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Redescription of *Heterodera rostochiensis* (Nematoda: Heteroderidae) with a Key and Notes on Closely Related Species

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ABSTRACT: *Heterodera rostochiensis* is redescribed on the basis of topotype specimens from Rostock, and a neotype is designated. Morphology of the stylet guide and vulval bodies are briefly discussed, and "race I" is the suggested designation for this nematode in the United States rather than "pathotype A" as in England. New data on the original cysts of *H. leptonepia* are presented and types established for the species. *Heterodera pseudorostochiensis* is placed as a new synonym under *H. tabacum*. The nomenclatural status of the "Mexican cyst nematode" is discussed, and it is considered to be conspecific with *H. virginiae*. A key to the six *Heterodera* species of the *rostochiensis* group (round cysts) is presented.

The golden nematode, *Heterodera rostochiensis* Wollenweber, 1923, is a major pest of potatoes, and recently was reported by Spears (1968) as occurring in 40 countries throughout the world. Since then its occurrence has been established in two additional countries, Tunisia² and Venezuela.³ Within the United States, this potato parasite is known only in Steuben County and Long Island in New York state, but still poses a potential threat to potato production in other states. It was found in Delaware (Spears, 1969) on a single farm, but was subsequently reduced below detection levels by vigorous regulatory procedures.

This cyst nematode was first reported on potatoes in Germany by Kuhn (1881) at which

time it was thought to be the sugar beet nematode, *H. schachtii* Schmidt, 1871. [See Franklin (1951) for historical details to about end of 1948.] Wollenweber (1923) first recognized morphological differences between the sugar beet nematode and the cyst nematode on potato, and at the same time he briefly described the latter as *H. rostochiensis*. For the next few years the specific status of this form was not generally recognized or accepted, and most workers considered it a "strain," or at most a subspecies of *H. schachtii*. Franklin (1940) presented a more complete description of *H. rostochiensis*, and gave it full recognition as a valid species with authorship credited to Wollenweber as we do today.

During the last 20 years the description of additional species in the "*rostochiensis* group" has increased greatly the need for a more complete description of the golden nematode. This paper presents a redescription of *H. rostochiensis* based on specimens obtained from potatoes in Rostock, German Democratic

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³ Specimens submitted for identification to senior author through Dr. W. F. Mai, Cornell University, Ithaca, New York, by Dr. F. Dao D. of Aragua, Venezuela.

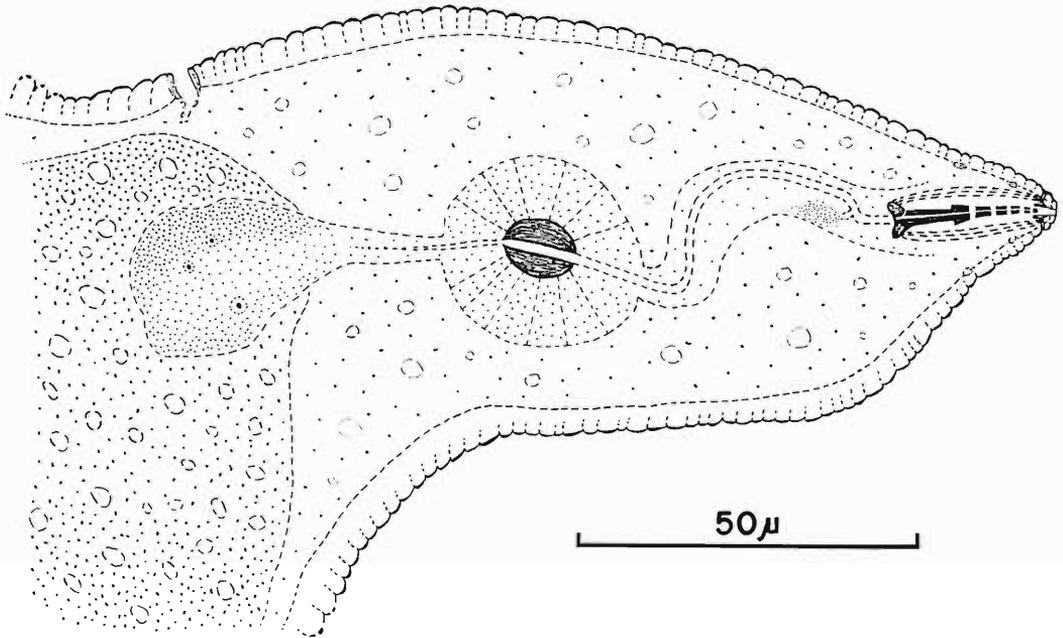


Figure 1. Drawing of anterior portion of female of *H. rostochiensis*.

Republic,⁴ with designation of a neotype; new details and lectotype designation for *H. leptonepia* Cobb and Taylor, 1953; comments on the relationship of the Mexican cyst nematode and *H. virginiae* Miller and Gray, 1968; and a key to the described species of the "*rostochiensis* group."

