64) regard the *Sarisodera* specimens from Idaho and others from California to represent at least five new species. However, sufficient specimens were not available at that time for adequate description.

Heterodera betulae Hirschmann & Riggs, 1969
(Figs. 65–71; Tables 5–8)

Thoroughly described and illustrated by Hirschmann and Riggs (24). Mulvey (39) assigned this species to the *cacti* group based on having a very short vulva slit. The markedly different morphology of *H. betulae,* as documented by Golden and Raski (18) and also illustrated herein, places this species apart from all described *Heterodera.* Therefore, we have not assigned this species to the genus *Cactodera* or to any of the present groups within the genus *Heterodera,* pending further action on this by one of us (AMG).

Type host and locality: River birch roots (*Betula nigra* L.). South bank of Middle Fork, White River, 1.75 miles upstream from Highway 16 bridge, Washington County, Arkansas.

Distribution: Western Hemisphere—Lawrence, Mississippi, and Washington counties of Arkansas and in Northwest Arkansas; Mississippi county, Missouri; and near Mason City, Iowa, USA.

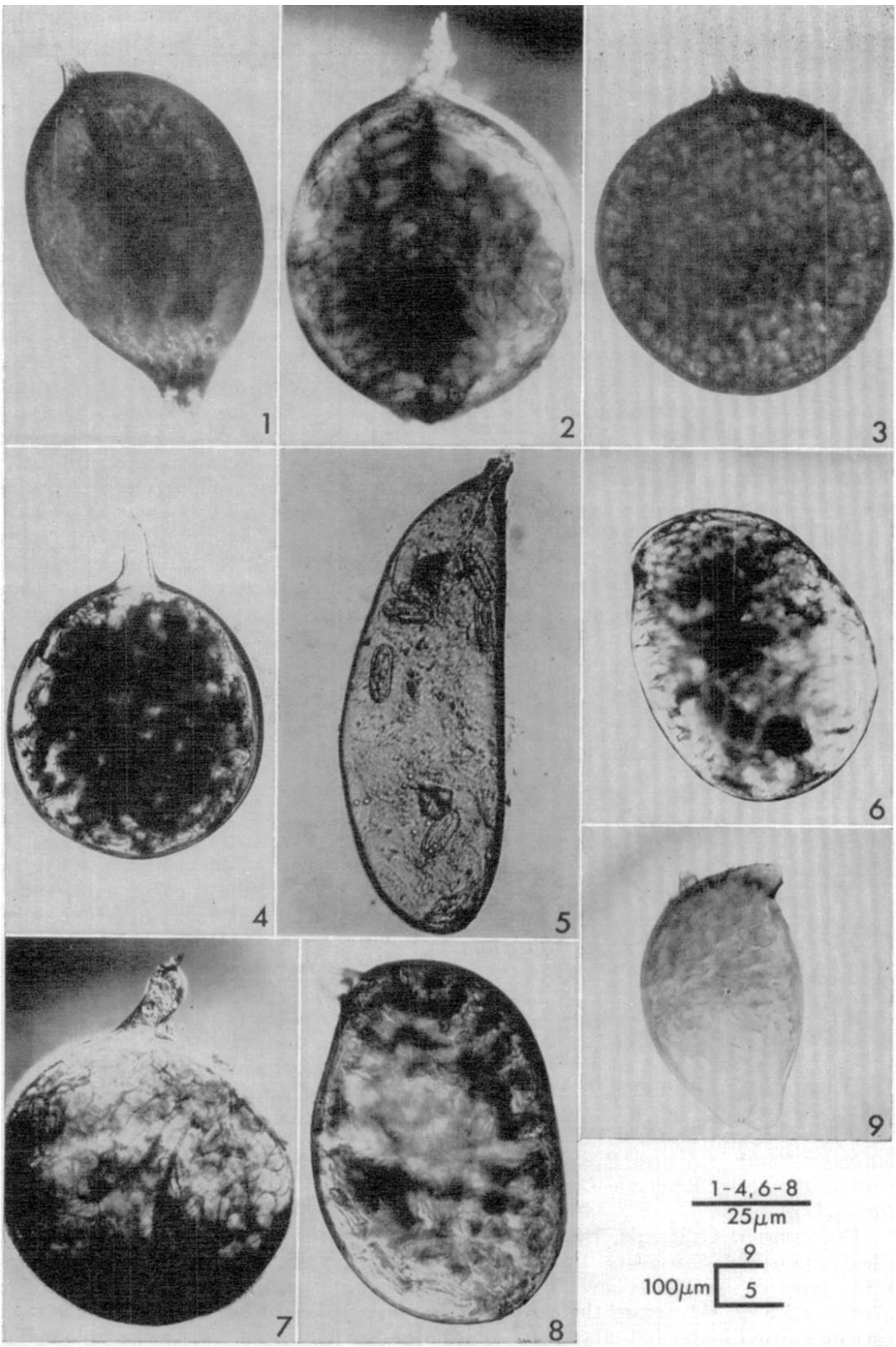
Discussion: Examination of 10 cysts (6 young and 4 older) from the type material revealed no bullae-like structures, as reported by Hirschmann and Riggs (24), in the vulva cone of the young cysts and only one of the older cysts had similar bullae-like structures.

Since we examined only a few cysts, future studies of many cysts may reveal a much higher frequency of occurrence of these bullae-like structures in the vulva cone. At present, however, we consider these bullae-like structures to have little or no diagnostic value for this species.

Genus *Globodera* Skarbilovich, 1959
(Tables 9–12)

Diagnosis: After Mulvey & Stone (42).

Mature female and cyst: Posterior protuberance absent, spherical shape, cuticle with lacelike pattern of ridges. Vulval slit short (<15 μm). Underbridge and bullae rarely present. Perineal tubercles present.


1
2
3
4
5
6
7
8
9
1-4, 6-8
25μm
9
100μm
5

Vulval fenestration circumfenestrate; no anal fenestra. Anus dorsal, not on vulval lip.

Second-stage juvenile: Stylet less than 30 μm. Esophageal glands fill body width. Phasmids without lenslike structure in muscle layer.

Male: To 1.5 mm long. Labial disc present but with low profile. Tail present, length less than half body width.

Type species: Globodera rostochiensis (Wollenweber, 1923) Behrens, 1975 (2).

Globodera leptonepia (G.S. Cobb & Taylor, 1953) Behrens, 1975

Golden and Ellington (15) redescribed and provided photomicrographs of this species based on cysts from the original material. They designated a lectotype and paralectotypes based on cysts, larvae, and eggs—the only stages known of this species.

Type host and locality: Unknown, possibly the roots of some solanaceous plant. Thought to be from some area in Peru, South America.

Distribution: Possibly Peru.

Globodera solanacearum (Miller & Gray, 1972) Behrens, 1975
(Figs. 39, 44, 50, 53)

Described and illustrated by Miller and Gray (38).

Type host and locality: Horse nettle (*Solanum carolinense* L.). Near Scott's Fork, Amelia County, Virginia, USA.

Distribution: Only Virginia, USA.

Globodera tabacum (Lownsbery & Lownsbery, 1954) Behrens, 1975
(Figs. 40, 51)

Described and illustrated by Lownsbery and Lownsbery (34).

Type host and locality: Tobacco (*Nicotiana tabacum* L.). Hazardville, Connecticut, USA.

Distribution: Western Hemisphere—Hazardville and Windsor in Connecticut, Hatfield in Massachusetts, USA. *World*—Bulgaria.

Globodera virginiae (Miller & Gray, 1968) Behrens, 1975
(Figs. 38, 43, 45, 52)

Described and illustrated by Miller and Gray (37). Golden and Ellington (15) consider the Mexican cyst nematode described by Campos-Vela (3) as conspecific with *G. virginiae.*

Type host and locality: Horse nettle (*Solanum carolinense* L.). Suffolk, Virginia, USA.

Distribution: Only Virginia, USA, and Mexico (Campos-Vela, 1967) (3).

Globodera pallida (Stone, 1973) Behrens, 1975
(Figs. 36, 41, 46, 47, 54)

Described by Stone (52) as a new species based on pathotypes ("B" and "E" of English designation) of *Heterodera rostochiensis* (Wol., 1923).

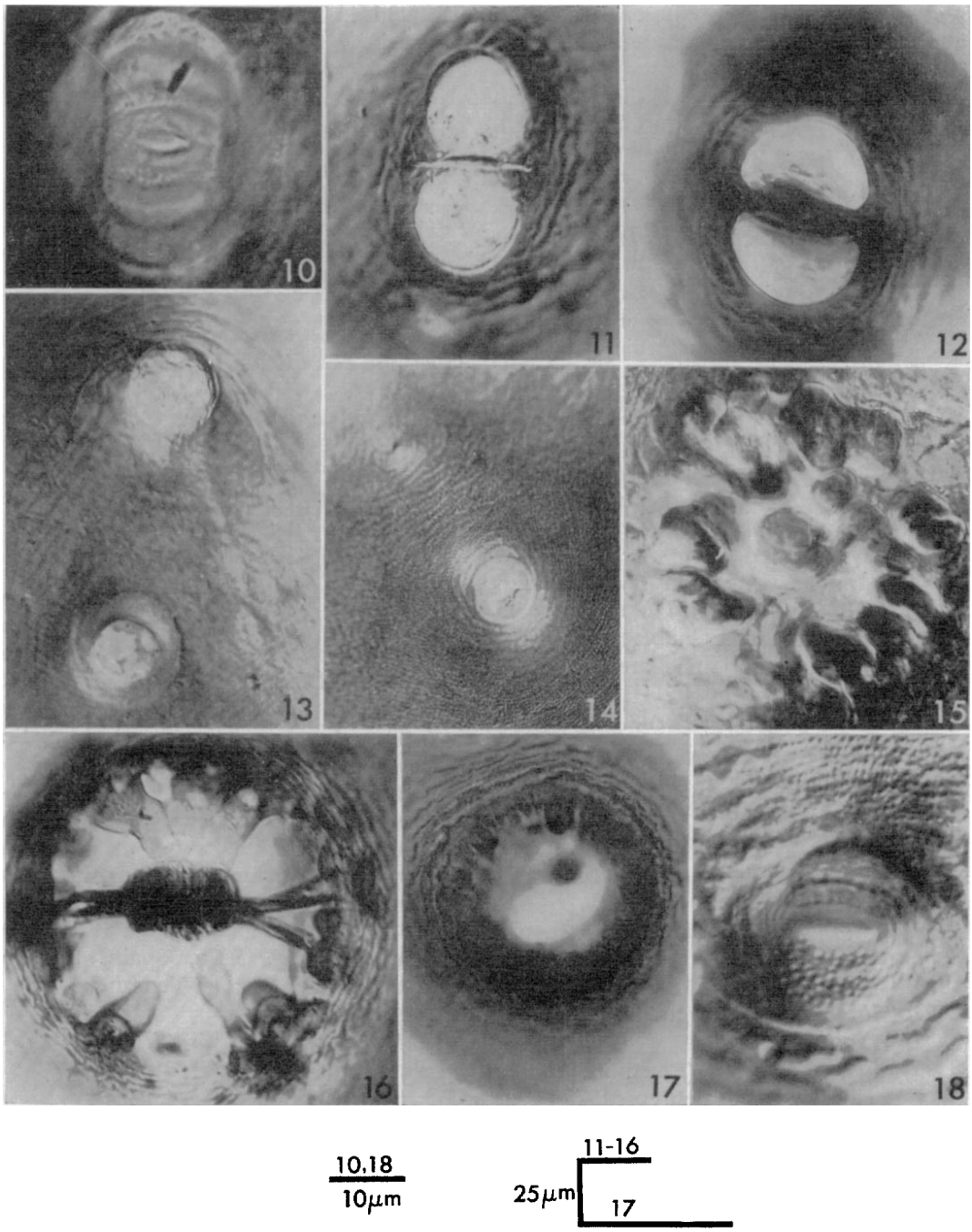
Type host and locality: Potato (*Solanum tuberosum* L.). Epworth, Lincolnshire, England.

Distribution: Western Hemisphere—Newfoundland in Canada, Peru, Bolivia, Colombia, and Ecuador. *World*—Algeria, Canary Islands, Channel Islands, Faroe Islands, France, East Germany, West Germany, Holland, Iceland, India, Italy, New Zealand, Norway, Peru, Spain, Sweden, Switzerland, USSR, and Venezuela.

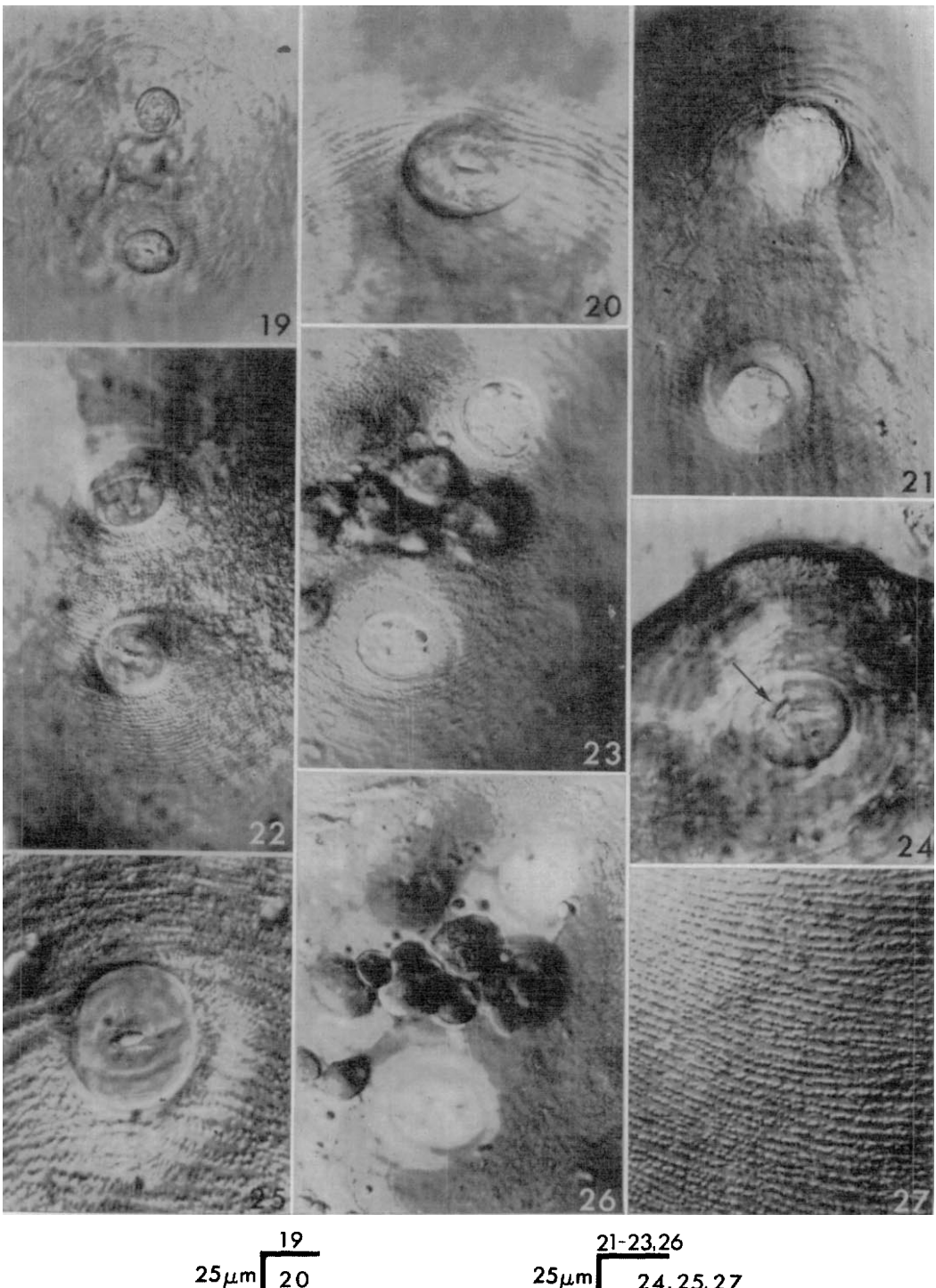
Globodera rostochiensis (Wollenweber, 1923) Behrens, 1975
(Figs. 37, 42, 48, 49, 55)

This destructive pest of potatoes was first noted by Kuhn (33) in Germany in 1881. Wollenweber (62) was first to recognize this was a distinct species. Over the years several workers, including Stone (52), have presented detailed data or brief descriptions of this species. In 1972 Golden and Ellington (15) provided a description

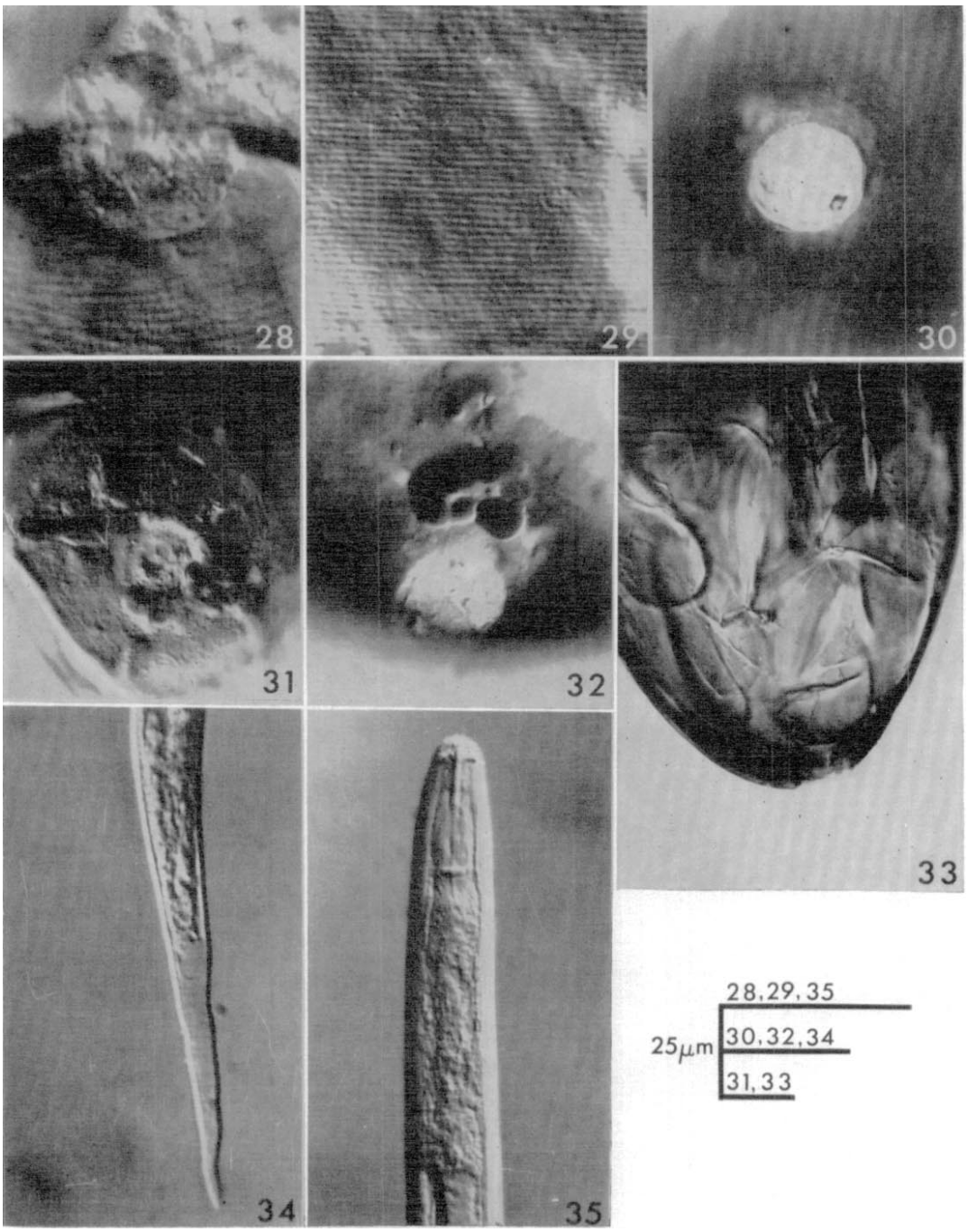
Figs. 1–9. Representative cyst shapes of cyst-forming Heteroderidae. 1, 2, 9) With posterior protuberance. 3-8) Without posterior protuberance. 1) Lemon shaped with vulva cone. 2) Spherical shaped with vulva cone. 3) Spherical (*Globodera*), anus and vulva terminal. 4) Subspherical (*Globodera*). 5) Elongate ovoid. 6) Ovoid. 7) Spherical (*Punctodera*). 8) Pear shaped. 9) Ovoid, vulva sunken into cone.