Heterodera rostochiensis
Wollenweber, 1923

Syn.: *H. schachtii* f. *solani* Zimmermann, 1927
H. schachtii *rostochiensis* Kemner, 1929
H. schachtii O'Brien and Prentice, 1930
H. (Globodera) rostochiensis Wollenweber, 1923 (Skarbilovich, 1959)

MEASUREMENTS: 50 females (Figs. 1, 3, 5, 6, 7, 8, and 9)—Length (including neck) 0.52 mm (0.42–0.64); width 0.34 mm (0.27–0.43); L/W ratio 1.5 (1.2–2.0); stylet 23 μ (22–24);

outlet of dorsal esophageal gland 6.2 μ (5.8–7.0).

Data on neotype (female): Length 0.47 mm; width 0.32 mm; L/W ratio 1.4; stylet 23.8 μ ; outlet of dorsal esophageal gland 6.4 μ ; excretory pore at base of neck and 130 μ from anterior end; vulva slit 10 μ in length; anus 41 μ from nearest edge of the hyaline vulval membrane, the latter measuring 13 μ in length (on the longer axis) and 7 μ in width.

DESCRIPTION OF FEMALES: Body pearly white, ovate to subspherical in shape, with elongate, protruding neck, rounded posteriorly. As maturity continues toward the cyst stage, body undergoes color changes through yellow to light golden. Cuticle thick, outer layer rugose, and punctations near or just beneath the surface. Head slightly set off, bearing two annules, and commonly appearing about as illustrated. Cephalic framework weakly developed. Stylet fairly strong, with slight curvature, and well-developed basal knobs sloping posteriorly. Anterior and posterior cephalids generally located as illustrated. Median bulb large, nearly spherical, with well-developed

⁴ For kindly providing this material, sincere appreciation is extended to Dr. H. Stelter and Dr. Ulrich, Amt. Institutsdirektor, Deutsche Akademie der Landwirtschaftswissenschaften zu Berlin, Institut für Pflanzenzüchtung, 2551 Gross-Lusewitz, Kreis Rostock, Deutsche Demokratische Republik.

valve. Esophageal glands often obscured but appearing custered near base of neck. Excretory pore prominent, located 131μ (105–175) from anterior end and always at or near base of neck. Vulva ellipsoid in shape, quite small, and measuring 12μ (7–14) in length and 7μ (5–11) in width. Vulva slit 9μ (6–11) in length. Often underneath the vulva and generally in a cluster (see Fig. 9) are vulval bodies, being highly variable in size and shape. Anus much smaller than vulva and is located 47μ (39–80) from the nearest edge of vulva and generally opposite the long axis of the latter.

MEASUREMENTS: 50 males (Figs. 2C, D, E, F, G, and H)—Length 1.08 mm (0.89–1.27); $a = 27$ (22–36); $b = 5.9$ (4.9–7.3); $c = 267$ (161–664); stylet 26μ (25–27); outlet of dorsal esophageal gland 6.4μ (5.3–7.0); spicules 35μ (32–39); gubernaculum 12μ (10–14); tail 4.4μ (1.7–6.7).

DESCRIPTION OF MALES: Body slender, vermiform, tapering slightly at both extremities. Cuticle with prominent annulation; subcuticular annulation less distinct and occurring twice as often as on cuticle. Lateral field measuring 7.0μ (6.7–8.4) in width at midbody, with 4 equally spaced lines except at its beginning in anterior portion. About midway, body measures 39μ (31–46) in width. Head slightly set off, hemispherical, with six annules. Cephalic framework heavily sclerotized. Stylet very stong, with prominent knobs appearing in lateral view generally as illustrated. Stylet guide seen anteriorly as the usual lyre-shaped structure with a ring at its base encircling the stylet; attached to the base of this lyre-shaped guide is a membranous, sleeve-like extension of the guide reaching about half the length of the basal stylet shaft, ending in another ring encircling the stylet at that point (see Fig. 2, D). Anterior and posterior cephalids present, located about as illustrated (Fig. 2, D). Median bulb ellipsoidal with its center located 99μ (85–112) from anterior end. Excretory pore about two annules posterior to commonly distinct hemizonid. One testis. Spicules

slightly arcuate, with tips rounded, unnotched. Tail short, variable in both length and shape (see Figs. 2 C, E, F, G, and H).

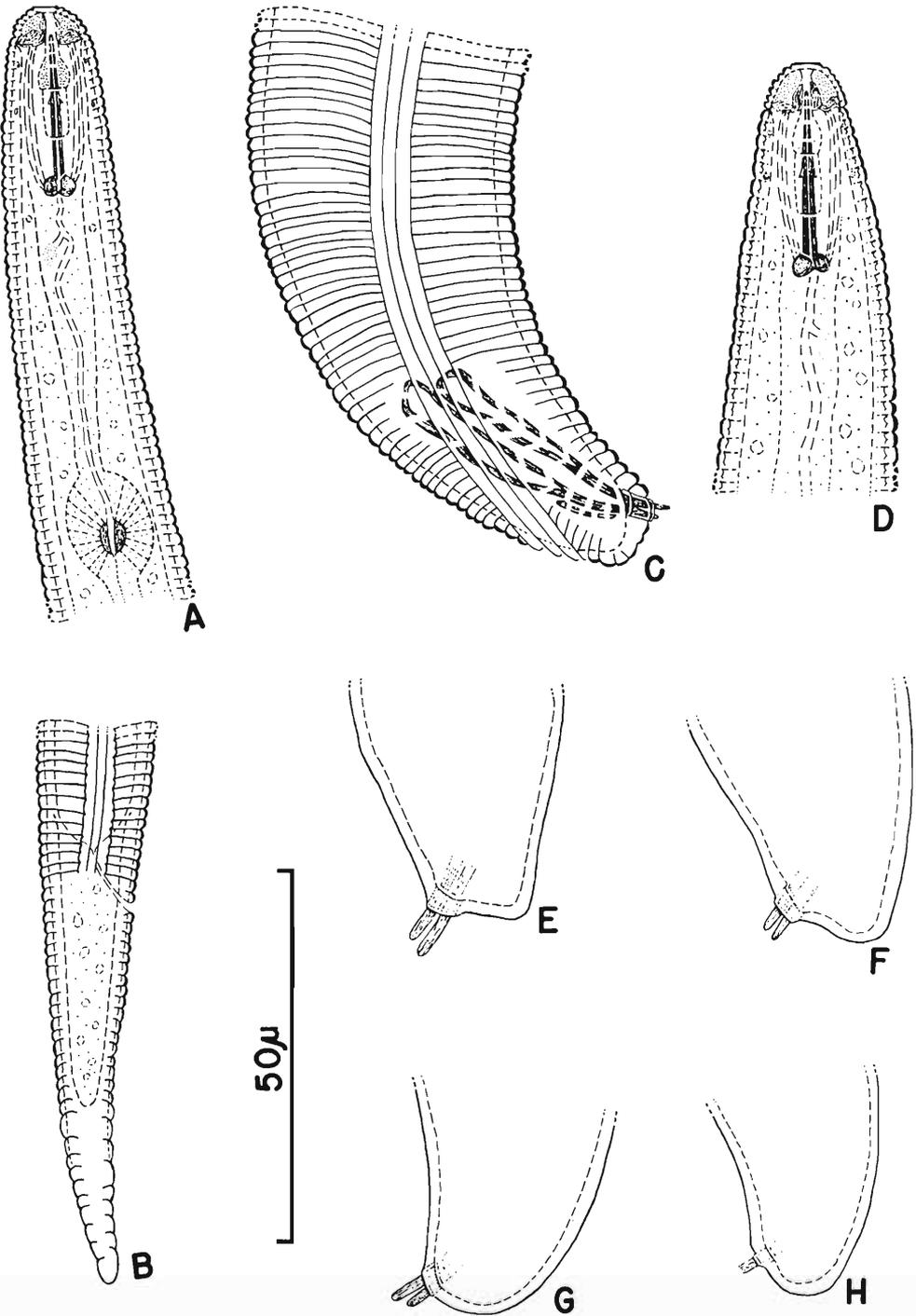
MEASUREMENTS: 50 second-stage larvae (Figs. 2A and B)—Length 0.43 mm (0.37–0.47); $a = 19$ (16–23); $b = 2.3$ (2.2–2.5); $c = 8$ (7–9); stylet 22μ (21–23); outlet of dorsal esophageal gland 5.5μ (5.0–6.7); tail 51μ (44–57); hyaline tail terminal 24μ (18–30); caudal ratio A = 3.4 (2.8–4.4); caudal ratio B = 10.8 (5.5–17.0).

DESCRIPTION OF SECOND-STAGE LARVAE: Body tapering at both extremities but much more so posteriorly. Subcuticular annulation twice as frequent as on cuticle. Lateral field with four lines for most of body length, the outer two crenate but without aeration. Body measures 23μ (19–26) at widest part. Head slightly set off, bearing five annules, and considerably wider at its base than in height, presenting a rounded though rather anteriorly flattened appearance as in Fig. 2 A. Cephalic framework heavily sclerotized. Stylet well developed, with prominent knobs appearing in lateral view as illustrated. Stylet guide as described above for males. Anterior and posterior cephalids present, located about as shown. Valvated median bulb prominent, ellipsoidal, with its center located 68μ (64–76) from anterior end. Isthmus and esophageal glands typical for the genus. Excretory pore posterior and almost adjacent to hemizonid. Genital primordium located slightly posterior to midbody and commonly consists of four cells. Tail tapering to small, rounded terminus. Phasmids generally difficult to see, located about halfway on tail.