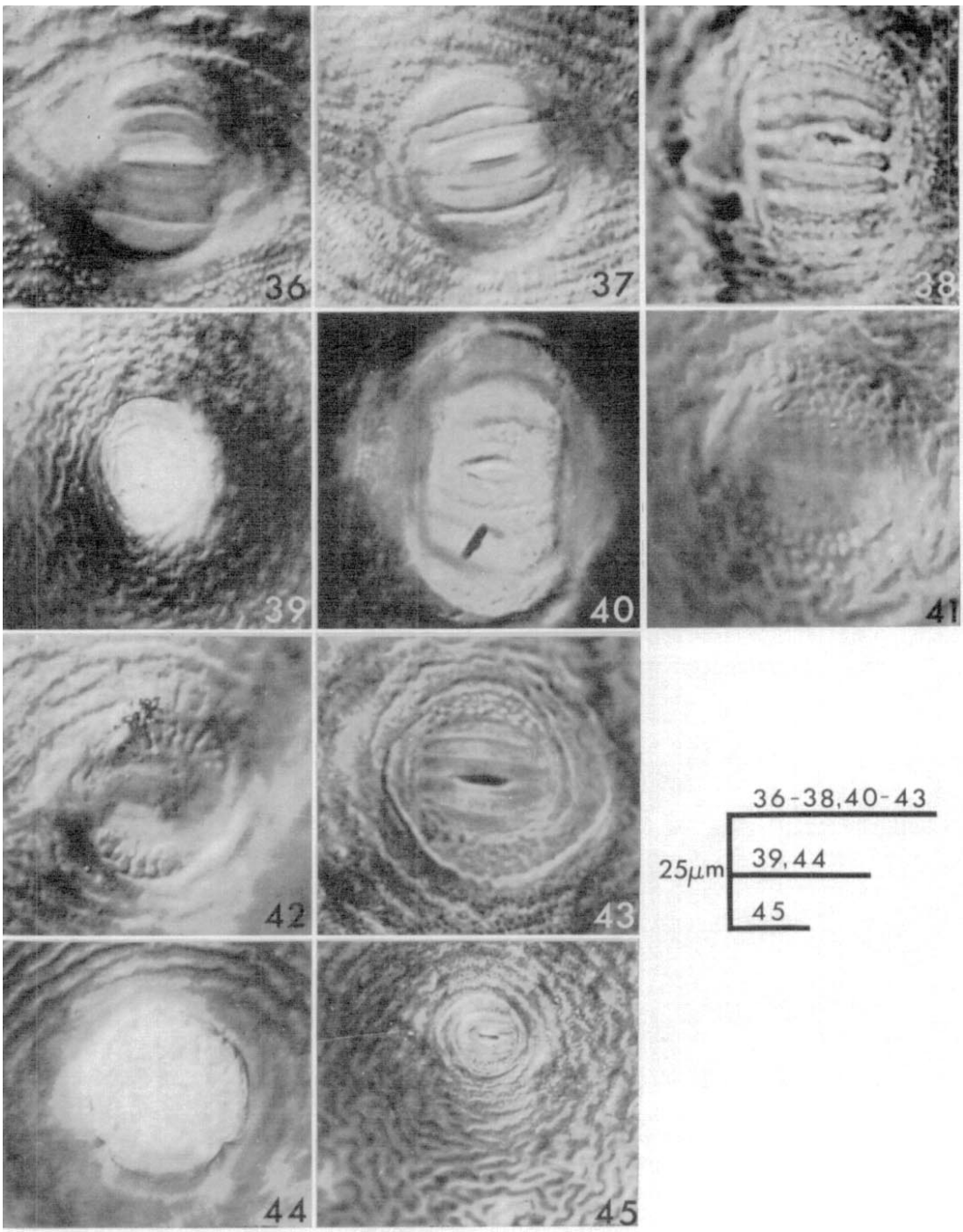
Figs. 10–18. Photomicrographs of representative fenestrae and underbridges of cyst-forming Heteroderidae. 10) Circumfenestrate. 11)Bifenestrate. 12) Ambifenestrate, *H. trifolii* showing vulva slit, vulva bridge, semifenestra and surrounding basin. 13) Equal size vulva and dorsally located anal fenestra. 14) Vulva fenestra large, anal area small and without fenestration. 15) Heavy bullae, *avenae* group, located immediately below fenestra. 16) Underbridge, end-on view. 17) Vulva denticles, slightly below fenestral level. 18) Perineal tubercles in vulva area, *Globodera* species.



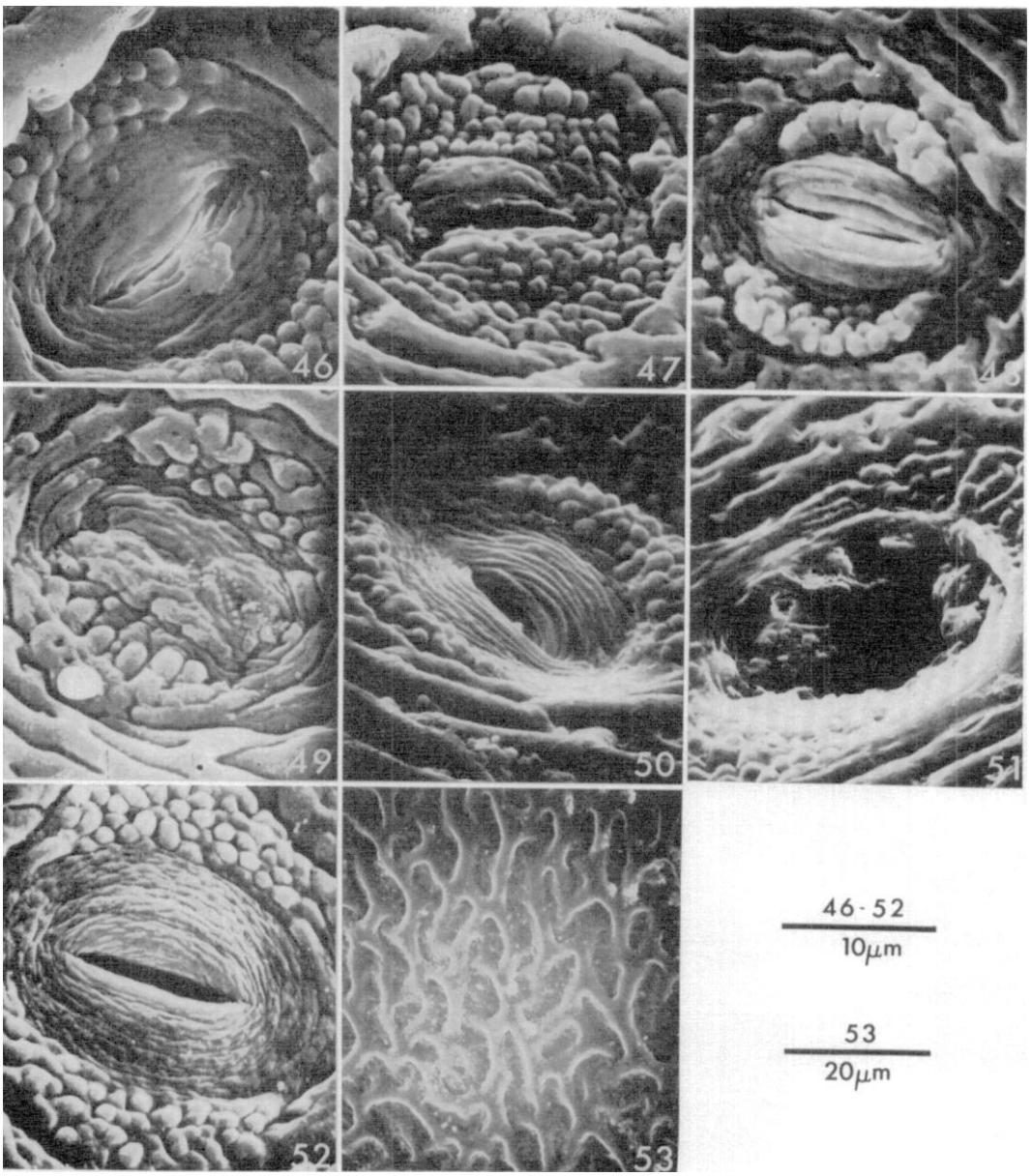
Figs. 19–27. Photomicrographs of the terminal areas of *Punctodera* species. 19) *P. punctata,* anal fenestra (dorsal) and vulva fenestra of female from Thorne's collection of 1927 from Saskatchewan, Canada. 20) *P. punctata,* enlarged photo of vulva fenestra (circumfenestrate) and vulva slit, same data as Figure 19. 21) *P. punctata,* vulva and anal fenestra, from Ontario, Canada. 22) *P. chalcoensis,* vulva and anal fenestra, from Mexico. 23) *P. matadorensis,* vulva and anal fenestra, from Saskatchewan, Canada. 24, 25) Enlarged photo of anal fenestra (anus [arrow] offset from center) and vulva fenestra (slit central) of *P. matadorensis.* 26) *P. matadorensis,* heavy bullae just below vulva and anal fenestra. 27) Subcuticular punctations near posterior level of neck of *P. matadorensis.*



Figs. 28–35. Photomicrographs of fenestra and second-stage larva of *Dolichodera fluvialis*. 28) Female, lateral view of terminal area showing large rounded fenestra. 29) Cuticular striations at midbody of female. 30) Fenestral area of cyst, deteriorated to form a round aperature. 31) Bullae around fenestral area. 32) Heavy bullae between anus (arrow) and vulva fenestra. 33) Lateral view of terminal fenestra of cyst. 34) Second-stage larva tail. 35) Second-stage larva anterior region showing stylet and dorsal esophageal duct opening.



Figs. 36–45. Photomicrographs of fenestral area of female *Globodera* species. 36) *G. pallida,* circummenestrate. 37) *G. rostochiensis.* 38) *G. virginiae.* 39) *G. solanacearum.* 40) *G. tabacum.* 41) *G. pallida,* perineal tubercles, small and discrete. 42) *G. rostochiensis, perineal* tubercles, large and clumped together. 43) *G. virginiae,* perineal tubercles. 44) *G. solanacearum,* circumfenestral area. 45) *G. virginiae* mazelike pattern of cuticle between anus and vulva fenestra.



Figs. 46–53. Scanning electron micrographs of perineal tubercles in the vulva area of *Globodera* species females. 46) *G. pallida,* Dutch population. 47) *G. pallida,* United Kingdom population. 48) *G. rostochiensis,* Newfoundland, Canada, population. 49) *G. rostochiensis,* United Kingdom population 50) *G. solanacearum.* 51) *G. tabacum.* 52) *G. virginiae.* 53) *G. solanacearum,* deeply etched cuticle in terminal area of cyst.

and illustrations of all stages of *G. rostochiensis* based on specimens from the type host and locality and designated a neotype from this material.

Type host and locality: Potato (*Solanum tuberosum* L.). Rostock, German Democratic Republic (East Germany).

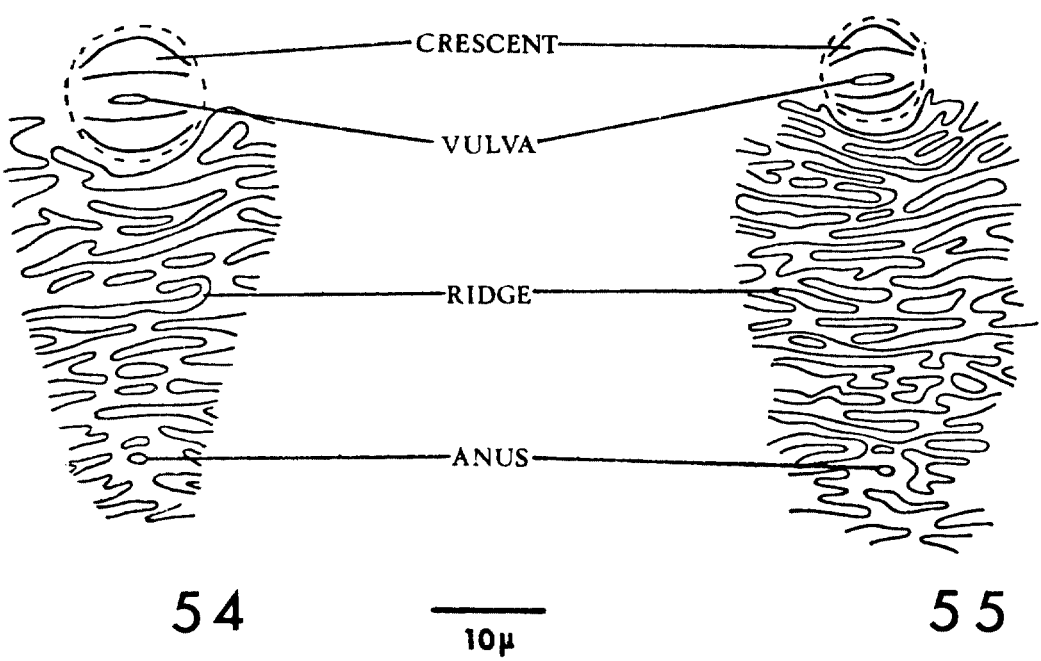
Distribution: Western Hemisphere—Newfoundland and British Columbia (only Vancouver Island) in Canada; New York State (Long Island and Steuben, Wayne, and Orleans counties) in USA; Bolivia, Chile, Colombia, Ecuador, Peru, Panama, Venezuela, and Mexico. *World*—Algeria, Austria, Belgium, Canary Islands, Cyprus, Czechoslovakia, Denmark, Egypt, England, Estonia, Finland, Faroe Islands, France, East Germany, West Germany, Guernsey Island, Greece, Holland, Iceland, Italy, India, Ireland, Israel, Japan, Jersey Island, Lapland (Finnish), Lebanon, Latvia, Lithuanian Republic, Luxembourg, Northern Ireland, New Zealand, Norway, Poland, Portugal, Scotland, South Africa, Spain, Sweden, Switzerland, Tunisia, USSR, Wales, and Yugoslavia.

Discussion: Stone (52) emphasized the differences in color between *G. pallida,* having white or cream colored females (former pathotypes "B" and "E" of English designation for *G. rostochiensis),* and *G. rostochiensis* (pathotype "A" of English designation for that species) females which became golden yellow shortly after they ruptured the root cortex. He described *G. pallida* as a new species representing the group with white or cream females and other characters. Recently, scanning work by Mulvey (unpublished) revealed distinct differences between the size and arrangement of the perineal tubercles of *G. pallida* (small, many, and discrete) and *G. rostochiensis* (large and coalesced). Several populations of each species from Canada, England, Switzerland, and Holland were studied. Those differences are easily seen under light microscopy and are very distinct when observed with scanning electron microscopy.

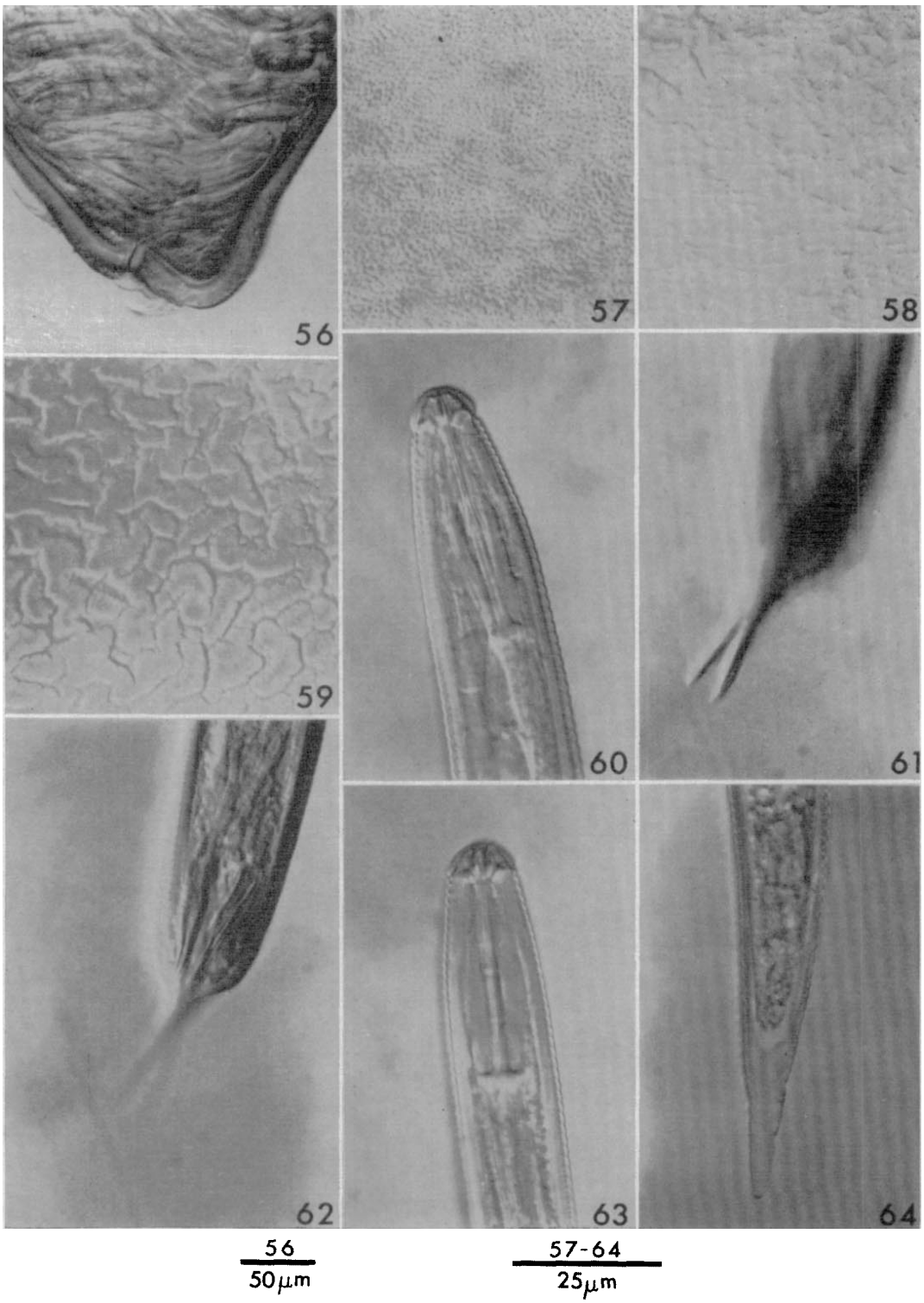
G. leptonepia differs significantly from all of the species in this genus by the very thin body of the second-stage larvae, short stylet, and long distance of the dorsal esophageal gland duct opening from the base of the stylet. The external pattern of the cyst wall at midbody and around the fenestral area is diagnostic for this species.

Cactodera Krall & Krall, 1978
(Tables 13–16)

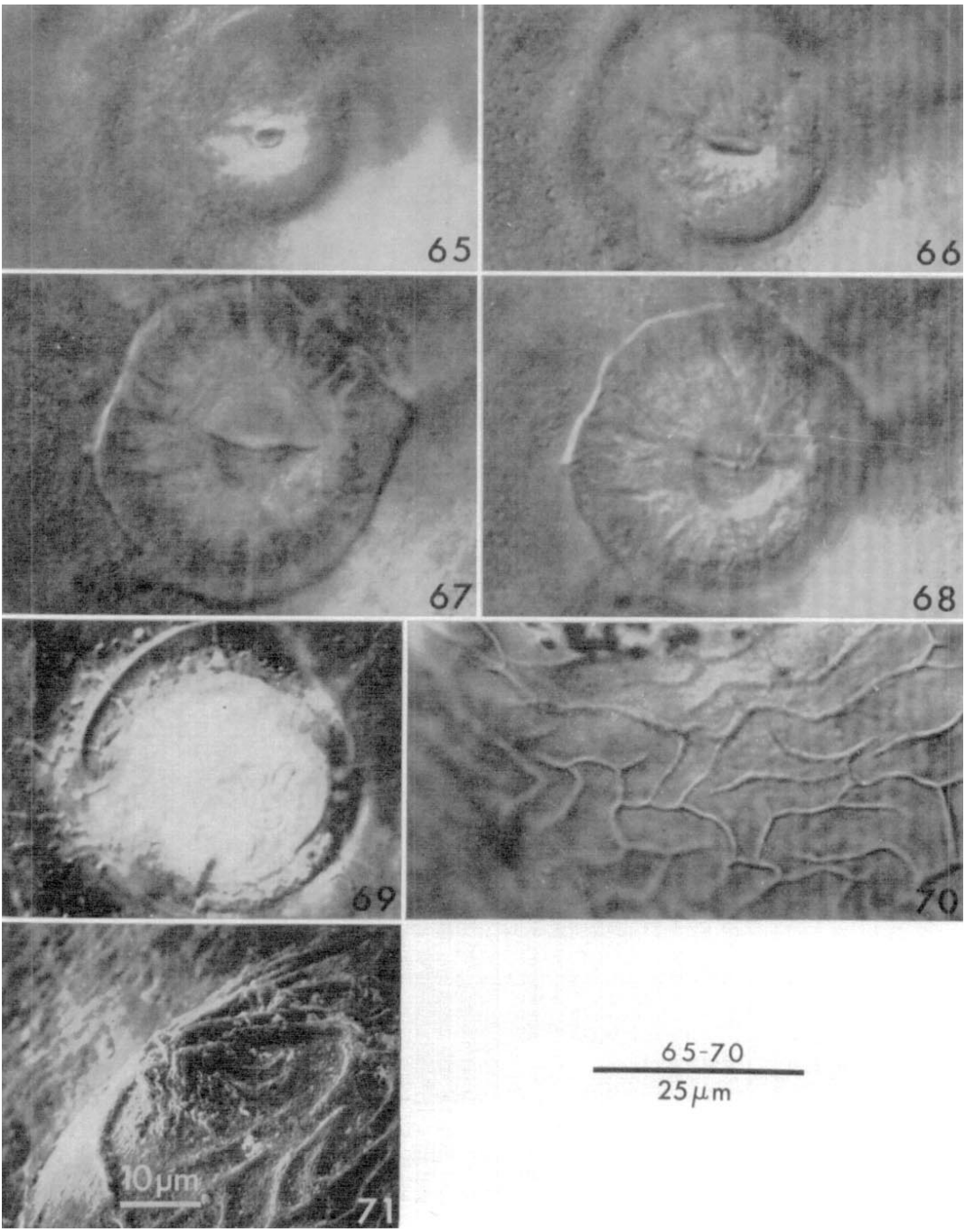
Diagnosis: Emended from Krall and



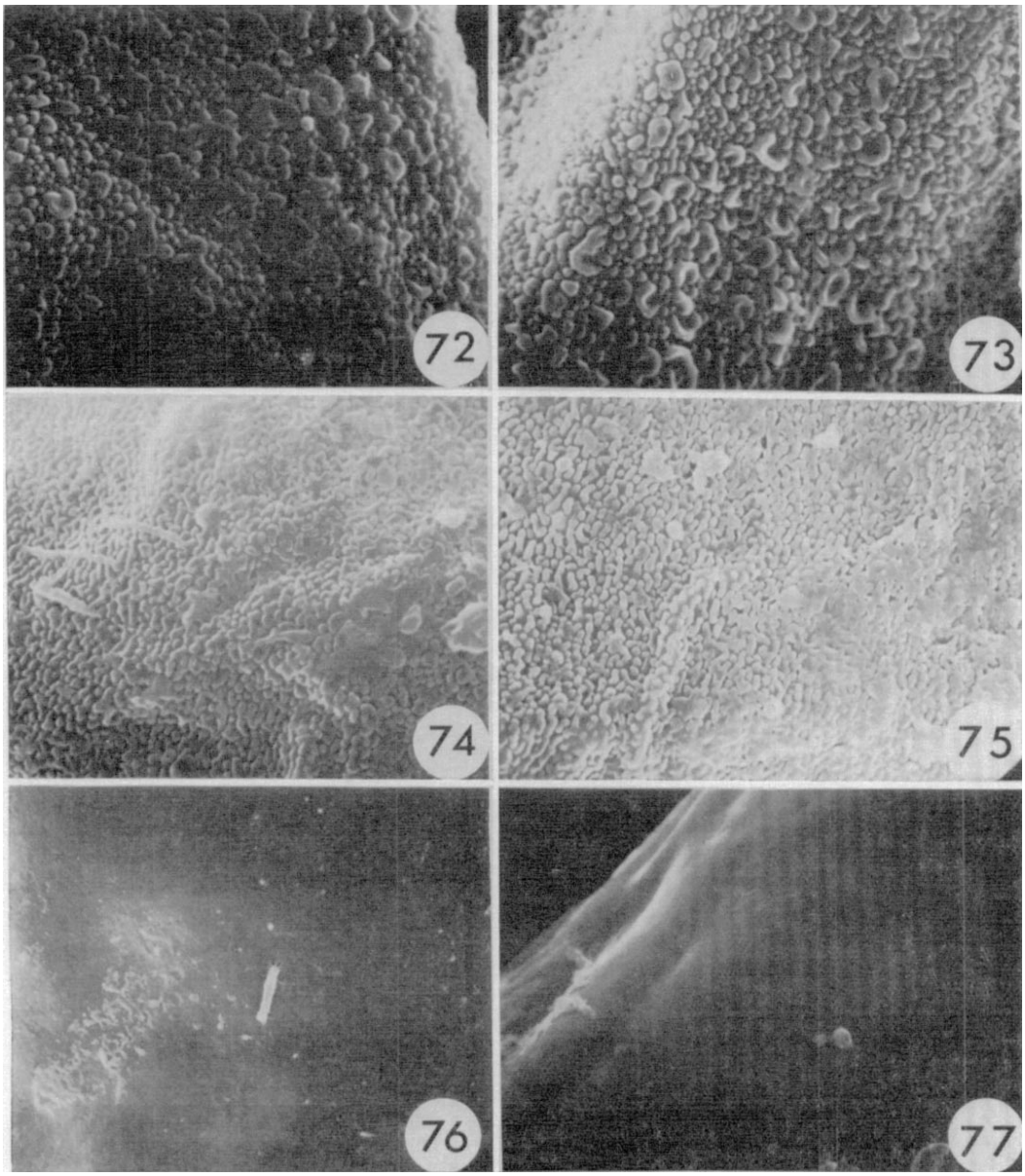
Figs. 54–55. Cuticular ridges in anal-vulva region of *Globodera* species 54) *G. pallida.* 55) *G. rostochiensis* (after Stone [52]).



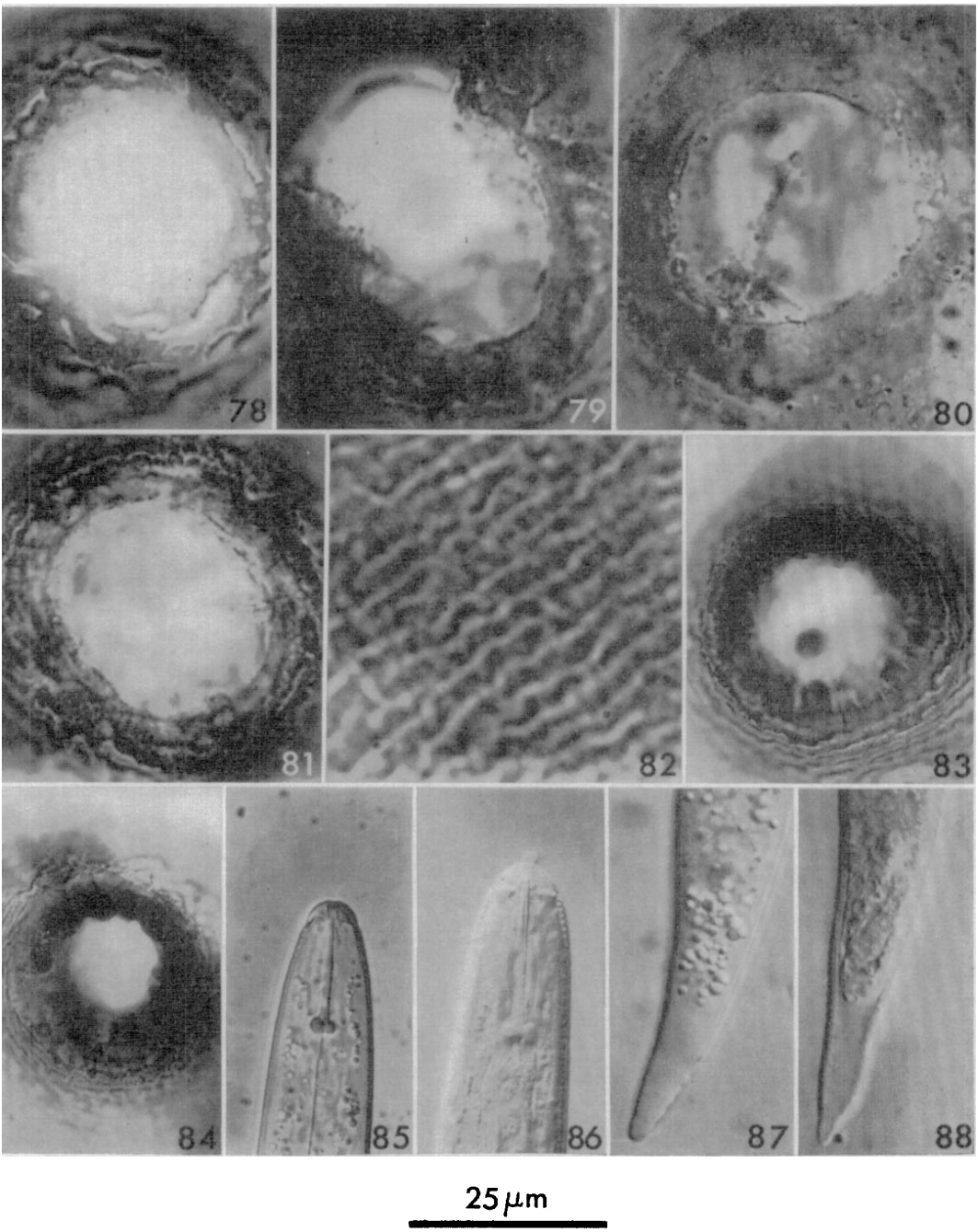
Figs. 56–64. Photomicrographs of cyst, second-stage larva, and male of *Sarisodera hydrophila*. 56) Vulva cone showing vulva sunken into cone. 57) Subcuticular punctations at midbody of cyst. 58) Layer between subcuticlar punctations and external cuticle. 59) External cuticle, note lacelike pattern. 60) Male, stylet. 61) Male, tips of spicules. 62) Male, proximal end of spicules (male has no tail). 63) Second-stage larva, stylet. 64) Second-stage larva, tail.



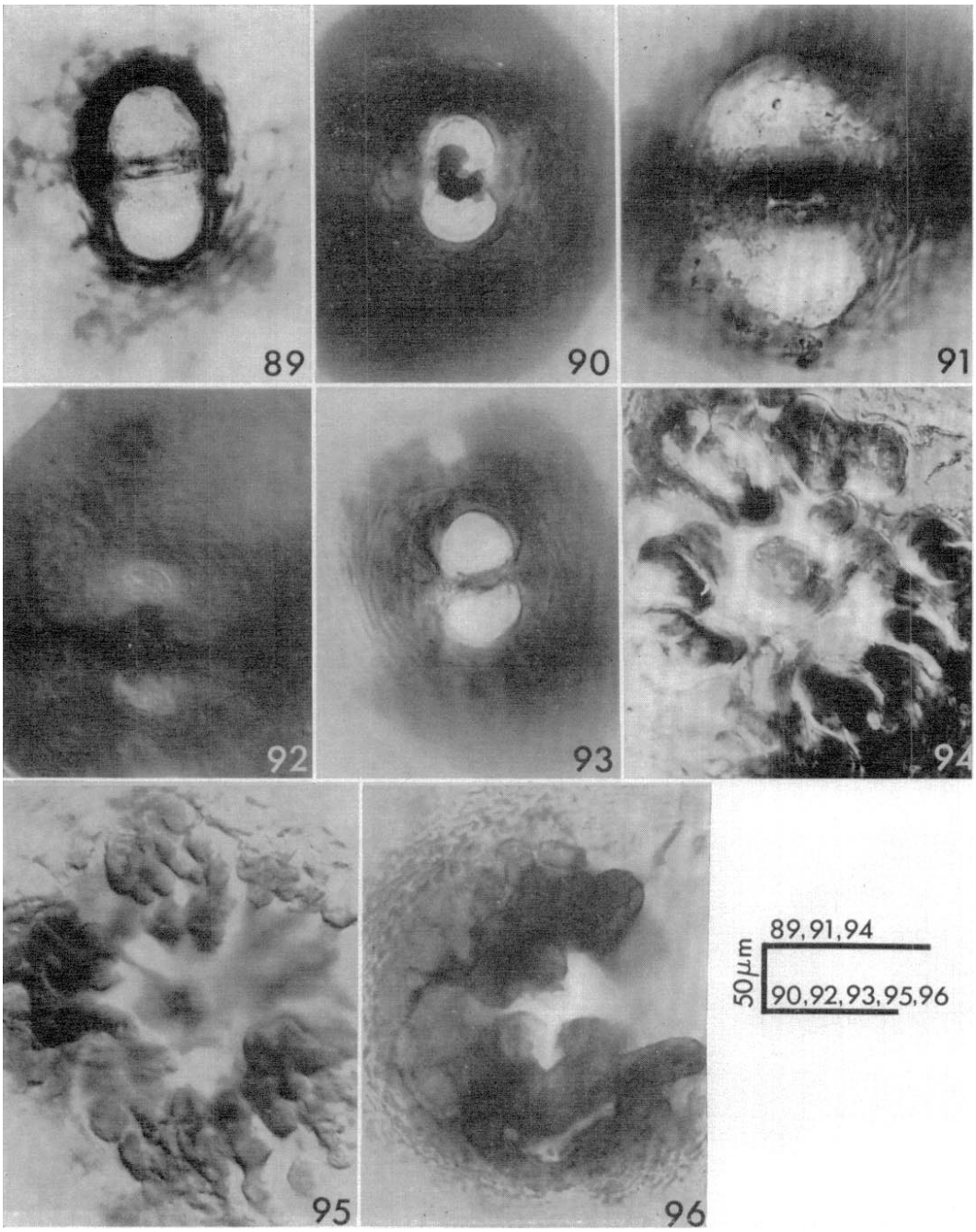
Figs. 65-71. Photomicrographs of vulva cone and cuticle of female and cyst of *Heterodera betulae*. 65) Vulva slit. 66) Slightly below vulva slit, beginning of three-layered core. 67) Lower level of core (approx. 12 μm below vulva slit) showing serrated wall of vagina and muscular bands extending out from wall. 68) Core area about 20 μm below level of vulva slit. 69) Newly formed cyst, fenestral area. 70) Cuticular pattern at midbody of cyst. 71) Scanning electron micrograph of mature female showing short vulva cone and unique external cuticular pattern.



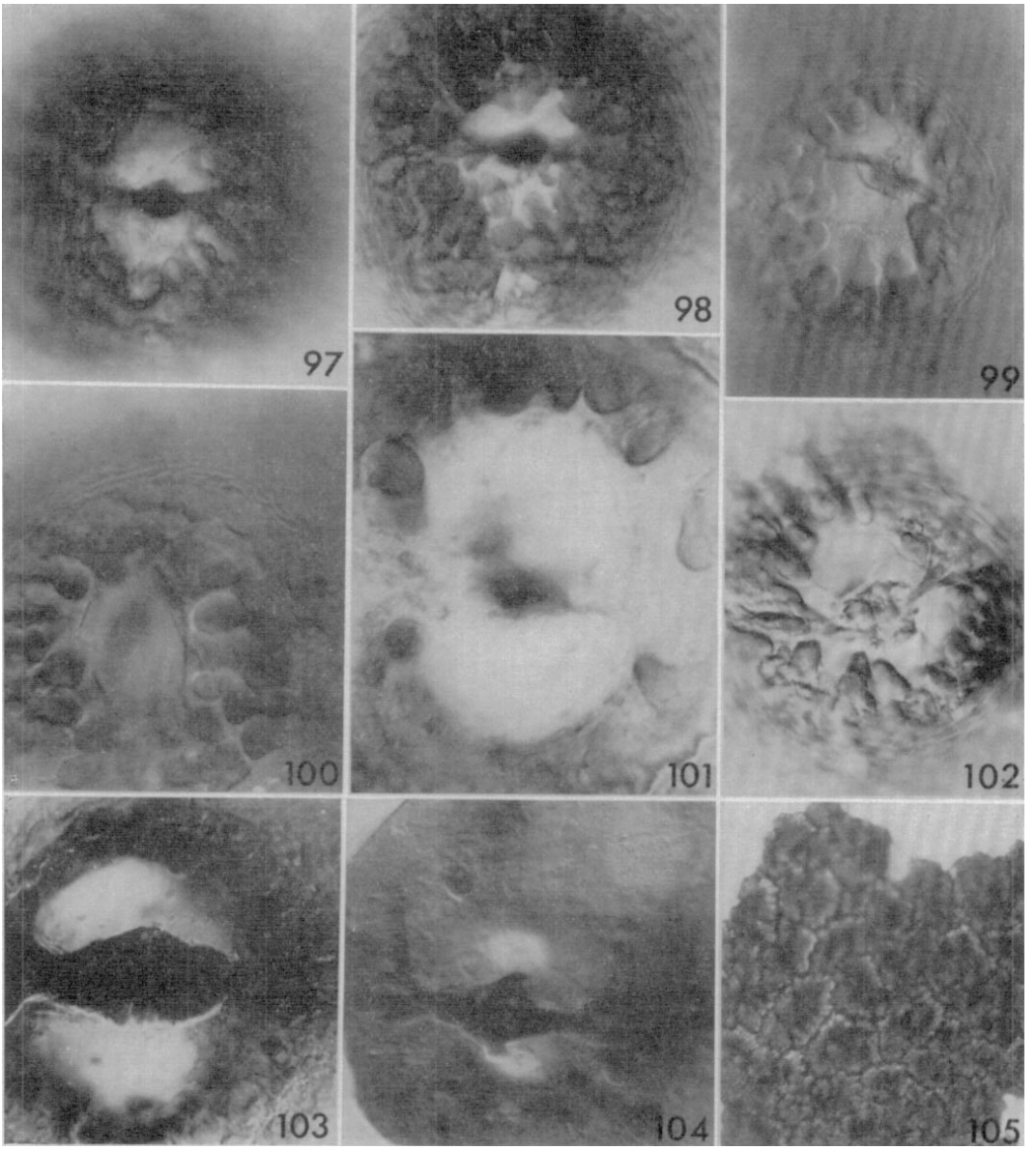
Figs. 72–77. Scanning electron micrographs of the egg shell surface of *Cactodera* species. 72, 73) *C. cacti,* shell heavily punctate. 74, 75) *C. thornei,* shell distinctly punctate. 76) *C. amaranthi,* shell without visible markings. 77) *C. weissi,* shell without visible markings. (From Golden and Raski [18]; the magnification given in the original publication of 5000 × is the same here.)

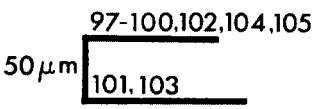


Figs. 78–88. Photomicrographs of fenestral areas and wall pattern of cysts, and heads and tails of second-stage larvae of *Cactodera* species. 78) *C. amaranthi,* fenestra. 79) *C. cacti,* fenestra. 80) *C. thornei,* fenestra. 81) *C. weissi,* fenestra. 82) External cyst wall pattern near midbody of *Cactodera* species. 83) *C. amaranthi,* vulval denticles. 84) *C. weissi,* vulval denticles. 85, 87) *C. weissi,* head and tail, stylet averaging 20 μm in length. 86, 88) *C. thornei,* head and tail, stylet averaging 27 μm in length.