MEASUREMENTS: 50 cysts (Figs. 4, 10, 11, 12, 13, 14, 15, and 16)—Length (including neck) 0.68 mm (0.45–0.99); width 0.54 mm (0.25–0.81); L/W ratio = 1.27 (1.0–1.8); diameter, or longest axis of fenestra (A) 15μ (8–20); distance from anus to nearest edge of fenestra (B) = 68μ (29–116); B/A ratio (Granek's ratio) = 4.5 (2.0–7.0).

DESCRIPTION OF CYSTS: Cysts brown in color, ovate to spherical in shape, with protruding

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Figure 2. Drawings of *H. rostockiensis*. Second-stage larva: A—Anterior; B—Posterior. Male: C—Posterior; D—Anterior; E—H—Outline of posterior portion showing variations in tail shape.



neck; circumfenestrate, abullate, and without the distinct "vulval bodies" commonly seen in white females. Fenestra much larger than the small but distinct, V-shaped anus. Cyst wall pattern basically as in female but often more prominent, and especially near midbody, tends to form wavy lines going latitudinally around body (see Fig. 16). Punctuation generally present but variable in intensity and arrangement.

MEASUREMENTS: 50 eggs—Length $105\ \mu$ (95–115); width $45\ \mu$ (42–48); L/W ratio = 2.3 (2.0–2.6). Egg shell hyaline, without visible markings. (See key for the distinguishing specific characteristics.)

NEOTYPE: Female: Collected by Dr. H. Stelter in May 1970. Slide T-203t, United States Department of Agriculture Nematode Collection, Beltsville, Maryland.

TYPE HABITAT, HOST, AND LOCALITY: Roots of potato (*Solanum tuberosum*) in Rostock, German Democratic Republic (East Germany).

Communication from Dr. Stelter indicated this nematode material to be "Rasse A," which is not known to break the *andigena* source of resistance.

Discussion

1. The golden nematode is perhaps the single most important species of plant nematode, and is subject to strict regulatory actions in the United States and other countries. Accurate identification of *H. rostochiensis* is, therefore, particularly critical, but has become increasingly difficult because of descriptions of closely related forms in recent years. The prospect of another species being split from *H. rostochiensis* (Jones et al., 1970) further intensifies the need for clear identity of the golden nematode. The designation of a neotype from topotype material in the present description is especially important in firmly establishing this species.