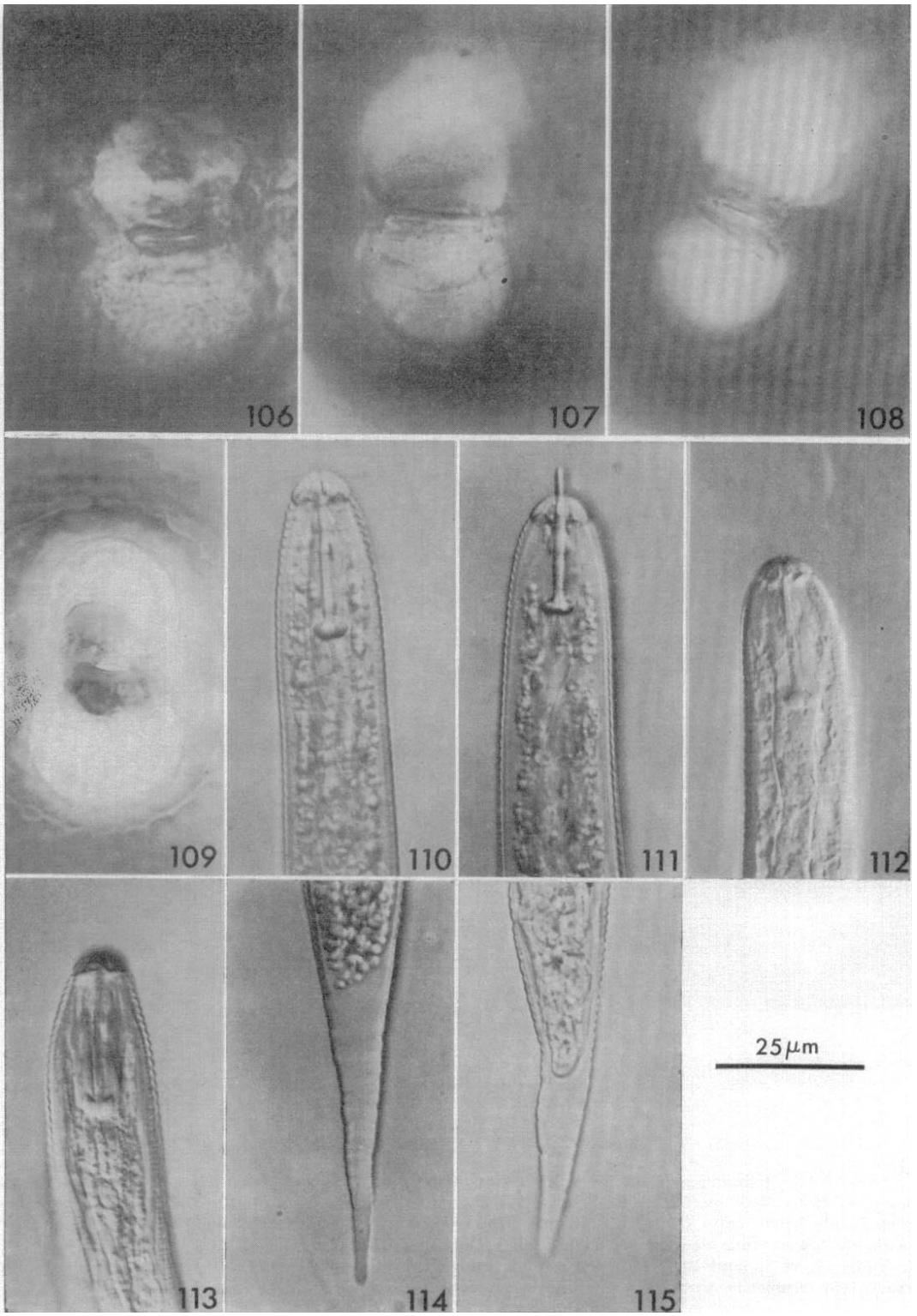


Figs. 89–96. Photomicrographs of fenestra, underbridge and bullae of *Heterodera* species cysts, *avenae* group. 89) *H. avenae,* fenestra, from Ontario, Canada. 90) *H. iri,* fenestra, from Ireland. 91) *H. latipons,* fenestra, from P.E.I., Canada. 92) *H. latipons,* fenestra, from Israel. 93) *H. mani,* fenestra, from Ireland. 94)*H. avenae,* bullae, from Canada. 95) *H. iri,* bullae, from Ireland. 96) *H. mani,* bullae, from Ireland.





Figs. 97–105. Photomicrographs of vulva cones of cysts showing vulva denticles, bullae, and underbridge of *Heterodera* species, *avenae* group. 97) *H. iri,* vulva denticles, from Ireland. 98) *H. iri,* bullae immediately below vulva denticles of Figure 97. 99) *H. iri,* vulva denticles, from USA. 100) Bullae immediately below vulva denticles of Figure 99. 101) *H. mani,* vulva denticles, from USA. 102) *H. iri,* underbridge, from Ireland 103) *H. latipons,* underbridge, from Canada. 104) *H. latipons,* underbridge, from Israel. 105) *H. avenae,* thick subcrystalline layer of mature female from Oregon, USA.


106
107
108
109
110
111
112
113
114
115
25 μm

Krall (31).

Mature female and cyst: With posterior protuberance, spherical to lemon shaped, vulva slit short (less than 20 μm), circumfenestrate, bullae and underbridge absent, vulva denticles present, characteristic cuticular pattern.

Second-stage larva: Stylet to 28 μm in length, labial disc present but with low profile, esophageal glands fill body width, phasmids without lenslike structure in muscle layer.

Male: Length up to 1.7 mm, labial disc present but with low profile, tail present, length less than one-half body width.

Eggs: Shell heavily punctate to hyaline without visible markings.

Type species: Cactodera cacti (Filipjev & Schuurmans Stekhoven, 1941) Krall and Krall, 1978.

Cactodera amaranthi (Stoyanov, 1972) Krall & Krall, 1978 (Figs. 76, 78, 83)

Described and illustrated by Stoyanov (57). Golden and Raski (18) redescribed and illustrated all stages of this species in great detail based on specimens from Cuba and Florida.

Type host and locality: Amaranthus viridis L. Terrenos del Institute de Investigaciones Tropicales, Santiago, de las Vegas, Havana, Cuba.

Distribution: Western Hemisphere—Havana, Cuba; Florida, Colorado, Illinois, Kansas, Missouri, and Tennessee, USA; Mexico.

Cactodera cacti (Filipjev & Schuurmans Stekhoven, 1941) Krall & Krall, 1978 (Figs. 72, 73, 79)

Described first by Adam (1). Golden and Raski (18) redescribed and illustrated all stages of this species based on specimens from Georgia in USA, Mexico, and Yugoslavia.

Type host and locality: Collected by Adam (1) from cactus plants (*Phyllocactus akkermani* Walp. and *Cereus speciosus* K. Schumacher) from Maartensdiijk near Utrecht, The Netherlands.

Distribution: Western Hemisphere—Brazil, Canada, Colombia, Mexico, and Colorado, Florida, Georgia, Minnesota, and New York, USA. *World*—Algeria, Austria, Australia, Argentina, Belgium, Czechoslovakia, England, France, Germany, Hungary, India, Italy, Israel, Japan, Korea, Malta, Sweden, Switzerland, The Netherlands, Vietnam, and Yugoslavia.

Occurrence of this species in Canada, also reported by Golden and Raski (18), is based on USDA Nematode Collection records showing a U.S. mail interception of "Cacti" from Ontario, Canada, in 1955. From the soil with the unidentified cactus, 200 cysts were recovered and identified as "*Heterodera cacti.*" No further collection of this species has been made in Canada.

Cactodera thornei (Golden & Raski, 1977) Krall & Krall, 1978 (Figs. 74, 75, 80, 86, 88)

Described and illustrated by Golden and Raski (18).

Type host and locality: Miner's lettuce (*Montia perfoliata* (Donnex Wild) Howell). Persian walnut orchard near San Jose, California, USA.

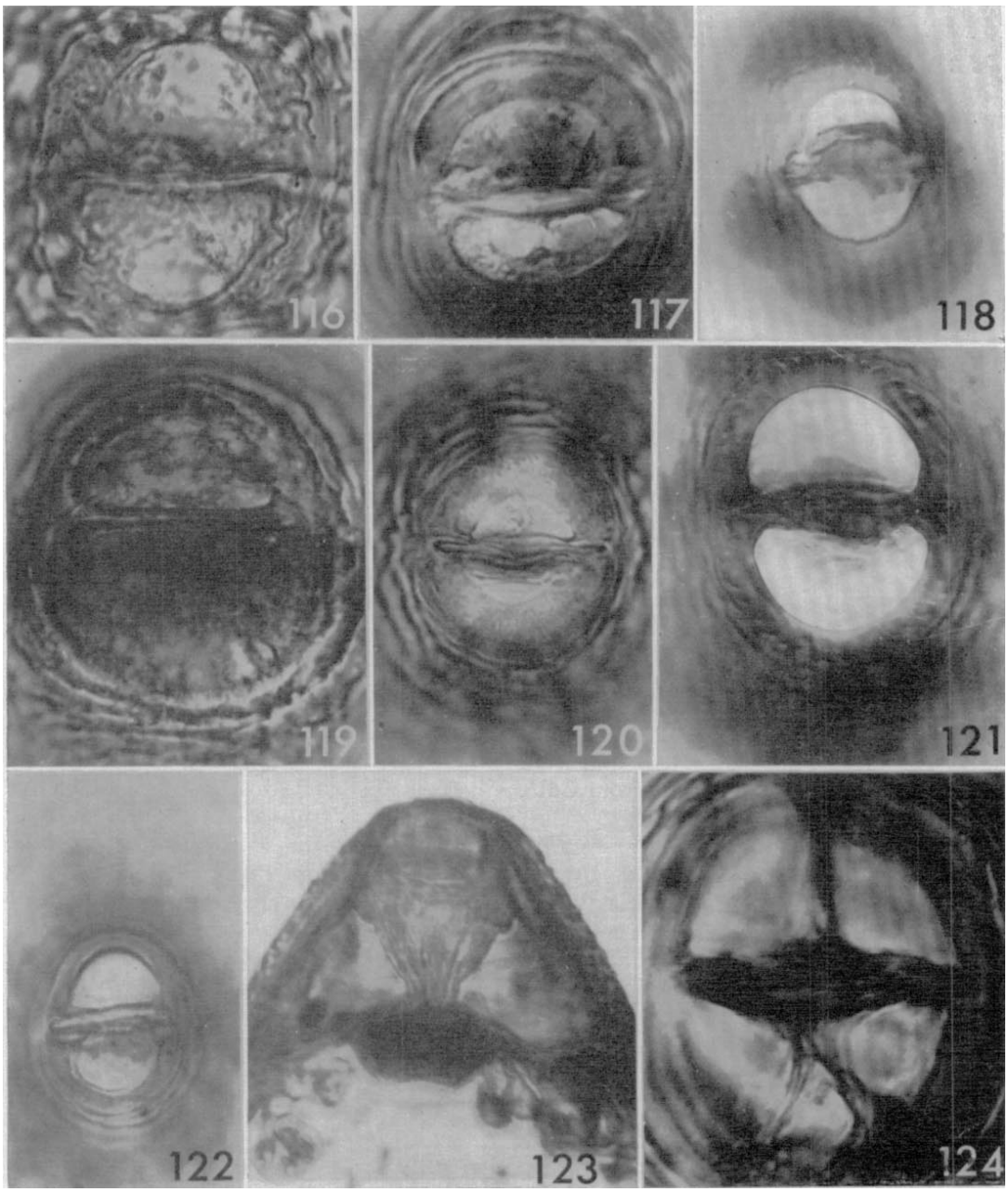
Distribution: Only San Jose, Santa Clara, Linden, and Sacramento in California, USA.

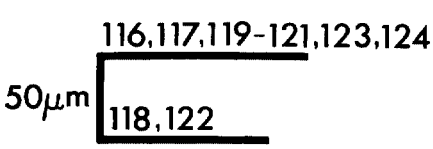
Cactodera weissi (Steiner, 1949) Krall & Krall, 1978 (Figs. 77, 81, 84, 85, 87)

First described by Steiner (51), and later Golden and Raski (18) provided additional information on all stages of this species and designated lectotypes.

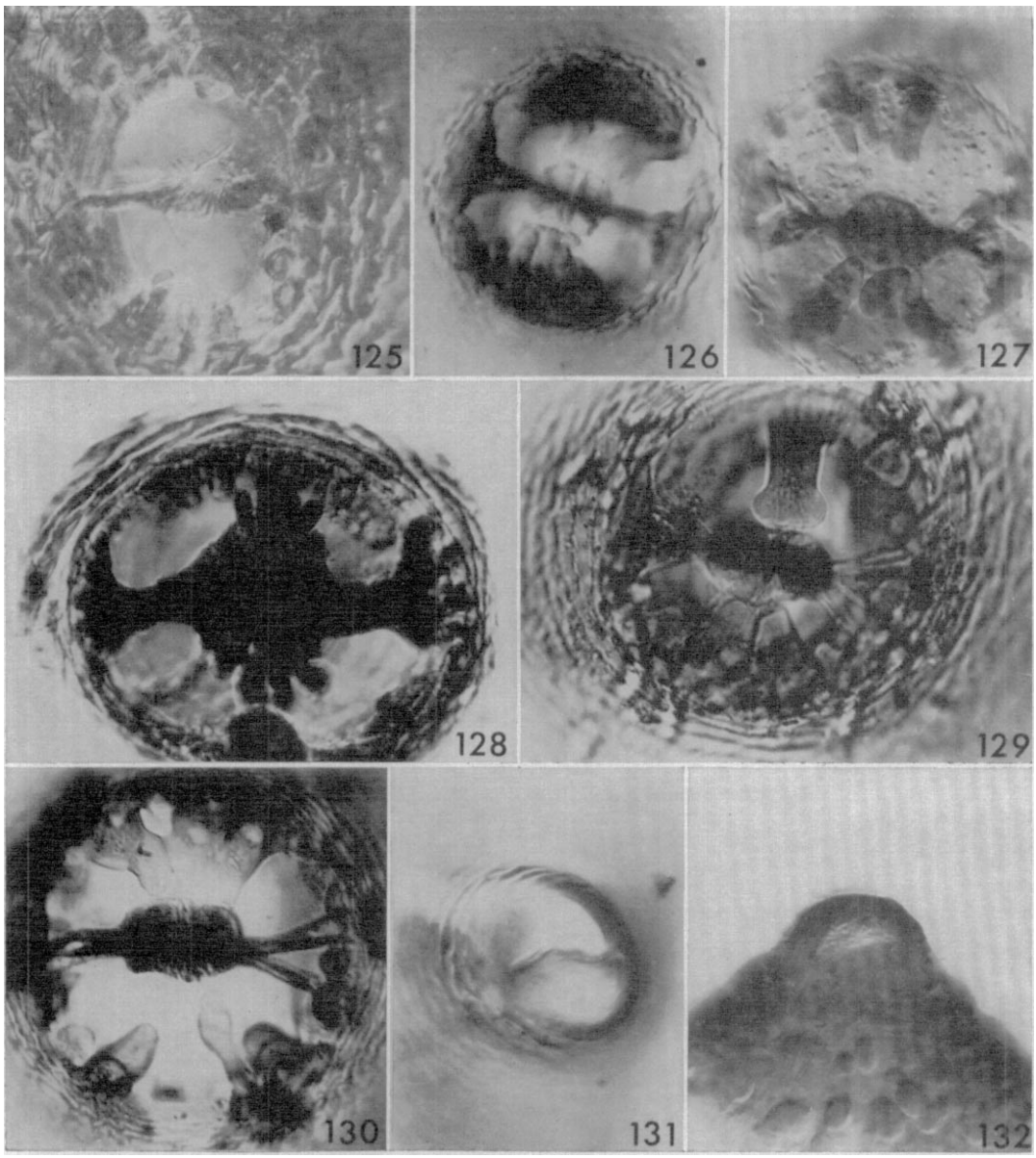
Type host and locality: Knot-weed (*Polygonum pennsylvanicum* L.). Near

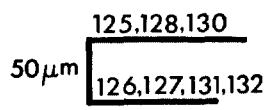
Figs. 106–115. Photomicrographs of vulva slit (106–109) of female, and head and tail of second-stage larva (110–115) of *Heterodera* species of the *avenae* group. 106) *H. avenae*, USA. 107) *H. iri*, USA. 108) *H. mani*, Ireland. 109) *H. mani*, USA, 110) *H. avenae*, United Kingdom, stylet knobs shallowly concave anteriorly. 111) *H. avenae*, Oregon, USA, stylet knobs shallowly concave anteriorly. 112) *H. iri*, USA, stylet knobs rounded. 113) *H. mani*, from The Netherlands, stylet knobs deeply concave anteriorly. 114) *H. avenae*, tail, from Oregon, USA. 115) *H. mani*, tail, from The Netherlands.



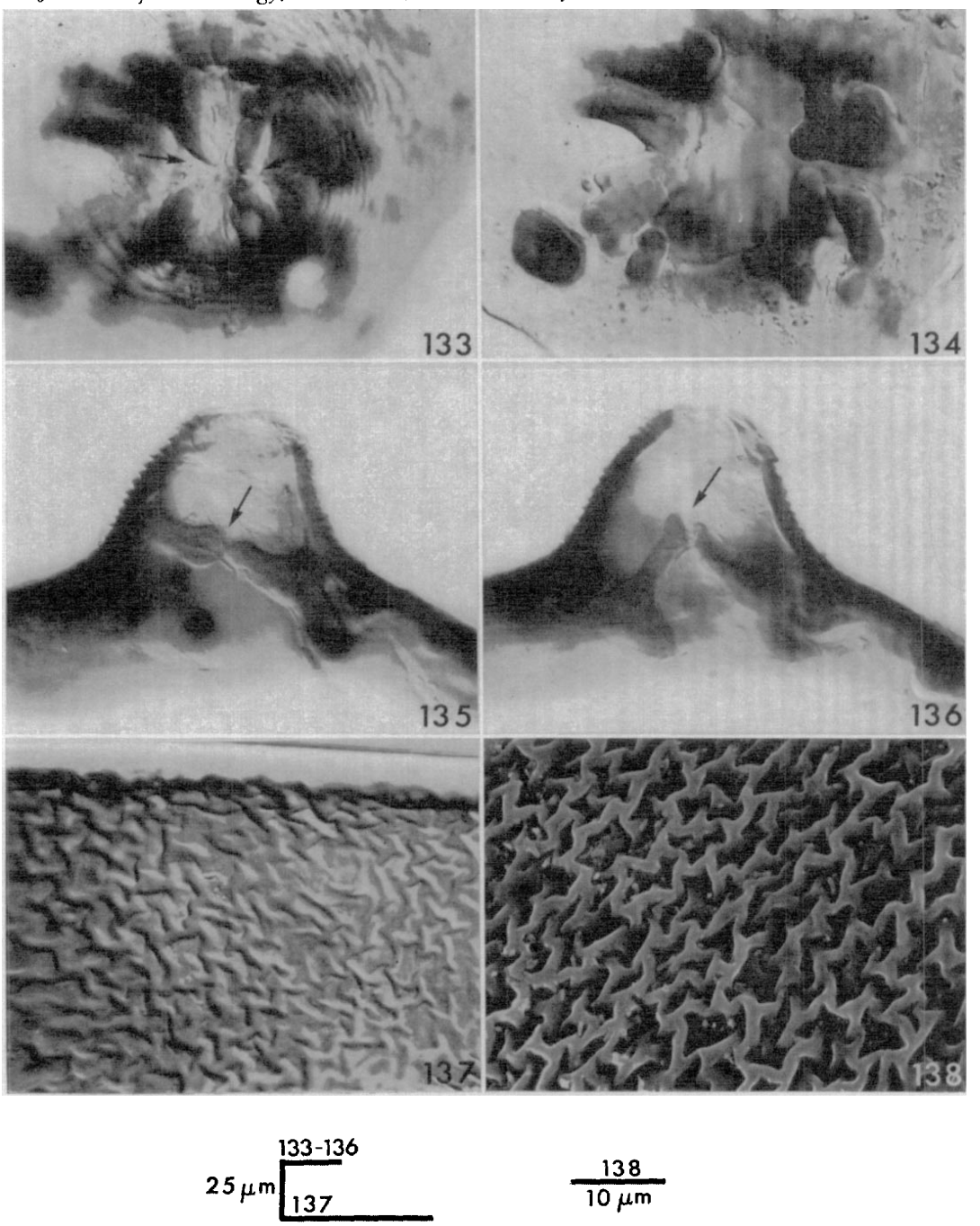


Figs. 116–124. Photomicrographs of fenestra (116–122) and underbridge of *Heterodera* species cysts, *schachtii* group. 116) *H.* fici, California, USA. 117) *H. glycines,* USA. 118) *H. lespedezae,* USA. 119) *H. leuceilyma* 120) *H. schachtii,* Canada. 121) *H. trifolii,* Canada. 122) *H. zeae,* USA. 123) *H. trifolii,* dorso-ventral view of vulva cone showing heavy underbridge, sheaf-like vagina, and bullae. 124) *H. glycines,* two underbridges in newly developed cyst, also found sometimes in *H. trifolii* cysts.

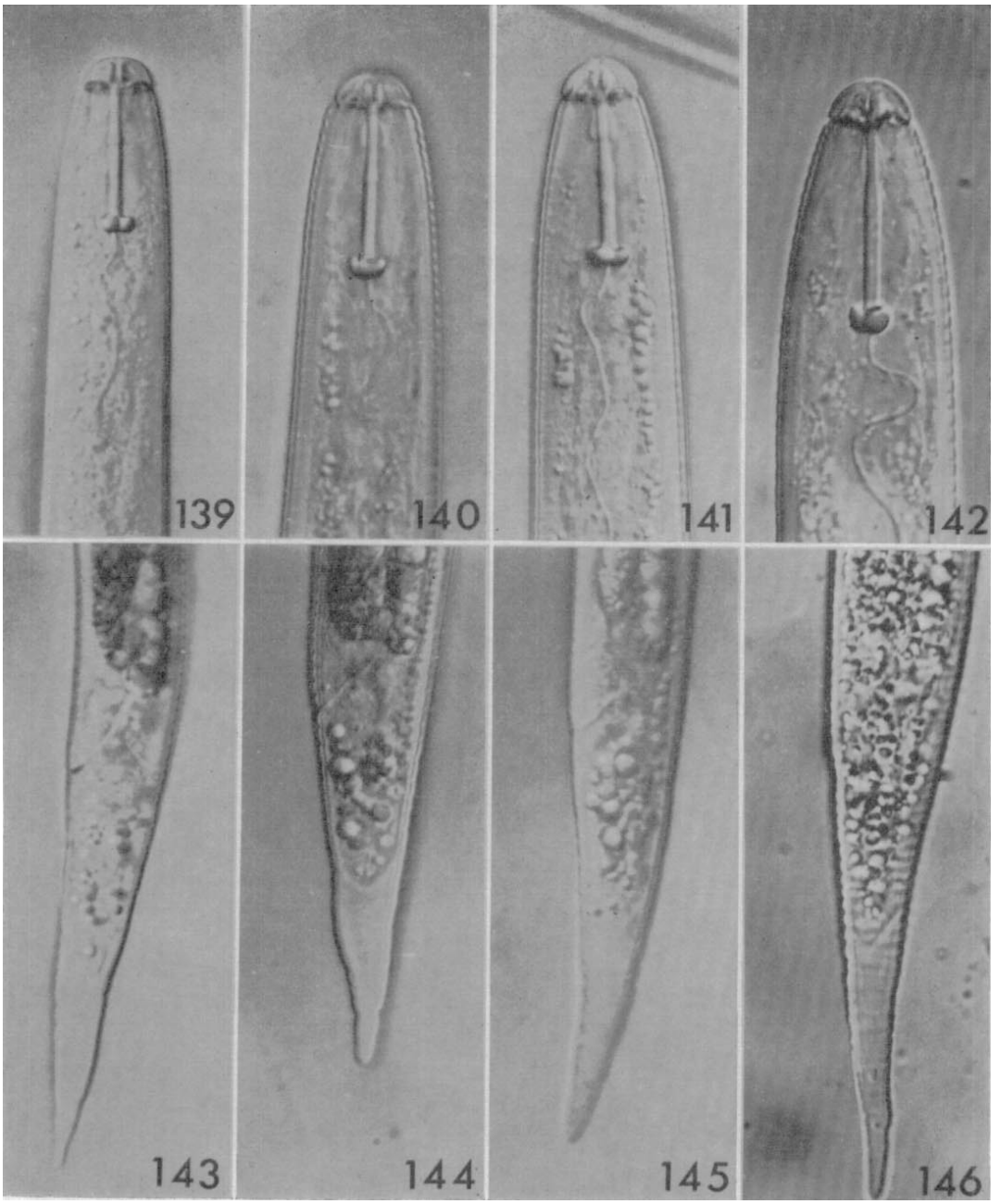




Figs. 125–132. Photomicrographs of underbridge (125–131) and bullae in cysts of *Heterodera* species, *schachtii* group. 125) *H. fici,* note small scattered bullae about underbridge. 126) *H. glycines.* 127) *H. lespedezae.* 128) *H. leuceilyma,* note fingerlike projections. 129) *H. schachtii.* 130) *H. trifolii.* 131) *H. zeae,* USA. 132) *H. fici,* lateral view of vulva cone showing many scattered bullae.

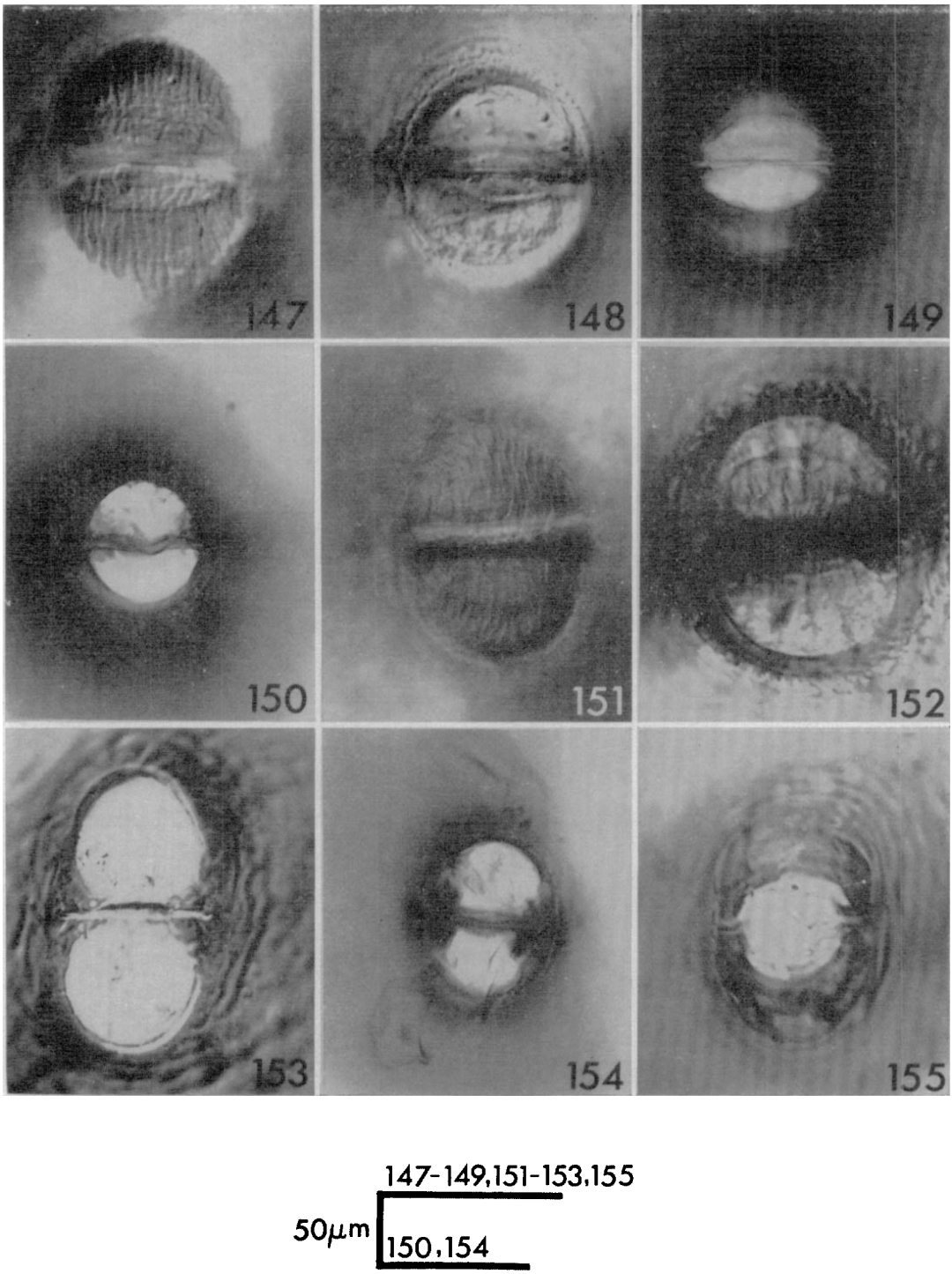


Figs. 133–138. Photomicrographs of *Heterodera zeae* cysts. 133) Four fingerlike bullae immediately below underbridge in vulva cone. 134) Bullae immediately below fingerlike bullae. 135, 136) Dorso-ventral view of two of the four fingerlike bullae at same level. 137) External cuticular pattern of cyst at midbody. 138) SEM micrograph of cyst external cuticular surface at midbody, interlocking ridges to form a zig-zag pattern.

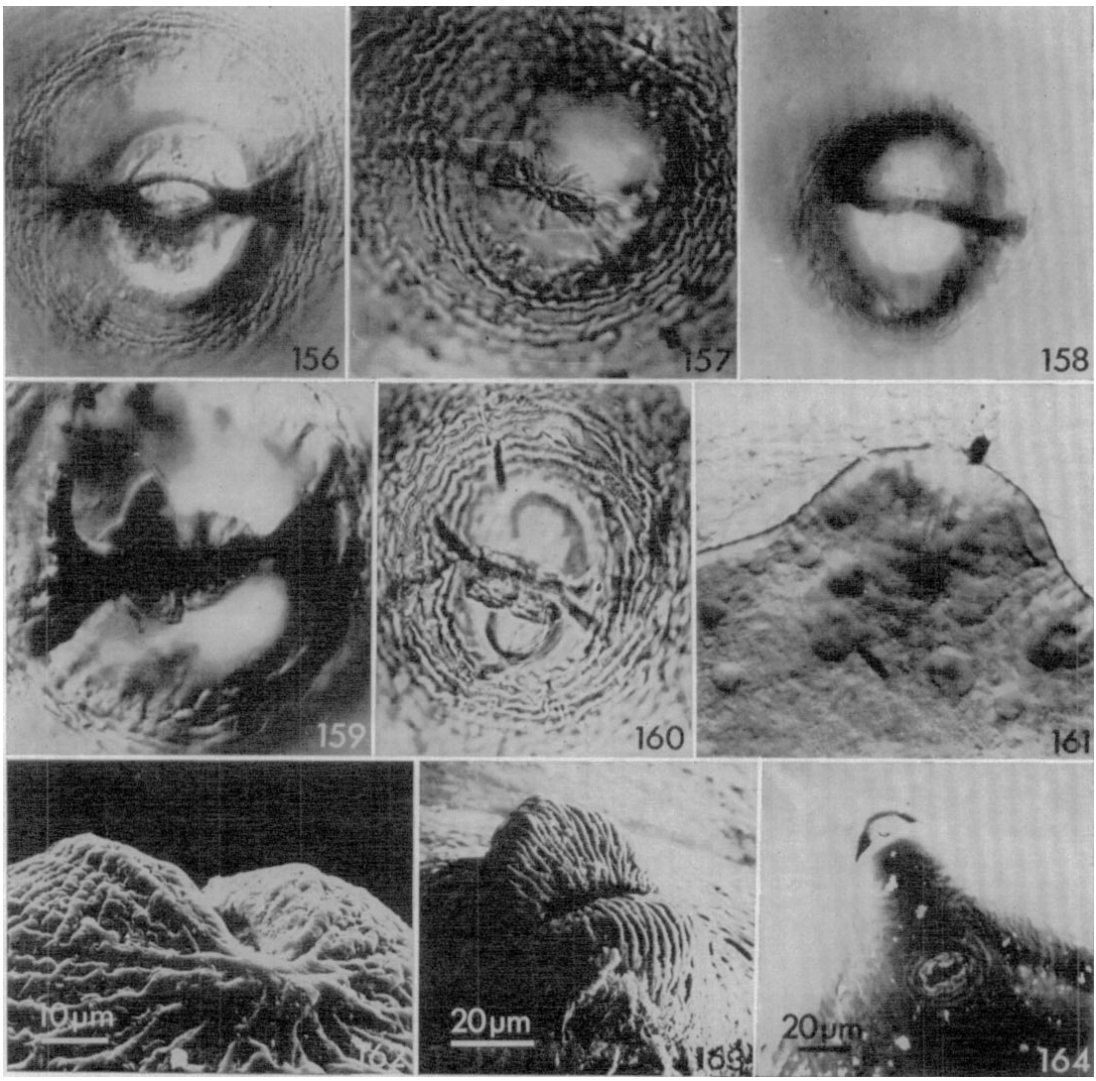


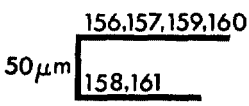
25μm

Figs. 139–146. Photomicrographs of second-stage larvae of *Heterodera* species, *schachtii* group, head and tails. 139, 143) *H. zeae*. 140, 144) *H. glycines*. 141, 145) *H. schachtii*. 142, 146) *H. trifolii*.



Figs. 147–155. Photomicrographs of fenestra of *Heterodera* species, *goettingiana* group. 147) *H. canadensis,* female. 148) *H. canadensis,* cyst. 149) *H. cruciferae,* cyst. 150) *H. cyperi,* cyst. 151) *H. graminophila,* female. 152) *H. graminophila,* cyst. 153) *H. humuli,* cyst. 154) *H. longicolla,* cyst. 155) *H. mothi,* cyst from India.





156–164. Photomicrographs of underbridge (156-160), bullae and fenestra of *Heterodera* species, *goettingiana* group. 156) *H. canadensis*. 157) *H. cruciferae*. 158) *H. cyperi*. 159) *H. graminophila*. 160) *H. humuli*. 161) *H. mothi*, lateral view of cone showing small, scattered bullae. 162) Scanning electron micrograph of *H. canadensis* female showing wavy lines extending from the outer edge of the fenestra to the vulva slit. 163) Scanning electron micrograph of *H. graminophila* female showing distinct wavy lines extending from the outer edge of the fenestra to the vulva slit. 164) *H. cyperi*, scanning electron micrograph, lateral view of vulva cone, showing perianal pattern.

Table 1. Measurements* (μm) of mature females and terminal structures of *Punctodera* species.

Species	Reference	Body			Fenestra		Vulva	Shape	Stylet	DGO
		Length**	Neck length	Width	Vulva (L/W)	Anal (L/W)	slit length		length	
P. chalcoensis	(55)	473 ± 105 (...)	142 ± 24 (...)	429 ± 120 (...)	30.7 ± 7.0 32.1 ± 7.0	29.5 ± 5.7 31.1 ± 5.3	4.0 ± 0.5 (...)	Sub-spherical	25.8 ± 0.9 (...)	5.7 ± 0.9 (...)
P. matadorensis	(42)	483 (430–560)	... (115–140)	403 (320–530)	20 20	20 20	4 (...)	Ovoid	22 (21–23)	5.0 (...)
P. punctata	(59)	520 (...)	... (...)	... (...)	... ...	... ...	... (...)	Pear	... (...)	... (...)
	(***)	... (...)	... (...)	... (...)	16.5 20.3	17.8 diam.	3.8 (...)	Pear	... (...)	... (...)

*Averages outside parenthesis; ranges within parenthesis.
**Body length of females and cysts includes neck length unless otherwise specified.
***Authors' measurement of specimens in Thorne's 1927 collection.

Table 2. Measurements* (μm) of cysts and terminal areas of *Punctodera* species.

Species	Reference	Body			Fenestra		Vulva	Bullae	Shape
		Length**	Neck length	Width	Vulva (L/W)	Anal (L/W)	slit length		
P. chalcoensis	(55)	441 ± 69 (...)	95 ± 26 (...)	416 ± 61 (...)	18.1 ± 2.7 19.8 ± 2.9	21.1 ± 3.4 22.4 ± 3.1	4.2 ± 0.4 (...)	Rare, small scattered	Spherical to sub-spherical
P. matadorensis	(42)	... (500–600)†	... (...)	... (480–500)	24 24	25 25	... (...)	Several large, in all cysts	Ovoid
P. punctata (Canada)	(39)	... (310–750)†	... (...)	... (260–500)	(18–30) (18–40)	Same size as vulva	... (...)	None	Pear
	(***)	499.41 ± 64.39 (...)	86.61 ± 18.07 (...)	345 ± 38 (...)	... ...	... ...	... (...)	None	Pear

*See Table 1.
**See Table 1.
***See Table 1.
†Excluding neck.

Table 3. Measurements* (μm) of males of *Punctodera* species.

Species	Reference	Body length	Spicule length	Stylet length	DGO	Tail length
P. chalcoensis	(55)	985 ± 69 (...)	31.9 ± 1.8 (...)	26.8 ± 0.8 (...)	4.0 ± 0.6 (...)	2.8 ± 1.4 (...)
P. matadorensis	(42)	... Male unknown ...				
P. punctata	(59)	... (900–1300)	32.0 (...)	24 (...)	2.6 (...)	1.8 (...)
	(***)	900 ± 99 (...)	32.4 ± 0.7 (...)	23.7 ± 1.0 (...)	3.8 (...)	... (...)

*See Table 1.
***See Table 1.

Table 4. Measurements* (μm) of second-stage larvae of *Punctodera* species.

Species	Reference	Body length	Lateral lines	Stylet length	Tail length	Hyaline terminal length	Head tip to base of esophageal gland	DGO
P. chalcoensis water mounts	(55)	542 ± 26 (...)	4	24.4 ± 0.2 (...)	66.2 ± 3.5 (...)	38.6 ± 3.4 (...)	176 ± 15.1 (...)	5.5 ± 0.8 (...)
glycerol mounts	(55)	533 ± 29 (...)	4	24.7 ± 0.6 (...)	63.2 ± 3.3 (...)	38.2 ± 3.1 (...)	... (...)	5.1 ± 0.7 (...)
P. matadorensis water mounts	(42)	540 (510–580)	4	24 (23–25)	62 (60–65)	36.5 (35–40)	... (...)	5.5 (5–6)
lactophenol mounts	(42)	526 (500–570)	4	24.6 (24–25)	61.7 (58–65)	39.1 (35–42)	222 (200–250)	... (...)
P. punctata	(59)	... (350–470)	... (...)	26 (...)	... (...)	... (...)	... (...)	... (...)
(England)	(8)	... (550–582)	... (...)	... (...)	... (...)	... (...)	... (...)	... (...)
(Canada)	(42)	... (480–530)	... (...)	... (...)	... (...)	... (...)	... (...)	... (...)
	(***)	464 (438–490)	4	25 (24.2–25.8)	70.1 (62.7–77.5)	40 (38.5–41.4)	175 (...)	4.5 (...)

*See Table 1.
***See Table 1.

Table 5. Measurements* (μm) of mature females of *Heterodera betulae* and species of *Dolichodera* and *Sarisodera*.

Genus & species	Reference	Body Length**	Body Width	Stylet length	DGO	Vulva-anus distance	Vulva slit length
H. betulae	(24)	618 ± 57 (381–945)†	512 ± 43 (342–720)	30.2 ± 0.48 (28.8–32.6)	4.8 ± 0.16 (4.1–5.3)	93 ± 10 (58–150)	5.84 ± 0.16 (5.1–6.6)
D. fluvialis	(44)	... (400–550)†	... (140–270)	15 (...)	... (...)	Short	... (...)
S. hydrophila	(64)	565 (359–688)	385 (238–481)	51 (45–56)	... (...)	... (...)	72 (62–85)

*See Table 1.
**See Table 1.
†Excluding neck.

Table 6. Measurements* (μm) of cysts and terminal areas of *Heterodera betulae* and species of *Dolichodera* and *Sarisodera*.

Genus & species	Reference	Body Length**	Body Width	Fenestra Length	Fenestra Width	Bullae
H. betulae	(24)	762 ± 56 (435–1,150)†	616 ± 43 (340–920)	21.96 ± 1.16 (11.9–29.8)	18.76 ± 1.12 (10.2–22.7)	Few cysts with bullae-like structures
D. fluvialis	(44)	575 (450–700)	235 (140–300)	20 diam.		Present in all cysts
S. hydrophila	(64)	(See female; no fenestra)				None

*See Table 1.
**See Table 1.
†Excluding neck.

Table 7. Measurements* (μm) of males of *Heterodera betulae* and species of *Dolichodera* and *Sarisodera*.

Genus & species	Reference	Body length	a	b	c	Spicule length	Stylet length	DGO	Tail length
H. betulae	(24)	1063 ± 121 (831–1,280)	... (...)	... (...)	... (...)	22.8 ± 1.5 (23.3–30.6)	29.1 ± 0.27 (28.5–29.6)	4.5 ± 0.49 (3.6–5.8)	6.2 ± 1.03 (5.1–10.2)
D. fluvialis	(44)	... Male unknown ...							
S. hydrophila	(64)	1053 (597–1,405)	46 (33–55)	7.3 (5.0–9.4)	... (...)	39 (33–46)	43 (38–46)	... (3.5–4.0)	No tail

*See Table 1.

Table 8. Measurements* (μm) of second-stage larvae of *Heterodera betulae* and species of *Dolichodera* and *Sarisodera*.

Genus & species	Reference	Total length	Lateral lines	Stylet length	Tail length	Hyaline terminal length	DGO
H. betulae	(24)	461 ± 3.59 (407–508)	3	26 ± 0.11 (24.6–27.6)	43.8 ± 0.46 (39–51)	21 ± 0.31 (15–26)	6.0 ± 0.1 (5.0–7.8)
D. fluvialis	(44)	600 (570–610)	3	23 (22–24)	103 (95–120)	... (...)	... (7–8)
S. hydrophila	(64)	479 (466–558)	4	40 (39–43)	54 (44–61)	31 (26–36)	5.0 (...)

*See Table 1.

Table 9. Measurements* (μm) of mature females and terminal areas of *Globodera* species.