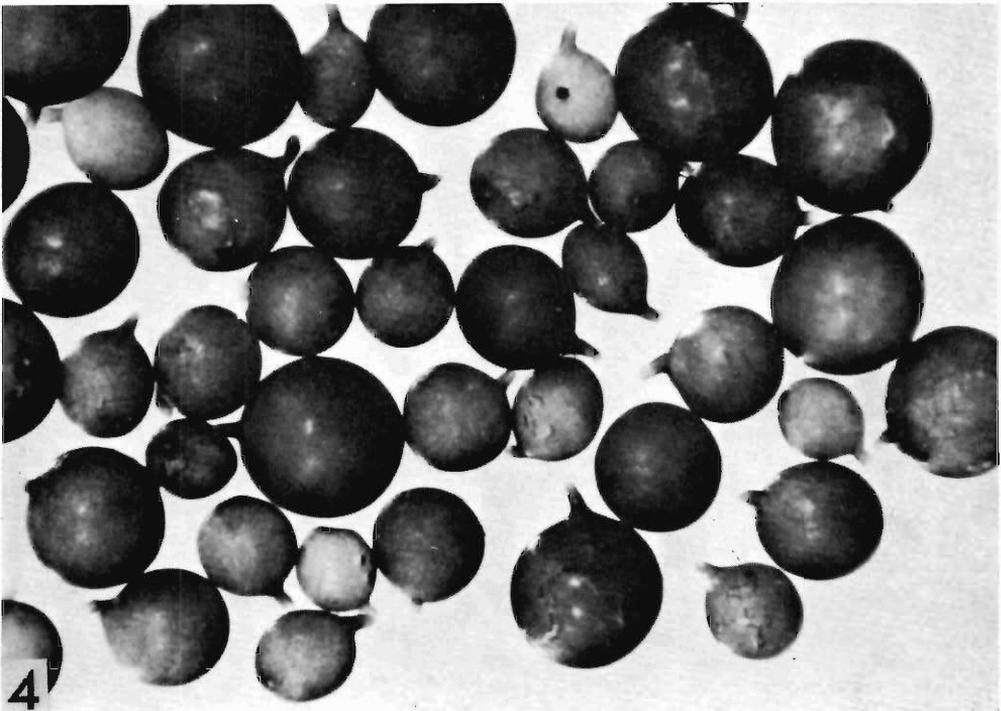
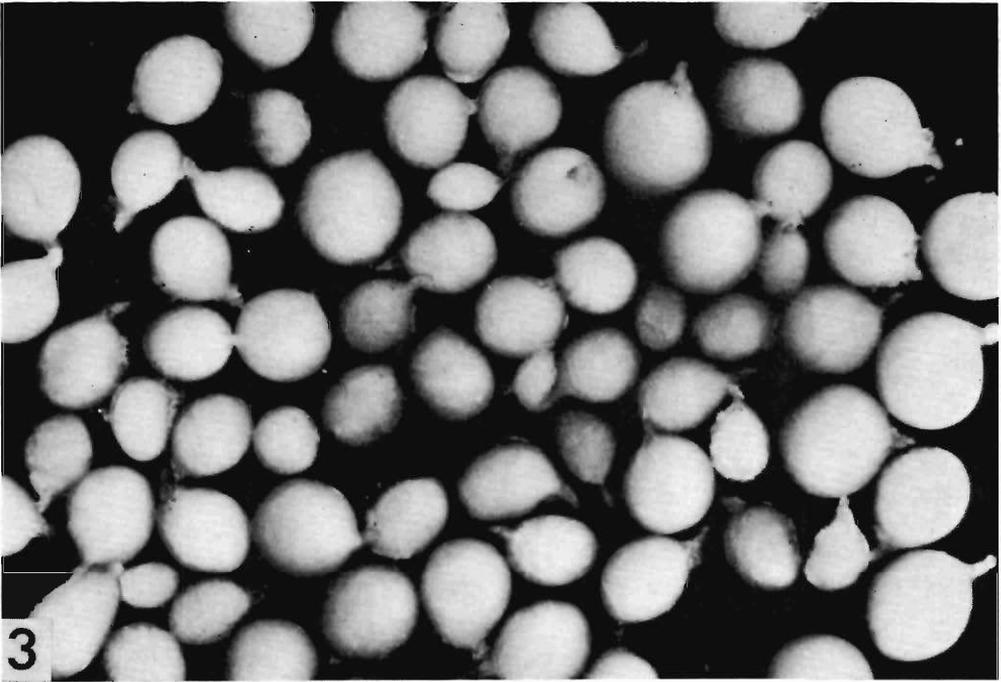
2. As background information for the present study, we collected and examined populations of *H. rostochiensis* from most countries of occurrence during the past several years. As

have other workers [ex. Evans and Webley (1970), Webley (1970), and Jones et al. (1970)], we noted that certain populations, including those from Peru, were in many respects not morphologically identical. However, specimens examined in great detail from Belgium and from the two areas of occurrence in the United States (Long Island and Steuben County, New York) proved to be morphologically similar to those from Rostock in all essential points. In view of its morphology and failure to attack potato varieties having the *andigena* source of resistance (Peconic and Wauseon), the nematode in the United States is clearly equivalent to "pathotype A" in England (Jones et al., 1970; Webley, 1970). We therefore suggest the use of the term, race 1 (or race A), for the population in this country rather than "pathotype A." This would be consistent with terminology in use for such infraspecific forms in *H. glycines* (Golden et al., 1970); in other nematodes, as races of *H. avenae* Wollenweber, 1924, and *Ditylenchus dipsaci* (Kuhn, 1857) Filipjev, 1936; and in other disciplines, as parasitology, zoology, and plant pathology.

3. The stylet guide, as illustrated for larvae in Figure 2A and for males in Figure 2D, is accurate for this species as far as could be determined with fixed material (in formalin or glycerin). However, in certain other *Heterodera* species where shown, the sleeve-like extension from the anteriorly placed lyrelike structure is different than depicted herein for *H. rostochiensis*. Hirschmann (1959) showed in *H. glycines* Ichinohe, 1952, a short sleeve-like extension ending in a ring encircling the anterior portion of the basal shaft of the stylet (in *H. rostochiensis* the ring is located at about one-half the basal shaft). In *H. betulae*, Hirschmann and Riggs (1969) showed the sleeve-like extension reaching almost to the stylet knobs and with no indication of its having a ring at its terminus. Miller and Gray (1968) illustrated the guide ring in a similar manner in their description of *H. virginiae*. It appears now that the stylet guide, when clearly and

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Photomicrographs of whole specimens of *H. rostochiensis*. Fig. 3—White females; Fig. 4—Cysts. (Both at same magnification.)



completely described for all of the various *Heterodera* species, might prove to be of taxonomic value.