Species	Reference	Body			Fenestra		Vulva slit length	Cuticle between vulva and anus	Stylet length	DGO
		Length**	Neck length	Width	Length	Width				
G. pallida (England)	(52)	... (500–800)	... (100–130)	... (375–625)	24.8 ± 3.7 diam. (Vulva basin)		11.5 ± 1.3 (...)	12.5 ± 3.1 ridges	27.4 ± 1.1 (...)	5.4 ± 1.1 (...)
G. rostochensis (England)	(52)	... (...)	... (...)	... (...)	22.4 ± 2.8 diam. (Vulva basin)		9.7 ± 1.9 (...)	21.6 ± 3.4 ridges	22.9 ± 1.2 (...)	5.7 ± 0.9 (...)
(East Germany)	(15)	520 (420–640)	... (...)	340 (270–430)	... (...)	... (...)	9 (6–11)	...	23 (22–24)	6.2 (5.8–7.0)
G. solancearum	(38)	632 ± 70 (411–873)	144 ± 32.5 (58–215)	430 ± 81 (293–614)	17.3 ± 2.0 (14–25)	21.2 ± 2.9 (16–29)	9.4 ± 1.5 (5–13)	Deeply etched	26.2 ± 1.7 (21–30)	6.0 ± 1.4 (3–11)
G. tabacum	(34)	464 (327–688)	... (...)	310 (201–516)	... (...)	... (...)	... (8–9)	Shallowly etched	22.4 (18.5–24.1)	5.5 (3.8–8.0)
G. virginiae	(37)	688 ± 78.7 (528–966)	152 ± 32.9 (59–231)	450 ± 67.5 (313–614)	19.3 ± 2.2 (14–26)	14.1 ± 1.4 (11–18)	9.2 ± 0.76 (8–11)	Maze-like	25 ± 1.58 (21–29)	6.1 ± 1.75 (3–11)

*See Table 1.
**See Table 1.

Table 10. Measurements* (μm) of cysts and terminal areas of *Globodera* species.

Species	Reference	Body			Fenestra		Vulva slit length	Tubercular crescents	Granek's ratio
		Length**	Neck length	Width	Length	Width			
G. pallida	(52)	579 ± 70 (...)	118 ± 20 (...)	534 ± 66 (...)	24.5 ± 5 diam. (...)		... (...)	Wide, tubercles discrete	2.1 ± 0.9 (...)
G. rostochensis (Canada)	(39)	... (360–650)†	... (...)	... (310–550)	... (10–30)	... (12–20)	... (10–11)	Narrow, tubercles clumped	3.7 (1.29–9.5)
(England)	(52)	445 ± 50 (...)	104 ± 19 (...)	382 ± 61 (...)	18.8 ± 2.2 diam. (...)		... (...)	As above	3.6 ± 0.8 (...)
(East Germany)	(15)	680 (450–990)	... (...)	540 (250–810)	15 diam. long axis (8–20)		... (...)	...	4.5 (2.0–7.0)
G. solanacearum	(38)	717 ± 58.7 (533–907)	154 ± 27.5 (98–256)	496 ± 55 (375–639)	23.7 ± 3.3 (15–32)	21.0 ± 2.4 (12–28)	... (...)	Wide, tubercles discrete	2.2 ± 0.4 (1.3–3.8)
G. tabacum (USA)	(34)	536 (337–740)	... (...)	459 (232–645)	... (...)	... (...)	... (...)	...	... (...)
	(39)	... (...)	... (...)	... (...)	... (22–30)	... (20–25)	... (10–11)	Wide, tubercles discrete	1.7 (1.02–2.2)
G. virginiae	(37)	767 ± 69.2 (537–937)	145 ± 31.3 (85–230)	528 ± 65.6 (383–660)	19.7 ± 3.1 (13–28)	18.7 ± 2.3 (13–25)	... (9–10)	Wide, tubercles discrete	2.8 ± 0.5 (1.5–4.2)

*See Table 1.
**See Table 1.
†Excluding neck.

Table 11. Measurements* (μm) of males of *Globodera* species.

Species	Reference	Body length	a	b	c	Spicule length	Stylet length	DGO	Tail length
G. pallida	(52)	1,198 ± 104 (...)	... (...)	... (...)	... (...)	36.3 ± 4.1 (...)	27.5 ± 1.0 (...)	3.4 ± 1.0 (...)	5.2 ± 1.4 (...)
G. rostochiensis (England)	(52)	1,197 ± 100 (...)	... (...)	... (...)	... (...)	35.5 ± 2.8 (...)	25.8 ± 0.9 (...)	5.3 ± 0.9 (...)	5.4 ± 1.1 (...)
(East Germany)	(15)	1,080 (890–1,270)	27 (22–36)	5.9 (4.9–7.3)	267 (161–664)	35 (32–39)	26 (25–27)	6.4 (5.3–7.0)	4.4 (1.7–6.7)
G. solanacearum	(38)	1,108 ± 103 (750–1,450)	... (...)	... (...)	... (...)	32.9 ± 1.6 (29–35)	21.3 ± 0.9 (24–27)	2.3 ± 0.7 (1.5–4.0)	4.3 ± 1.2 (2–8)
G. tabacum	(34)	1,123 (710–1,355)	33 (27–40)	7.4 (6.3–8.7)	1,478 (284–5,325)	... (26–34)	26 (24–27)	3.6 (2.0–5.5)	... (0.2–3.6)
G. virginiae	(37)	1,163 ± 98.3 (850–1,325)	43.1 ± 4.05 (27–52)	... (...)	536 ± 330 (189–2,400)	32.8 ± 1.3 (30–35)	26.6 ± 0.97 (24–29)	3.5 ± 0.86 (2–6)	... (...)

*See Table 1.

Table 12. Measurements* (μm) second-stage larvae of *Globodera* species.

Species	Reference	Total length	Lateral lines	Stylet length	Tail length	Hyaline terminal length	DGO
G. pallida	(52)	486 ± 23 (...)	4	23.8 ± 1.0 (...)	51.1 ± 2.8 (...)	26.6 ± 4.1 (...)	2.7 ± 0.9 (...)
G. rostochiensis	(52)	468 ± 20 (...)	4	21.8 ± 0.7 (...)	43.9 ± 11.6 (...)	26.5 ± 1.8 (...)	2.6 ± 0.6 (...)
	(15)	430 (370–470)	4	22 (21–23)	51 (44–57)	24 (18–30)	5.5 (5.0–6.7)
G. solanacearum	(38)	497 ± 32.0 (390–577)	4	23.9 ± 0.5 (22–26)	50.3 ± 3.9 (33–60)	24 ± 2.7 (16–30)	5.5 ± 0.6 (5–7)
G. tabacum	(34)	476 (410–527)	4	24 (22–26)	52 (46–59)	28 (22–31)	5.5 (4.3–6.8)
G. virginiae	(37)	503.7 ± 31.7 (419–592)	4	23.7 ± 0.97) (19–28)	50.3 ± 3.8 (34–61)	27.1 ± 3.3 (19–35)	6.1 ± 0.8 (3–9)

*See Table 1.

Table 13. Measurements* (μm) of mature females and vulva cone structures of *Cactodera* species.

Species	Reference	Body			Fenestra		Vulva slit length	Stylet length	DGO
		Length**	Neck length	Width	Length	Width			
C. amaranthi (Cuba)	(57)	324 (135–462)	... (91–143)	196 (119–290)	22.1 (15.6–28.6)	22.1 (20.8–26.0)	15.2 (10.4–18.2)	23.4 (...)	... (...)
(USA)	(18)	563 ± 98 (404–688)	... (...)	366 ± 87 (181–464)	... (...)	... (...)	15 ± 1.2 (14–16)	25.3 ± 1.5 (24.9–26.6)	4.8 ± 0.5 (4.3–5.2)
C. cacti	(18)	... No female available ...							
C. thornei (USA)	(18)	561 ± 67 (456–704)	... (...)	326 ± 74.2 (194–459)	... (...)	... (...)	17 (16–19)	29.4 ± 0.8 (28.4–30.7)	5.6 ± 0.3 (5.2–6.0)
C. weissi (USA)	(18)	503 ± 76 (406–688)	... (...)	278 ± 65 (201–408)	... (...)	... (...)	15 ± 1.9 (13–20)	22.8 ± 0.53 (21.8–24.3)	5.2 ± 0.34 (4.5–5.6)

*See Table 1.
**See Table 1.

Table 14. Measurements* (μm) of cysts and vulva cone structures of *Cactodera* species..

Species	Reference	Body			Fenestra		Vulval denticles	Egg shell†
		Length**	Neck length	Width	Length	Width		
C. amaranthi (Cuba)	(57)	545.5 (261–713)	75.4 (33.7–128)	416 (242–485)	13.2 (...)	... (...)	...	Hyaline, no markings
(USA)	(18)	642 ± 62 (525–774)	... (...)	472 ± 54 (370–550)	31 ± 3.6 diam. (25–38)		Singly, small groups, partial or complete rings	As above
C. cacti (Yugoslavia)	(18)	587 ± 48 (496–662)	... (...)	475 ± 57 (387–550)	38 ± 5.5 diam. (29–48)		Generally present, singly or small groups	Heavily punctate under optical microscope
(Belgium)	(39)	... (430–450)	... (...)	... (400–420)	... (20–40)	... (18–30)	...	...
C. thornei (USA)	(18)	656 ± 83 (485–806)	... (...)	448 ± 81 (286–581)	34 diam. (31–36)		Singly, small clusters or partial ring	Small, discrete punctations under optical micro-scope
C. weissi (USA)	(18)	598 ± 87 (385–750)	... (...)	350 ± 68 (230–460)	34 diam. (29–38)		Singly, in clusters, partial or complete ring	Hyaline, without markings
(Canada)	(39)	... (320–576)	... (...)	... (220–540)	... (20–28)	... (15–20)	...	...

*See Table 1.
**See Table 1.
†Punctate egg shells appear villiform under SEM (18).

Table 15. Measurements* (μm) of males of *Cactodera* species.

Species	Reference	Body length	a	b	c	Spicule length	Stylet length	DGO	Tail length
C. amaranthi (USA)	(18)	974 ± 85 (792–1,195)	38 ± 5 (31–47)	6.2 ± 0.1 (5.4–6.8)	558 ± 274 (302–1,244)	30.5 ± 1.4 (27–33)	25.6 ± 0.5 (24.7–26.4)	3.7 ± 0.6 (2.6–4.3)	1.8 ± 0.6 (0.9–3.4)
C. cacti	(1)	1,010 (972–1,048)	35 (33–37)	9.7 (9.3–9.8)	... (<200)	33.5 (32.3–36.0)	28 (26–29)	... (...)	... (...)
C. thornei	(18)	1,503 ± 125 (1,315–1,708)	37 ± 4.2 (30–45)	8.8 ± 0.7 (7.3–9.8)	321 ± 97 (199–505)	43 ± 2 (39–46)	29.4 ± 1.4 (27.8–31.0)	6.8 ± 1.1 (5.5–8.0)	5.0 ± 1.7 (2–8)
C. weissi	(18)	1,034 ± 69 (943–1,240)	31 ± 2.1 (27–33)	6.0 ± 0.9 (5.1–6.7)	631 ± 112 (346–991)	32.4 ± 0.99 (30.8–33.6)	24.2 ± 0.9 (22.5–25.2)	4.8 ± 0.4 (4.5–5.6)	1.6 ± 0.5 (1.1–2.8)

*See Table 1.

Table 16. Measurements* (μm) of second-stage larvae of *Cactodera* species.

Species	Reference	Body length	Lateral lines	Stylet length	Tail length	Hyaline terminal length	Caudal ratio† A	Caudal ratio† B	DGO
C. amaranthi (Cuba)	(57)	409 (372–447)	4	23 (21.6–24.0)	39 (34–47)	... (...)	... (...)	... (...)	4.9 (4.8–5.2)
(Cuba)	(18)	368 ± 18 (343–402)	4	20.7 ± 0.4 (20.4–21.3)	35 ± 2.5 (31–40)	14 ± 1.0 (12–16)	2.0 ± 0.2 (1.9–2.4)	4.2 ± 0.3 (3.5–4.6)	4.6 ± 0.4 (4.0–5.2)
(USA)	(18)	374 ± 15 (340–406)	4	20.7 ± 0.4 (20.2–21.3)	35 ± 2.2 (32–40)	15 ± 1.9 (11–18)	2.1 ± 0.3 (1.6–2.6)	4.9 ± 1.0 (3.3–6.9)	4.5 ± 0.4 (3.9–5.1)
C. cacti (USA)	(18)	432 ± 17 (412–451)	4	22.9 ± 0.5 (22.4–24.0)	44 ± 2.2 (39–48)	17.2 ± 1.2 (14.5–19.6)	2.4 ± 0.2 (2.0–3.0)	6.8 ± 1.4 (4.3–8.8)	3.8 ± 0.3 (3.4–4.5)
(Mexico)	(18)	418 ± 38 (376–451)	4	23.4 ± 0.4 (22.4–24.0)	43 ± 3.6 (34–48)	19 ± 2.2 (14–21)	2.4 ± 0.3 (2–3)	5.2 ± 1.3 (3.4–7.6)	5.0 ± 0.5 (4.5–6.1)
C. thornei	(18)	554 ± 38 (446–620)	4	27 ± 0.9 (25–28)	56 ± 4.9 (49–64)	25 ± 1.5 (23–28)	2.9 ± 0.2 (2.5–3.3)	8.7 ± 1.2 (7.0–10.0)	6.0 ± 0.6 (5.0–7.0)
C. weissi	(18)	407 ± 12 (372–420)	4	20.4 ± 0.5 (19.6–21.8)	45.9 ± 1.9 (43–50)	20.2 ± 1.9 (17–24)	3.5 ± 0.3 (3.0–3.9)	8.4 ± 1.2 (6.6–10.5)	5.3 ± 0.3 (4.5–5.6)

*See Table 1.

†Caudal ratio A calculated by dividing the length of the hyaline tail terminal by its width at its beginning; caudal ratio B obtained by dividing the length of the hyaline tail terminal by its width at a point 5 μm from its terminus (13).

Table 17. Measurements* (μm) of mature female and vulva cone structures of *Heterodera* species (*avenae* group).

Species	Reference	Body			Vulva slit length	Stylet length	DGO
		Length**	Neck length	Width			
H. avenae (England)	(61)	... (550–770)	... (...)	... (360–500)	... (12–13)	... (26–32)	5.0 (...)
H. iri	(36)	676 (565–764)	125 (99–147)	548 (463–606)	... (...)	28 (25–30)	8 (5–11)
H. latipons	(9)	525 (348–645)	83 (58–103)	414 (277–510)	... (...)	25 (21–28)	3.7 (2.7–4.7)
H. mani	(36)	617 (485–721)	157 (146–164)	539 (418–679)	... (...)	30 (24–34)	8 (5–9)

*See Table 1.
**See Table 1.

Table 18. Measurements* (μm) of cysts and vulva cone structures of *Heterodera* species (*avenae* group).

Species	Reference	Body			Fenestra		Vulva slit length	Vulva bridge width	Bullae	Underbridge	
		Length**	Neck length	Width	Length	Width				Length	Width
H. avenae (England)	(61)	710 (...)	... (...)	500 (...)	... (...)	... (...)	... (...)	... (...)	Many	Absent	
(Canada)	(39)	... (...)	... (...)	... (...)	... (43–44)	... (21–23)	... (10–13)	... (6–8)	Heavy, many	Absent	
H. iri (Ireland)	(36)	675 (600–755)	119 (100–131)	520 (450–550)	42 (35–50)	24 (17–28)	11 (8–15)	... (...)	Fairly heavy, many	Mostly present	
(Ireland)	(39)	... (...)	... (...)	... (...)	... (32–40)	... (15–23)	12 (...)	... (6–8)	...	... (35–50)	... (10–16)
H. latipons (Israel)	(9)	See female			67 (58–76)	21 (15–27)	7 (6–9)	33 (18–39)	...	103 (80–125)	11 (7–14)
(Canada)	(39)	540 (...)	100 (...)	400 (...)	... (52–72)	... (15–20)	... (6–16)	... (18–39)	None-few	... (70–120)	... (20–28)
H. mani (Ireland)	(36)	590 (480–725)	139 (124–155)	494 (390–650)	52 (43–59)	27 (17–33)	7 (4–10)	7 (5–9)	Fairly heavy	Seldom present	

*See Table 1.
**See Table 1.

Table 19. Measurements* (μm) of males of *Heterodera* species (*avenae* group).

Species	Reference	Body length	a	b	Spicule length	Stylet length	DGO	Tail length
H. avenae (England)	(61)	1,380 (1,070–1,590)	45 (32–55)	9 (7–12)	36 (33–38)	28.5 (27–31)	3.6 (...)	6.0 (...)
H. iri	(56)	1,292 (1,060–1,450)	... (...)	... (...)	39 (36–43)	30 (28–33)	8 (6–10)	Very short
H. latipons	(9)	1,167 (960–1,406)	41 (32–51)	10.3 (8.9–11.3)	34 (32–36)	26.7 (22–29)	... (3–5)	Very short
H. mani	(36)	1,388 (1,100–1,750)	... (...)	... (...)	39 (35–43)	26 (22–30)	6 (3–8)	Very short

*See Table 1.

Table 20. Measurements* (μm) of second-stage larvae of *Heterodera* species (*avenae* group).

Species	Reference	Body length	Lateral lines†	Stylet length	Tail length	Hyaline terminal length	DGO
H. avenae (England)	(61)	575 (520–610)	4	27 (24–28)	54–58 (45–70)	... (35–45)	... (5–6)
H. iri	(36)	638 (573–694)	4	25 (23–28)	94 (83–103)	62 (51–75)	9 (8–10)
H. latipons	(9)	454 (401–478)	4	23.8 (23–25)	47.8 (42–54)	26.5 (20–31)	4.6 (4–5)
H. mani	(36)	578 (530–627)	4	24 (22–28)	67 (58–77)	40 (28–48)	6 (2–10)

*See Table 1.
†Particularly in *H. avenae* and *H. mani*, the two inner lines are prominent but the outer two are generally difficult to see and are areolated, if visible.

Table 21. Measurements* (μm) of female body and stylet lengths of *Heterodera* species (*schachtii* group).

Species	Reference	Body			Vulva slit length	Stylet length	DGO
		Length**	Neck length	Width			
H. fici	(28)	... (320–770)	... (...)	... (320–660)	... (...)	... (...)	... (...)
H. glycines (Japan)	(26)	... (470–790)	... (70–100)	... (210–580)	... (...)	27.5 (...)	... (2.5–5.5)
H. lespedezae	(13)	628 (495–865)	... (...)	345 (220–434)	... (...)	28.6 (28.0–29.7)	4.7 (4.5–5.0)
H. leuceilyma	(4)	... (...)	... (...)	... (...)	55 (...)	... (...)	5 (...)
H. schachtii	(46)	... (628–890)	... (...)	... (361–494)	... (...)	27 (...)	... (...)
H. trifolii (Canada)	(41)	... (520–650)†	... (...)	... (320–340)	... (...)	... (...)	... (...)
H. zeae (India)	(30)	592 (427–716)	... (...)	491 (325–684)	... (...)	... (24–25)	... (...)
(USA)	(20)	617 (459–796)	... (...)	366 (275–515)	32.9 (31.8–34.3)	24.7 (22.4–25.8)	4.8 (3.4–6.2)

*See Table 1.
**See Table 1.
†Excluding neck.

Table 22. Measurements* (μm) of cysts and vulva cone structures of *Heterodera* species (*schachtii* group).

Species	Reference	Body		Fenestra		Vulva	Underbridge		Bullae
		Length**	Width	Length	Width	slit length	Length	Width	
H. fici (USA)	(39)	... (...)	... (...)	... (45–68)	... (22–40)	... (35–60)	... (53–75)	... (15–20)	Weakly developed, scattered
H. glycines (Japan)	(26)	700 ± 60 (555–850)	450 ± 54 (370–589)	... (...)	... (...)	40 (...)	... (...)	... (...)	...
(USA)	(39)	... (...)	... (...)	... (38–62)	... (35–53)	... (45–60)	... (70–100)	... (15–28)	Heavy
H. lespedezae (USA)	(13)	678 (540–918)	371 (255–520)	50 (...)	35 (...)	45 (...)	Present		Heavy
(USA)	(39)	... (...)	... (...)	... (45–62)	... (35–43)	... (50–55)	... (90–115)	... (16–28)	Heavy
H. leuceilyma (USA)	(4)	830 (650–930)	480 (420–570)	... (...)	... (...)	... (...)	... (...)	... (...)	...
	(39)	... (...)	... (...)	... (48–50)	... (38–40)	... (50–65)	... (100–140)	... (50–80)	Few
H. schachtii (USA)	(46)	... (626–890)	... (361–494)	... (...)	... (...)	... (...)	... (...)	... (...)	...
(Canada)	(39)	... (...)	... (...)	... (24–38)	... (18–30)	... (35–46)	... (70–100)	... (18–25)	Heavy
H. trifolii (USA)	(23)	... (310–995)	... (190–615)	... (45–60)	... (31–49)	... (39–58)	... (...)	... (...)	...
(Canada)	(39)	... (...)	... (...)	... (40–58)	... (30–48)	... (39–50)	... (80–100)	... (20–28)	Heavy
H. zeae (India)	(30)	501 (342–684)	396 (260–537)	44 (37–53)	27.8 (20–32)	44.4 (36–58)	... (...)	... (...)	...
(USA)	(20)	588 (454–785)	347 (255–551)	40.4 (35–45)	26.3 (16–34)	36.5 (29–42)	36.8 (30–41)	10.3 (7.6–12)	Prominent

*See Table 1.
**See Table 1.