4. In describing *H. millefolii*, Kirjanova and Krall (1965) referred to "bullae" in both that species and *H. rostochiensis*. They also pointed out that in the latter species the "bullae" formed compact circles around the "fenestra" while in *H. millefolii* the "bullae" were not numerous and occurred singly or in small groups a short distance from the "fenestra." Wilson (1968), without reference to the work by Kirjanova and Krall, reported on similar structures in *H. rostochiensis*, *H. tabacum*⁵ Lownsbery and Lownsbery, 1954, and *H. schachtii*, calling them "vulval bodies." He stated they were embedded in the hypodermis and in close association with the "fenestra" in the species examined. Our findings support both of the above observations relative to *H. rostochiensis*, and we accept, pending a more appropriate choice, Wilson's name of "vulval bodies." As indicated in Figure 9 the vulval bodies in the golden nematode are deep in the hypodermis, and are compact and clustered in the immediate vulval area of the white female. Sometimes there are few, sometimes many, clustered in the area. The individual vulval bodies seem to be variable in size and shape, often appearing as irregular, deflated balloons. These vulval bodies also might prove in time to have some taxonomic value in the cyst nematodes.

Heterodera leptonepia Cobb and Taylor, 1953

This very interesting species was described almost 20 years ago by Cobb and Taylor (1953) on the basis of three cysts collected

⁵ Without explanation Kirjanova (1963) proposed the name "*H. pseudorostochiensis*, sp. nov." and placed *H. tabacum* in synonymy under it. Since no possible justification for this action is known to us, we propose the continued recognition of *H. tabacum* as a valid name and species, and the placement of *H. pseudorostochiensis* Kirjanova, 1963, as a new synonym under *H. tabacum*.

from soil with potatoes taken on as ship's stores at Callao, Peru. Presumably the cysts and potatoes came from Peru although the ship was known to travel the Pacific west coast almost entirely on the nitrate run from Peru and Chile to the United States. Two of these cysts contained eggs with larvae while the third was evidently empty. Since all of this material was retained, we remounted it in glycerin and examined the specimens again.

A striking feature emphasized in the excellent original description was the extreme slenderness of the larvae ($a = 39$). Other distinctive larval characters included an average length of 0.56 mm; a short stylet of 18 μ ; the outlet of the dorsal esophageal gland being 12 μ (or $\frac{2}{3}$ of stylet length) from the base of stylet; and no annules on the head. Our observations confirmed these and other points reported in the original description.

Through the years the opinion apparently developed among many workers that the cysts of *H. leptonepia* are essentially similar to those of *H. rostochiensis*. However, such is not the case, except for shape. In *H. leptonepia* the cyst wall pattern and B/A ratio are different from *H. rostochiensis* as shown in photomicrographs herein and described below.

LECTOTYPE: Cyst (Fig. 1D in original description and Figs. 17, 20, and 21 in present paper)—Circumfenestrate, abullate. Fenestra about 29 μ at greatest diameter; small anus 12 μ from nearest edge of fenestra, giving a B/A ratio (Granek's ratio) of 0.4.

PARALECTOTYPES: Two cysts, larvae, and eggs—cysts circumfenestrate, abullate. One cyst with fenestra about 24 μ at greatest diameter; small anus 23 μ from nearest edge of fenestra; B/A ratio = about 1. Second cyst (Figs. 18 and 19) with fenestra measuring 18 μ at greatest diameter; anus not located. Excretory pore in one cyst seen located at base of neck.

From original description—"Cysts: Light brown, more or less ovate, about 0.5 by 0.3

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Photomicrographs of posterior portion of a single female of *H. rostochiensis*. Fig. 5—Vulval-anal area at outer surface. Fig. 6—Enlarged vulval area on surface. Fig. 7—Same as Fig. 5, but at deeper focus to under surface (note difference in appearance of pattern). Fig. 8—Same as Fig. 6, but at deeper focus to under surface. "a" with arrow indicates anus.