Table 23. Measurements* (μm) of males of *Heterodera* species (*schachtii* group).

Species	Reference	Body length	a	b	c	Spicule length	Stylet length	DGO	Tail length
H. fici	(28)	... (865–900)	... (29–36)	4.5 (...)	... (144–150)	... (30–35)	30 (...)	... (...)	... (...)
H. glycines (USA)	(23)	1,265 ± 51 (1,085–1,400)	... (...)	... (...)	... (...)	34.3 ± 1.2 (33.5–36.8)	26.9 ± 0.4 (25.5–28.4)	3.9 ± 0.1 (3.2–4.2)	5.3 ± 0.5 (3.7–8.4)
(Japan)	(26)	1,330 (1,200–1,400)	... (...)	... (...)	... (...)	34 (...)	... (26–27)	4 (...)	... (1.7–5.5)
H. lespeaezae	(13)	... Male unknown ...							
H. leuceilyma	(4)	1,230 (950–1,450)	34.8 (25.0–41.9)	6.7 (5.0–8.6)	... (...)	35.5 (30–37)	35 (32–40)	... (2–3)	Very short
H. schachtii (England)	(10)	... (1,120–1,440)	... (32–38)	... (...)	... (...)	... (34–38)	29 (...)	4.5 (...)	... (...)
H. trifolii		... Male rarely found ...							
H. zeae		... Male unknown ...							

*See Table 1.

Table 24. Measurements* (μm) of second-stage larvae of *Heterodera* species (*schachtii* group).

Species	Reference	Body length	Lateral lines	Stylet length	Tail length	Hyaline terminal length	DGO
H. fici (England)	(65)	402 ± 5.5 (...)	4	23.2 ± 0.2 (...)	51 ± 1.36 (...)	26.5 ± 0.87 (...)	... (...)
(USSR)	(28)	... (320–460)	...	... (25–26)	... (...)	... (...)	... (...)
H. glycines (USA)	(23)	439 ± 6.7 (375–490)	4	23 ± .01 (22–24)	50.4 ± 1.0 (42–59)	26.6 ± 0.7 (20–33)	4.0 ± 0.2 (3.0–5.2)
(Japan)	(26)	471 (437–504)	4	23.0 (...)	45.0 (42–47)	... (...)	... (...)
H. lespedezae	(13)	457 (400–510)	4	25.2 (24–26.3)	55.9 (47–66)	29.6 (23.5–35.8)	4.5 (3.9–5.04)
H. leuceilyma	(4)	550 (520–580)	3	26 (23–28)	65 (...)	38 (31–41)	5.0 (...)
H. schachtii (USA)	(46)	... (435–492)	4	25 (...)	... (...)	... (...)	... (...)
(USA)	(65)	452 ± 49.7 (...)	4	25.6 ± 0.11 (...)	48.5 ± 0.73 (...)	27.1 ± 0.61 (...)	3.4 (...)
H. trifolii (Canada)	(41)	510 (490–530)	4	27 (25–29)	59 (55–65)	36 (30–38)	... (5–9)
(USA)	(23)	497 (443–547)	4	27.5 (25.5–29.5)	60 (51–71)	30.7 (24.2–39.6)	7.3 (5.6–9.0)
H. zeae (India)	(30)	410 ± 40 (360–440)	4	23.3 ± 0.3 (20–25)	41.0 ± 1.1 (32–50)	24.0 ± 0.7 (16–30)	... (4–5)
(USA)	(20)	431 ± 14 (399–460)	4	19.9 ± 0.4 (19–20.7)	44.2 ± 2.4 (40–49)	21.9 ± 1.7 (16.8–25.2)	4.3 ± 0.4 (3.4–5)

*See Table 1.

Table 25. Measurements* (μm) of females fenestra, vulva, and stylet lengths of *Heterodera* species (*goettingiana* group).

Species	Reference	Body			Fenestra		Vulva			
		Length**	Neck length	Width	Length	Width	slit	Shape	Stylet length	DGO
H. canadensis	(43)	508 (480–520)	... (110–160)	480 (430–510)	... (...)	... (...)	47 (40–50)	Basically spherical	... (24–25)	... (...)
H. cyperi	(12)	526 (459–663)	... (...)	275 (228–345)	... (...)	... (...)	... (...)	Basically lemon	22.4 (22.0–22.4)	4.9 (4.5–5.6)
H. cruciferae	(54)	... (...)	... (...)	... (...)	... (...)	... (...)	... (...)	Basically spherical	26.5 ± .5 (...)	4.8 ± 1.1 (...)
H. graminophila	(16)	460 (290–650)	... (...)	310 (160–560)	... (...)	... (...)	38 (35–43)	Basically lemon	22.6 (21.3–23.8)	5.0 (4.0–6.7)
H. humuli (England)	(56)	... (...)	... (...)	... (...)	Semi (20–22)	... (22–24)	37 (...)	Basically lemon	25.4 ± 1.5 (...)	5.7 ± 0.8 (...)
H. longicolla	(17)	474 (366–585)	131 (60–186)	255 (156–337)	... (...)	... (...)	32 (28–37)	Basically lemon	20 (19–21)	4 (...)
H. mothi (India)	(27)	525 (460–590)	... (...)	300 (110–350)	... (...)	... (...)	... (...)	Basically lemon	... (17–21)	... (5.5–6.5)

*See Table 1.
**See Table 1.

Table 26. Measurements* (μm) of cysts and vulva cone structures of *Heterodera* species (*goettingiana* group).

Species	Reference	Body			Fenestra		Underbridge		Shape	Vulva
		Length**	Neck length	Width	Length	Width	Length	Width		slit length
H. canadensis	(43)	580 (490–615)	... (...)	543 (450–610)	51 (47–55)	45 (42–50)	88 (80–95)	... (18–20)	Basically spherical	... (41–48)
H. cyperi	(12)	640 (459–742)	... (...)	325 (229–382)	... (27–35)	... (20–28)	... (40–60)	... (10–12)	Basically lemon	... (30–35)
H. cruciferae (England)	(54)	429 ± 67 (...)	76 ± 18 (...)	333 ± 56 (...)	34.5 ± 5.9 (...)	34.4 ± 5.3 (...)	85.2 ± 11.1 (...)	10.9 ± 2.0 (...)	Basically spherical	45.5 ± 5.5 (...)
	(39)	... (380–500)	... (...)	... (300–400)	... (20–38)	... (30–50)	... (90–110)	... (12–33)	Basically spherical	... (45–55)
H. graminophila	(16)	650 (520–780)	... (...)	450 (350–550)	... (52–58)	... (43–50)	... (115–140)	... (15–20)	Basically lemon	45 (40–52)
H. humuli (England)	(56)	452 ± 57 (...)	66 ± 14 (...)	330 ± 53 (...)	22.3 ± 2.6 (...)	24.7 ± 2.4 (...)	85.6 ± 8.8 (...)	5.3 ± 0.9 (...)	Basically lemon	34.6 ± 3.5 (...)
(Canada)	(39)	... (400–490)	... (...)	... (320–410)	... (40–65)	... (18–35)	... (40–70)	... (6–15)	Basically lemon	... (32–45)
H. longicolla	(17)	496 (362–632)	136 (101–185)	359 (275–459)	48 (...)	40 (...)	Absent		Basically lemon	45 (...)
H. mothi (India)	(27)	630 (470–790)	... (...)	360 (230–480)	36 (...)	27 (...)	... (...)	... (...)	...	32 (...)
	(39)	... (500–620)	... (...)	... (330–440)	... (33–40)	... (30–38)	55 (...)	10 (...)	Basically lemon	... (38–46)

*See Table 1.
**See Table 1.

Table 27. Measurements* (μm) of males of *Heterodera* species (*goettingiana* group).

Species	Reference	Body length	a	b	c	Spicule length	Stylet length	DGO	Tail length
H. canadensis	(43)			... Male unknown ...					
H. cruciferae	(54)	1,170 ± 79 (...)	40.8 ± 5.8 (...)	... (...)	... (...)	34.5 ± 2.4 (...)	24.9 ± 1.1 (...)	7.2 ± 0.8 (...)	Short
H. cyperi	(12)	964 (874–1,159)	38.6 (32.9–42.0)	5.5 (4.5–6.7)	196 (90.0–351.4)	28.8 (28.0–30.8)	22.1 (21.2–22.9)	3.9 (3.3–4.5)	Short
H. graminophila	(16)	990 (850–1,110)	32 (28–37)	6.0 (5.3–6.5)	... (...)	34 (31–36)	24.7 (22.4–25.8)	5.3 (4.0–6.2)	Very short
H. humuli (England)	(56)	941 ± 67 (...)	34.0 ± 3.7 (...)	... (...)	... (...)	31.1 ± 0.9 (...)	28.1 ± 0.7 (...)	5.2 ± 0.5 (...)	1.7 ± 0.3 (...)
H. longicolla	(17)	784 (660–885)	29 (23–32)	5.0 (4.1–7.0)	590 (215–1,580)	26.9 (25.2–28.6)	19.2 (17.9–20.2)	5.4 (5.0–6.2)	1.8 (0.6–3.4)
H. mothi	(27)	... (830–1,200)	... (35–46)	... (5.8–8.0)	... (148–330)	... (24–30)	... (19–23)	... (4.0–4.5)	Short

*See Table 1.

Table 28. Measurements* (μm) of second-stage larvae of *Heterodera* species (*goettingiana* group)

Species	Reference	Body length	Lateral lines	Stylet length	Tail length	Hyaline terminal length	DGO
H. canadensis	(43)	558 (520–600)	3	24 (23–25)	115 (110–120)	60 (55–65)	8 (7–9)
H. cruciferae	(54)	431 ± 19 (...)	4	24.1 ± 1.6 (...)	50 ± 2.7 (...)	25.2 ± 2.7 (...)	5.5 ± 0.7 (...)
H. cyperi	(12)	441 (414–465)	3	20.0 (19.2–20.7)	60 (56–63)	24.7 (18.1–31.0)	5.2 (4.8–6.1)
H. graminophila	(16)	430 (380–460)	3	22.7 (21.8–23.5)	62 (57–67)	32 (25–38)	5.6 (...)
H. humuli (England)	(56)	378 ± 22 (...)	4	22.5 ± 0.5 (...)	50.3 ± 3.5 (...)	26.7 ± 3.6 (...)	5.2 ± 0.6 (...)
H. longicolla	(17)	353 (312–378)	3	17.5 (16.8–18.5)	50 (45–54)	27 (20–33)	5.2 (3.4–6.1)
H. mothi	(27)	... (380–430)	3	... (16–17)	... (60–75)	... (30–40)	... (5.0–6.5)

*See Table 1.

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

Distribution: Western Hemisphere—Ontario and Quebec, Canada; Arkansas, Maryland, Florida, Illinois, Iowa, Michigan, Missouri, New Jersey, New York, North Carolina, Pennsylvania, Virginia, West Virginia, and Wisconsin, USA.

Other species: Not found in the Western Hemisphere but is included here as one of the group of species studied by Golden and Raski (18).

Cactodera estonica (Kirjanova & Krall, 1963) Krall & Krall, 1978

Described and illustrated by Kirjanova and Krall (29). Golden and Raski (18) provided additional information based on cysts from Poland and second-stage larvae from the type locality.

Type host and locality: Host unknown; collected from soil around several grasses. Village of Markas, Tartu district, Estonia SSR.

Distribution: Estonia, Poland, Yugoslavia, and Turkey.

Discussion: Golden and Raski (18) described and first recognized the taxonomic value of tooth-like structures, which they named vulval denticles, in the vulva cone of certain species, including all those assigned to *Cactodera*. The presence of vulval denticles, the characteristic external cuticular pattern, and the short vulva slit provide a sound basis for accepting *Cactodera* as a valid genus containing the above species. Species are readily identified by differences in second-stage larvae measurements of stylet, tail, and tail terminal; punctate or non-punctate egg shells; and cyst shape.

Genus *Heterodera* Schmidt, 1871

Diagnosis: After Mulvey & Stone (42).

Mature female and cyst: With posterior protuberance (the vulval cone) more or less lemon shaped; cuticle with lacelike pattern of ridges. Vulval slit short to long (10–60 μm); sited at apex of vulval cone; underbridge and bullae present or absent. Perineal tubercles (40) absent. Vulval cone bifenestrate circum- or ambi-fenestrate. Anus dorsal, not on vulval lip.

Second-stage juvenile: Stylet less than 30 μm. Esophageal glands fill body width. Phasmids without lenslike structure in muscle layer.

Male: To 1.5 mm in length. Labial disc present but with low profile. Tail present, length less than half body width.

Type species: Heterodera schachtii Schmidt, 1871.

Heterodera avenae group: In 1978 Krall and Krall (31) established a new genus, *Bidera,* and placed the following *Heterodera* species in it as new combinations: *avenae* (as type species of the new genus), *arenaria, bifenestra, hordecalis, iri, latipons, longicaudata, mani, turcomanica,* and *ustinovi.*

We prefer to recognize these species as belonging in the genus *Heterodera* and propose that *Bidera* Krall & Krall, 1978 be placed as a new synonym under the genus *Heterodera* Schmidt, 1871. For measurements of species in this group see Tables 17–20.

Female and cyst with posterior protuberance, basically lemon shaped, vulva slit short (6–16 μm), bifenestrate, bullae, vulva denticles and underbridge present or absent. Second-stage larvae (species from the Western Hemisphere) 520–627 μm (*H. latipons* exception 401–480 μm). Male present.

Heterodera avenae Wollenweber, 1924 (Figs. 15, 89, 94, 105, 106, 110, 111, 114)

First recorded by Kuhn (32) in Germany, designated as *H. schachtii* var. *avenae* by Wollenweber (63), and later described in detail by Schmidt (50) and Franklin (8). Williams and Siddiqi (61) provided more detailed information on all stages of this species.

Type host and locality: Oats (*Avena sativa* L.). Aschersleben, East Germany (D.D.R.).

Distribution: Western Hemisphere—Ontario, Canada; Oregon, USA. *World*—Algeria, Australia, Belgium, Czechoslovakia, East Germany, England, Denmark, Greece, Holland, India, Israel, Japan, Morocco, New Zealand, Norway, Pakistan, Scotland, Sweden, USSR, Italy, Ireland, Lebanon,

The Netherlands, Spain and West Germany.

Heterodera iri Matthews, 1971
(Figs. 90, 95, 97-100, 102, 107, 112)

Described and illustrated by Matthews (36).

Type host and locality: Brown top grass (*Agrostis tenuis* Sibth.). Draperstown, Northern Ireland.

Distribution: Western Hemisphere—Michigan and New York, USA. *World*—German Federal Republic, The Netherlands, Northern Ireland, and Pakistan.

Heterodera latipons Franklin, 1969
(Figs. 91, 92, 103, 104)

Described and illustrated by Franklin (9).

Type host and locality: Wheat (*Triticum aestivum* L.). Gilat, Israel.

Distribution: Western Hemisphere—Prince Edward Island, Canada. *World*—Bulgaria, Greece, Israel, Italy, Japan, Libya, Poland, Scotland, Tripoli, and USSR (European).

Heterodera mani Matthews, 1971
(Figs. 93, 96, 101, 108, 109, 113, 115)

Described and illustrated by Matthews (36).

Type host and locality: Perennial rye grass (*Lolium perenne* L.). Magilligan, Northern Ireland.

Distribution: Western Hemisphere—California, USA. *World*—German Federal Republic, Northern Ireland, Spain, and The Netherlands.

Discussion: North American species assigned to the *avenae* group are fairly closely related, except *H. latipons* which differs significantly by having a well-developed underbridge and widely separated semifenestrae. *H. iri* is easily separated from *H. avenae* and *H. mani* by having a medium sized underbridge, by cyst color, and by a much longer tail and hyaline tail terminal of the second-stage larvae. *H. avenae* and *H. mani* are identified by the shape of stylet knobs of the second-stage larvae, only slightly concave anteriorly for *H. avenae* and deeply concave anteriorly for *H. mani*. Additionally, the vulva slit length of the female and cyst of *H. avenae* is much longer than that of *H. mani*. Unpublished data (excerpts of this information were published by Golden in Nematropica. 1979. 9: 99-100) of vulva slit length measurements of *H. avenae* cysts from Oregon, USA, gave a mean length of 9.24 ± 1.11 μm (7.5–11.0); from Sweden 10.14 ± 1.17 μm (8.1–11.6). For *H. mani* from California, USA, the mean length was 6.01 ± 0.77 μm (4.6–7.5); from paratype collection, Ireland, 6.44 ± 1.81 μm (5.2–9.2); and from The Netherlands, 6.42 ± 0.87 μm (5.2–8.1).

All three species have well-developed vulval denticles; *H. avenae* and *H. mani* females have a thick subcrystalline layer which persists to the brown cyst stage, whereas that of *H. iri* is thin and nonpersistent. *H. mani* does not attack cereals as does *H. avenae*.

Heterodera schachtii group: For measurements of the following seven species see Tables 21–24.

Females and cysts with posterior protuberance, basically lemon shaped, vulva slit long (> 30 μm), bullae present, underbridge generally strongly developed, ambifenestrate. Male present or absent.

Heterodera fici Kirjanova, 1954
(Figs. 116, 125, 132)

Described by Kirjanova (28) in 1954.

Type host and locality: Rubber plant (*Ficus elastica* Roxb.). Harbin, People's Republic of China. Type material not designated but deposited at the Zoological Institute, Academy Sciences of the USSR, Leningrad.

Distribution: Western Hemisphere—California, Florida, and Virginia in USA; Brazil. *World*—Australia, Germany, Italy, Poland, South Africa, Spain, Turkey, USSR, and Yugoslavia.

Heterodera glycines Ichinohe, 1952
(Figs. 117, 124, 126, 140, 144)

First described by Ichinohe (25) in 1952 and additional details were given by him in 1961 (26). Hirschmann (23) and Taylor (58) redescribed and illustrated the various stages of this species.

Type host and locality: Soybean (*Glycine max* Merr.). Opihiro-shi, Hokkaido, Japan.

Distribution: Western Hemisphere—Alabama, Arkansas, Delaware, Florida, Georgia, Indiana, Illinois, Iowa, Kentucky, Louisiana, Minnesota, Maryland, Missouri, Mississippi, North Carolina, Oklahoma, Ohio, South Carolina, Tennessee, Texas, Virginia, and Wisconsin in USA. *World*—China, Japan, Korea, and Manchuria.

Heterodera lespedezae Golden & G. S. Cobb, 1963
(Figs. 118, 127)

Described and illustrated by Golden and Cobb (13).

Type host and locality: Kobe lespedeza (*Lespedeza striata* Hook). Near Monroe in Union County, North Carolina, USA.

Distribution: Ohio, North Carolina, Illinois, and Tennessee, USA.

Heterodera leuceilyma Di Edwardo & Perry, 1964
(Figs. 119, 128)

Described and illustrated by Di Edwardo and Perry (4).

Type host and locality: St. Augustine grass (*Stenotaphrum secundatum* [Walt.] Kuntzo). West Palm Beach, Florida.

Distribution: Only Atlantis and West Palm Beach in Florida, USA.

Heterodera schachtii Schmidt 1871
(Figs. 120, 129, 141, 145)

Described first by Schacht (48) and by Schmidt (49) who described the genus and named the species after Schacht. Raski (46) provided the first comprehensive study of the life history and morphology of *H. schachtii*. Franklin (10) gave up-to-date data with illustrations and measurements of the female, cysts, and larva. Although (*H. schachtii* is the type species of the genus *Heterodera*, no type specimen was ever designated.

Type host and locality: Sugar beet (*Beta vulgaris* L.). Near Aschersleben, East Germany.

Distribution: Western Hemisphere—Ontario and Alberta in Canada; Chile; Arizona, California, Colorado, Florida, Idaho, Kansas, Michigan, Montana, New York, Nebraska, North Dakota, Ohio, Oregon, South Dakota, Utah, Washington, Wisconsin, and Wyoming in USA. *World*—Australia, Austria, Belgium, Czechoslovakia, Denmark, England, France, Finland, Germany, Holland, Poland, India, Israel, Italy, Senegal, South Africa, Spain, Sweden, USSR, Wales, Pakistan, and Yugoslavia.

Heterodera trifolii Goffart, 1932
(Figs. 16, 121, 123, 130, 142, 146)

First described by Goffart (11) and redescribed and illustrated by Hirschmann (23). Mulvey and Anderson (41) described and illustrated the female, cyst, larva, and two males (from England) and collated other information concerning this species. Wouts and Sturhan (66) recently redescribed *H. trifolii* and designated a neotype.

Type host and locality: Red clover (*Trifolium pratense*). Schleswig Holstein, Germany.

Distribution: Western Hemisphere—Throughout Canada and USA including Hawaii. *World*—Australia, Europe, England, India, Israel, New Zealand, Northern Ireland, Tunisia, USSR, Belgium, and Yugoslavia.

Heterodera zeae Koshy, Swarup & Sethi, 1971
(Figs. 122, 131, 133-139, 143)

Described and illustrated by Koshy et al. (30). Redescribed by Golden and Mulvey (20).

Type host and locality: Maize (*Zea mays* L.). Chapli, District Udaipur, Rajasthan, India.

Distribution: Western Hemisphere—Maryland, USA. *World*—India, Egypt, and Pakistan.

Discussion: We have placed *Heterodera fici* in the *H. schachtii* group since many of the vulva cones of the cysts examined from California, USA, had small, scattered bullae and a slender, distinct underbridge. Further study of many specimens is required for proper placement of this species.

The bullae formation, fingerlike and at two levels, in the vulva cone of *H. zeae*, as shown herein and described in detail by Golden & Mulvey (20) and also Golden & Mulvey (19), is unique for the genus *Heterodera* and is a significant character in the identification of this species. Fingerlike

projections of the underbridge in the vulva cone of *H. leuceilyma* readily separates this species from others in the group. *Heterodera trifolii, H. lespedezae,* and *H. glycines* are closely related species, particularly in fenestral length and bullae characteristics, and, according to Stone (53), the larvae belong to lip pattern type "5." However, they are readily identified especially by stylet length, distance of dorsal esophageal gland duct opening from the base of the stylet, and tail measurements of the second-stage larvae. Field populations of *H. schachtii* are easily separated from these three species on the basis of much shorter average fenestral length and differences in the length of the larval stylet and tail.

According to Golden and Epps (14), *Heterodera glycines* is not morphologically uniform in all areas of occurrence. The variation in tail length and shape and length of the hyaline tail terminal of second-stage larvae indicate several forms or races. Race one, occurring mainly in the Wilmington area of North Carolina, and some other states now, has a tail length of 50 μm, with a long tapering hyaline tail terminal of 26 μm. Race two, found commonly in northeastern North Carolina and southeastern Virginia and occasionally in the Mississippi valley, has a tail length of 42 μm and hyaline tail terminal length of 22 μm, with a bluntly rounded terminus. Races three and four, occurring widely in the Mississippi valley, lie between races one and two, having tail lengths of 45 μm and hyaline tail terminal lengths of 23 μm. The race of *H. glycines* in Japan has tail and hyaline tail terminal measurements similar to races three and four occurring in United States. Although second-stage larval tail and tail terminal measurements differ between these races, the stylet length and distance of the dorsal esophageal gland duct opening from the stylet base always remain constant for these races and specimens from other populations examined, averaging 23 μm and 4 μm, respectively.

Heterodera goettingiana group: For measurements of species in this group see Tables 25–28).

Cyst and female always with posterior protuberance, lemon-shaped or somewhat spherical, vulva slit long (> 30 μm), underbridge present or absent, bullae (when present) small and scattered, circumfenestrate or bifenestrate.

Heterodera canadensis Mulvey, 1979
(Figs. 147, 148, 156, 162)

Described and illustrated by Mulvey (43).

Type host and locality: Spike-rush (*Eleocharis acicularis* [L.] R. & S.). Outskirts of Deschenes, Province of Quebec, Canada.

Distribution: Only Quebec, Canada.

Heterodera cruciferae Franklin, 1945
(Figs. 149, 157)

Described and illustrated by Franklin (7). Stone and Rowe (54) redescribed and illustrated all stages of this species.

Type host and locality: Cabbage (*Brassica oleracea* L. v. *capitata*). Syntypes marked Oster House, St. Albans (Hertfordshire, S. E. England), and verified by Franklin.

Distribution: Western Hemisphere—California in USA. *World*—Australia, Bulgaria, England, Belgium, Holland, USSR (possibly), Yugoslavia, Finland, and West Germany.

Heterodera cyperi Golden, Rau & G. S. Cobb, 1962
(Figs. 150, 158, 164)

Described and illustrated by Golden et al. (12).

Type host and locality: Yellow nut grass (*Cyperus esculentus* L.). Central Florida, Experimental Station, Sanford, Florida, USA.

Distribution: Only Sanford and Lee Counties, Florida, and Early County, Georgia, in USA.

Heterodera graminophila Golden & Birchfield, 1972
(Figs. 151, 152, 159, 163)

Described and illustrated by Golden and Birchfield (16).

Type host and locality: Barnyard grass (*Echinochloa colonum* (L.) Link.). Baton Rouge, Louisiana, USA.

Distribution: Louisiana, USA.

Heterodera humuli Filipjev, 1934
(Figs. 153, 160)

First described by Voigt (60), then by Percival (45), and later named *Heterodera humuli* by Filipjev (6). Stone and Rowe (56) reviewed the literature, redescribed all stages of this species, and established a neotype for this species.

Type host and locality: Hop (*Humulus lupulus* L.). Kent, England.

Distribution: Western Hemisphere—British Columbia in Canada; Washington, Oregon, and Idaho in USA. *World*—Australia, Bulgaria, Belgium, Germany, India, Israel, Greece, Holland, New Zealand, Sweden, Switzerland, Southern England, South Africa, USSR, and Yugoslavia.

Heterodera longicolla Golden & Dickerson, 1973
(Fig. 154)

Described and illustrated by Golden and Dickerson (17).

Type host and locality: Buffalo-grass (*Buchloe dactyloides* [Nutt.] Engelm.). Near Hays, Kansas, USA.

Distribution: Only Kansas in USA.

Heterodera mothi Khan & Husain, 1965
(Figs. 155, 161)

Described and illustrated by Khan and Husain (27).

Type host and locality: Nut grass (*Cyperus rotundus* L.). University Campus, Aligarh, U.P. India.

Distribution: Western Hemisphere—Georgia, USA. *World*—India, Iran, Iraq, and Pakistan.

Discussion: H. mothi is tentatively placed in this group pending further study of more specimens which may reveal the true nature of the bullae-like structures found in the vulva cone of some mature cysts. *H. mothi* is the only species in this group in the Western Hemisphere with vulval denticles. The wavy lines extending from the edge of the semifenestra to the vulva slit in white females of *H. canadensis* and *H. graminophila,* combined with only three lines in the lateral field of second-stage larva, provide easy identification of these species.

KEY TO THE GENERA AND SPECIES OF CYST FORMING HETERODERIDAE IN THE WESTERN HEMISPHERE

(based on cysts and second-stage larvae)

1. Cyst (and female) without posterior protuberance (Figs. 3–8) 2
   Cyst (and female) with distinct posterior protuberance (Figs. 1, 2, 9) 11
2. Vulva fenestra large (Fig. 14), anal area small and without fenestration; cysts spherical (Fig. 3), subspherical (Fig. 4), or elongate ovoid (Fig. 5) 5
   Vulva and anal fenestra large, both of equal size (Fig. 13); cysts ovoid or pear shaped ..... *Punctodera* Mulvey & Stone 3
3. Cysts pear shaped (Fig 8); second-stage larvae with body length of 350–490 μm ..... *P. punctata* (Thorne)
   Cysts spherical (Fig. 7) or ovoid (Fig. 6), second-stage larvae with body length greater than 500 μm 4
4. Massive bullae (Fig. 26) between vulva and anal fenestra; second-stage larvae with esophageal gland lobe extending to about 50% of body length; stylet knobs strongly concave anteriorly; host grasses ..... *P. matadorensis* Mulvey & Stone
   Bullae small, scattered or absent (Fig. 22); second-stage larva esophageal gland lobe extending to about 30% of body length; stylet knobs flattish to slightly concave anteriorly; host maize ..... *P. chalcoensis* Stone, Sosa Moss & Mulvey
5. Cysts spherical (Fig. 3) or subspherical (Fig. 4); bullae absent; second-stage larva with four lines in lateral field ..... *Globodera* Skarbilovich 6
   Cysts elongate ovoid (Fig. 5); bullae (Fig. 32) present; second-stage larvae with three lines in lateral field .. *Dolichodera* Mulvey & Ebsary-*D. fluvialis*
6. Cyst wall pattern with rugose striae at midbody primarily extending latitudinally; second-stage larvae with ratio "a" = about 18–25; stylet length 20 μm or more; dorsal gland duct opening about one-third or less of stylet length from its base 7
   Cyst wall pattern with prominent striae extending longitudinally from

fenestral area to near base of neck, body of second-stage larvae very thin, with "a" = 39; stylet length 18 μm, dorsal esophageal gland duct opening about two-thirds of stylet length from its base ..... *G. leptonepia* (G.S. Cobb & Taylor)

7. B/A ratio* averages 1.7 (1.0–2.8) 8
   B/A ratio averages 2.5 to 3.7 (range 1.3–9.5) 9
8. Cuticle between anus and vulva fenestra deeply etched (Fig. 53); distinct circumfenestral area (Fig. 44) present in yellow and mature cysts ..... *G. solanacearum* (Miller & Gray)
   Cuticle between anus and vulva fenestra moderately etched; circumfenestral area obscure in mature females ..... *G. tabacum* (Lownsbery & Lownsbery)
9. Cuticular pattern mazelike (Fig. 45) between anus and vulva fenestra ..... *G. virginiae* (Miller & Gray)
   Cuticular pattern not mazelike between anus and vulva fenestra (Figs. 54, 55), more or less straight lines or ridges 10
10. Number of cuticular ridges between anus and vulva fenestra 8–20 (av. 12.2) (Fig. 55) second-stage larvae stylet length 23.6 μm (21–26); body length 484 μm (440–525); if females are available, perineal tubercles (Figs. 18, 41, 47) small and discrete ..... *G. pallida* (Stone)
    Number of cuticular ridges between anus and vulva fenestra 21.6 (16–31) (Fig. 54); second-stage larvae stylet length 21.8 μm (21–23); body length 468 μm (425–505) if females are available, perineal tubercles (Figs. 42, 48) large and clumped together ..... *G. rostochiensis* (Wollenweber)
11. Cysts ovoid shaped (Fig. 9), vulva sunken into a terminal cone (Fig. 56), without fenestration; anus located on upper inside of dorsal vulva lip; second-stage larva stylet averaging 40 μm (Fig. 63) ..... *Sarisodera* Wouts & Sher-*S. hydrophila*
    Cysts generally lemon shaped, rarely spherical (Figs. 1, 2); vulva on a terminal cone bifenestrate (Fig. 11) circumfenestrate (Fig. 10) or ambifenestrate (Fig. 12); anus outside of vulva lip generally located on or near vulva cone; second-stage larvae stylet less than 30 μm ..... *Heterodera* Schmidt 12
12. Cysts spherical; vulval denticles absent, anal-vulva distance long (90–120 μm), vulva cone short (Fig. 71) and with distinct three-layered core (Figs. 66–68); lateral field of second-stage larva with three lines ..... *Heterodera betulae* Hirschmann & Riggs
    Cysts basically lemon shaped; vulval denticles (Fig. 17) present or absent; anal-vulva distance generally short (30–70 μm); vulva cone generally prominent and without core structure; lateral field of second-stage larva with either three or four lines 13
13. Vulva cone bifenestrate or ambifenestrate; bullae present or absent; cyst wall pattern zig-zag, (Figs. 137, 138); vulva slit (Figs. 106–109) very short (6–19 μm) to very long (> 30 μm) (Figs. 116–122) 17
    Vulva cone circumfenestrate (Figs. 78–81), cyst wall pattern at midbody straight to wavy lines encircling body, broken by short oblique or verticle lines (Fig. 82); bullae absent; vulva slit very short (6–19 μm); second-stage larva average body length 440 μm (368–554) ..... *Cactodera** Krall & Krall 14
14. Egg shells distinctly punctate (Figs. 72–75); stylet length of second-stage larvae averaging 23 μm or more (Fig. 86) 15
    Egg shells hyaline (Figs. 76, 77), without visible markings; stylet length of second-stage larvae averaging 20.6 μm (Fig. 85) 16
15. Second-stage larva stylet length averaging 23.5 μm; hyaline tail terminal short, blunt and measuring 12–20 μm ..... *C. cacti* (Filipjev & Schuurmans Stekhoven)
    Second-stage larva stylet length averaging 27 μm (Fig. 86), tail averaging 56

*Granek's ratio (21):

$$\frac{\text{Distance from anus to nearest edge of vulva opening } B}{\text{Diameter of vulva opening } A}$$

Also, see modification of this ratio by Hesling (22).

*Golden and Raski (18) provided a sound basis for accepting *Cactodera* as a valid genus.

μm, hyaline tail terminal (Fig. 88) relatively long, tapering to finely rounded tip and measuring 23–28 μm in length ..... *C. thornei* (Golden & Raski)

16. Tail of second-stage larva averaging 46 μm in length (Fig. 87), hyaline tail terminal about same length as stylet (Fig. 85) which averages 20.4 μm in length ..... *C. weissi* (Steiner)
    Tail of second-stage larva averaging 35 μm in length, hyaline tail terminal shorter than stylet length (av. 20.7 μm) and averaging 15 μm in length ..... *C. amaranthi* (Stoyanov)
17. Vulva slit long to very long (> 30 μm), vulva cone commonly ambifenestrate, occasionally bifenestrate (Figs. 11, 12) 21
    Vulva slit very short (6–19 μm), vulva cone always bifenestrate; vulva denticles present or absent; bullae few to many; second-stage larvae length averaging 561 μm (454–638) ..... *avenae* group 18
18. Semifenestra widely separated (Figs. 91, 92); vulva bridge 18–39 μm wide, underbridge (Figs. 103, 104) strongly developed; bullae few, scattered; second-stage larvae body length 454 μm (401–478) ..... *H. latipons* Franklin
    Semifenestra not widely separated (Fig. 89); vulval bridge less than 18 μm wide; bullae strongly developed (Figs. 94–96); underbridge, when present, weakly developed, (Fig. 102); second-stage larvae body length 561 μm (520-694) 19
19. Cysts mostly creamy brown in color, underbridge present (Fig. 102); second-stage larva tail 94 μm (83–103) in length, hyaline terminal 51–75 μm ..... *H. iri* Matthews
    Cysts mostly dark brown to black in color, underbridge rarely present; second-stage larva tail 54 to 67 μm (45–77) 20
20. Cysts under low power of microscope and in numbers of 10 or more, appear dark brown to black in color, second-stage larvae stylet knobs (Figs. 110, 111) shallowly concave anteriorly; vulva slit (Fig. 106) mean length 9.6 μm; cereals host ..... *H. avenae* Wollenweber
    Cysts under low power and in numbers greater than 10 appear brown in color; second-stage larvae stylet knobs (Fig. 113) deeply concave anteriorly; vulval slit (Figs. 108, 109) mean length 6.5 μm; grass hosts .. *H. mani* Matthews
21. Bullae present in vulva cone of all species, small to large in size; underbridge generally well developed; vulva cone ambifenestrate ..... *schachtii* group 22
    Bullae rarely present, underbridge either absent, slender or strongly developed; vulva cone ambifenestrate or bifenestrate ..... *goettingiana* group 28
22. Underbridge (Fig. 128) massive, with dorso-ventral fingerlike projections, bullae few on peripheral wall of cone; second-stage larvae with three lines in lateral field ..... *H. leuceilyma* Di Edwardo & Perry
    Underbridge weakly to strongly developed, without fingerlike projections, bullae few to many on peripheral wall of cone; second-stage larvae with four lines in lateral field 23
23. Bullae located at two levels in vulva cone (Figs. 133–136), level one immediately below (anterior) the underbridge and having four fingerlike bullae (Figs. 133, 135, 136), level two a mass of randomly located long heavy bullae (Fig. 134); second-stage larva stylet mean length 20.0 μm (Fig. 139).. ..... *H. zeae* Koshy, Swarup & Sethi
    Bullae at one level (Fig. 123), randomly located; second-stage larva stylet length 22–29.5 μm 24
24. Fenestral length 32.5 μm (24–38) (Fig. 120); anal bullae (Fig. 129) typically molar shaped; second-stage larva stylet (Fig. 141) mean length 25.6 μm ..... *H. schachtii* Schmidt
    Fenestral length 53 μm (36–68), anal bullae not molar shaped 25
25. Bullae small scattered (Figs. 125, 132) underbridge weakly developed (Fig. 125) ..... *H. fici* Kirjanova
    Bullae large, many; underbridge well to very strongly developed 26
26. Underbridge very strongly developed (Fig. 130), distinct in most specimens;

fenestra (Fig. 121) well delineated; distance of dorsal esophageal gland duct opening from base of stylet (Fig. 142) of second-stage larva averaging 7.3 μm; stylet length 27.9 μm (25.9–29.5) ..... *H. trifolii* Goffart

Underbridge fairly well developed (Figs. 126, 127); fenestra generally obscure in outline; distance of dorsal gland duct opening from base of stylet (Fig. 140) of second-stage larva averaging 4.0–4.5 μm; stylet length 23 and 25 μm (22–26) 27

27. Second-stage stylet 25 μm (24–26) in length; tail length 55.9 μm (47–66); hyaline tail terminal length averaging 30 μm, male unknown ..... *H. lespedezae* Golden & Cobb

Second-stage larva stylet length (Fig. 140) 23 μm (22–24); tail length averaging 42.0 to 50.4 μm and tail terminal length averaging 22.0 to 26.6 μm (depending on the race involved); males numerous ..... *H. glycines* Ichinohe

28. Semifenestra separated by a wide vulva bridge (Fig. 153); fenestral length generally twice width; vulva cone bifenestrate ..... *H. humuli* Filipjev

Semifenestra separated by a narrow (Fig. 150) to medium width (Fig. 152) vulva bridge; fenestral length generally slightly more than width; vulva cone ambifenestrate 29

29. Underbridge and bullae absent; vulva bridge thin (Fig. 154); second-stage larvae with three lines in lateral field ..... *H. longicolla* Golden & Dickerson

Underbridge weakly to strongly developed; bullae and vulva denticles present or absent; second-stage larva with either three or four lines in lateral field 30

30. Vulva denticles present; scattered bullae sometimes found in vulva cone (Fig. 161); fenestral length 32–40 μm (Fig. 155); second-stage larva with three lines in lateral field; stylet length 16–17 μm ..... *H. mothi* Khan & Husain

Vulva denticles and bullae absent in cone; fenestral length 37–54 μm; second-stage larva with either three or four lines in lateral field, stylet length 19–25 μm 31

31. Underbridge strongly or very strongly developed with furcations at both ends (Fig. 159); semifenestra with wavy lines (Figs. 147, 151) extending from outer edge to vulva slit; second-stage larva with three lines in lateral field 32

Underbridge weakly developed (Fig. 158) without furcations at ends; semifenestra without wavy lines; second-stage larva with either three or four lines in lateral field 33

32. Underbridge (Fig. 159) very strongly developed, 115–140 μm in length; semifenestra of mature cyst (and female) with distinct wavy lines (Figs. 151, 163) extending from outer edge to vulva slit; cysts basically lemon shaped; second-stage larva body length 430 μm (380–460), tail length 62 μm (57–67) .. *H. graminophila* Golden & Birchfield

Underbridge strongly developed (Fig. 156), 80–95 μm in length; semifenestra of female with distinct wavy lines (Figs.. 147, 162) extending from outer edge to vulva slit, but generally absent in mature cysts which are basically spherical in shape; second-stage larvae body length 558 μm (520–600) tail length 110–120 μm ..... *H. canadensis* Mulvey

33. Cysts appearing rather spherical but with distinct vulva cone; perianal pattern absent; fenestral arch (Fig. 149) very low, fenestral width greater than length; second-stage larva with four lines in lateral field ..... *H. cruciferae* Franklin

Cysts basically lemon shaped; perianal pattern (Fig. 164) present; fenestral arch (Fig. 150) high; fenestral length/width ratio less than 1.5; second-stage larva with three lines in lateral field ..... *H. cyperi* Golden, Rau & Cobb

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