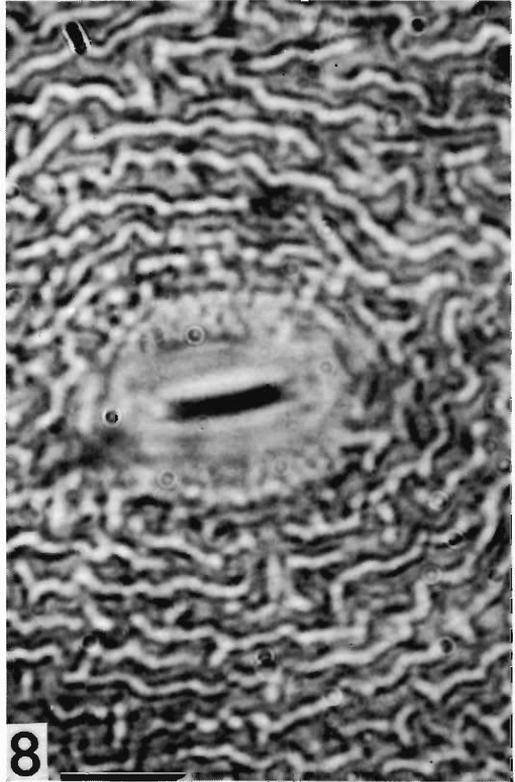
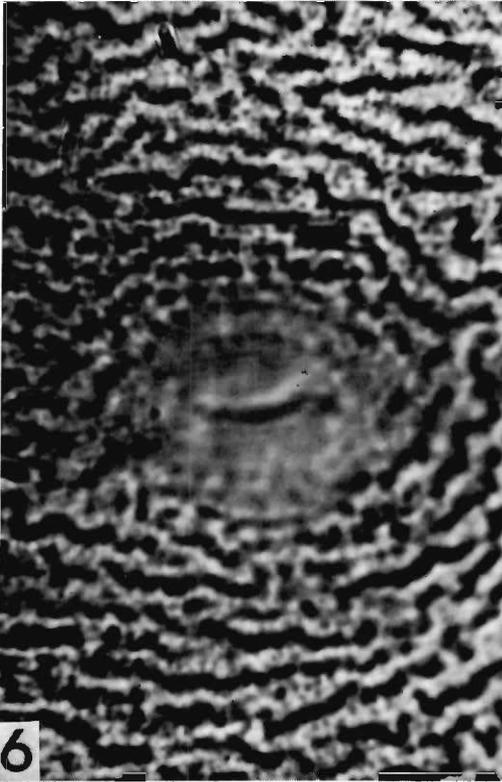
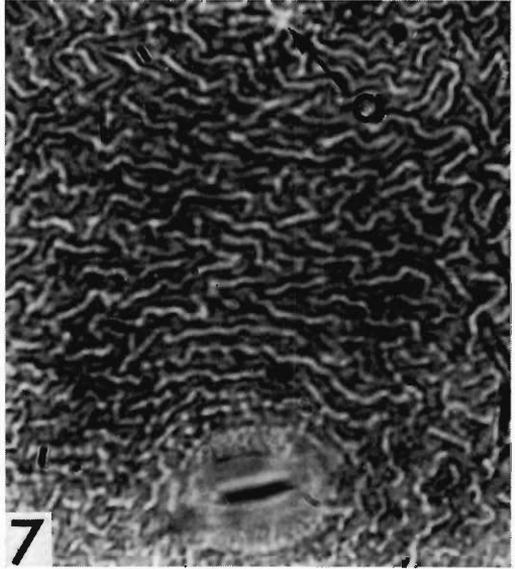
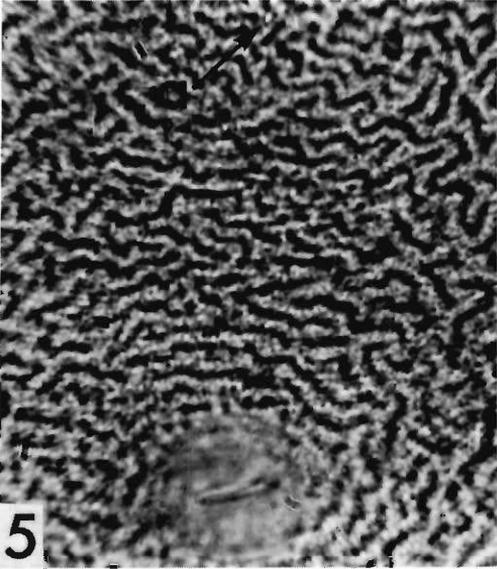




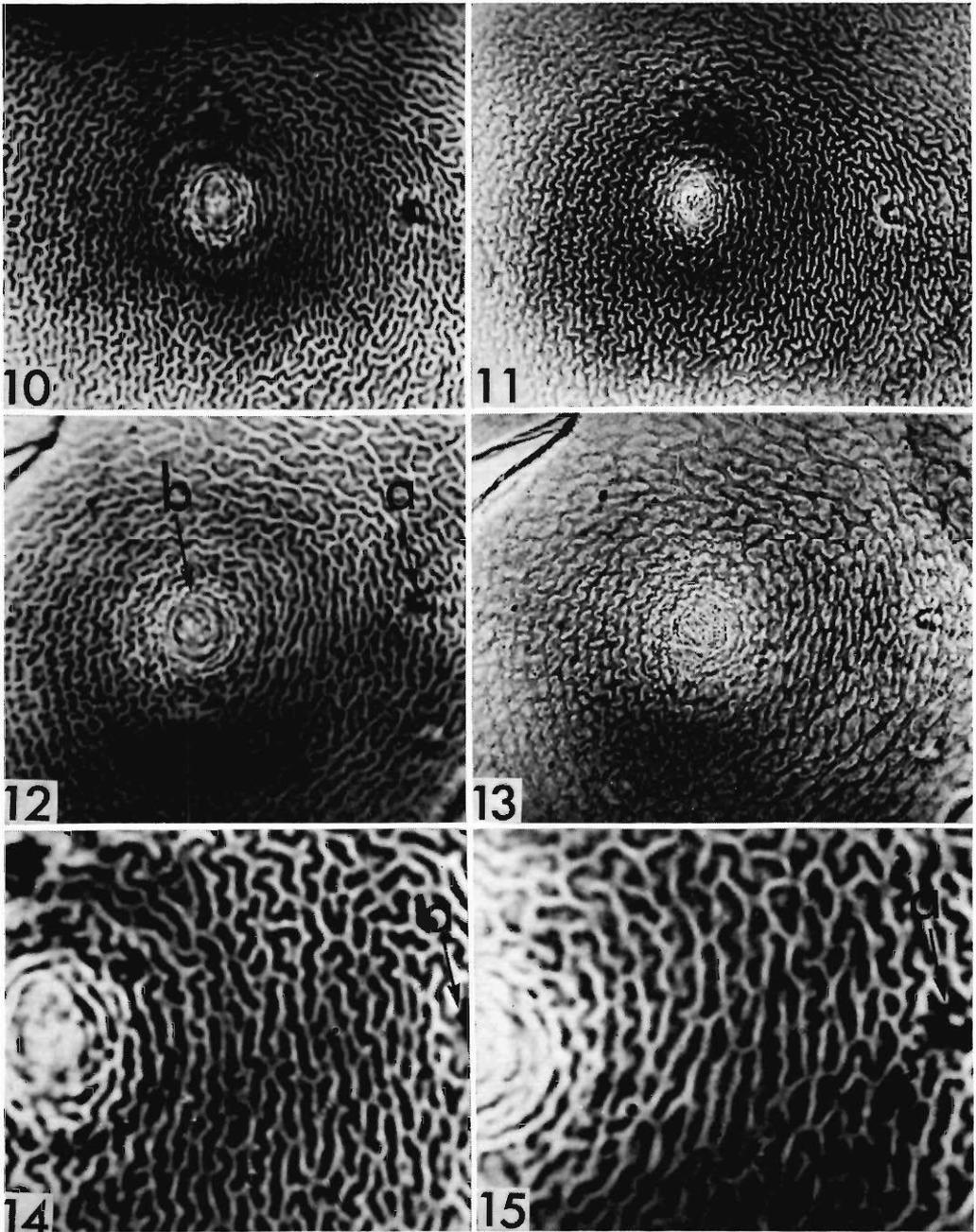
Figure 9. Photomicrograph of vulval bodies in white female of *H. rostochiensis*. "a" with arrows indicate vulval bodies. "b" with arrow indicates inner area of vulva.

mm, with distinct neck; smoothly rounded posteriorly as in *H. rostochiensis* and *H. punctata* Thorne, 1928. Vulvar opening round and much larger than the minute, pore-like anus, as is the case with *H. rostochiensis*; different from *H. punctata* which has anus located at a thin spot of cyst wall so that vulvar and anal openings appear about same size (Franklin

1940). Outer layer of cyst wall with rugose pattern of striae extending from neck to near vulva; immediately around vulva, striae interrupted, forming an irregular pattern as shown in Figure 1D. A lower layer of the cyst wall distinctly punctate, with minute dots arranged in closely spaced parallel rows at right angles to axis of cyst; dots irregularly spaced in rows."

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Photomicrographs of posterior portion of two cysts of *H. rostochiensis*. Fig. 10—Fenestral-anal area of one cyst at outer surface. Fig. 11—Same area and cyst as Fig. 10 but at deeper focus to under surface. Fig. 12—Fenestral-anal area of the second cyst at outer surface. Fig. 13—Same area and cyst as Fig. 12 but at deeper focus to under surface. (Note differences in pattern between the two cysts and at different



focus.) Fig. 14—Cyst wall pattern of Fig. 10 between fenestra and anus at higher magnification. Fig. 15—Cyst wall pattern of Fig. 12 between fenestra and anus at higher magnification. “a” with arrow indicates anus. “b” with arrow indicates fenestra.

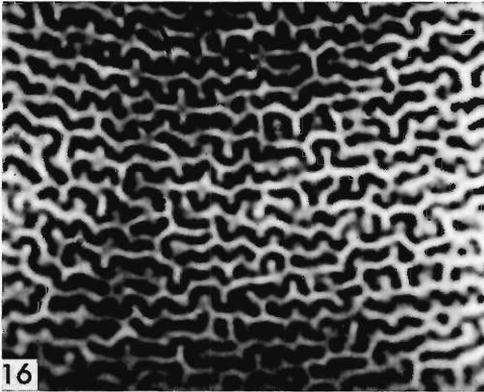


Figure 16. Enlarged photomicrograph of *H. rostockiensis* cyst near midbody.

For details on larvae, eggs, and diagnosis, see the original description, and the above comments on the larvae. Also, note certain characters in key to some *Heterodera* species in this paper.

LECTOTYPE: Cyst: Collected April 26 1952 by Inspector C. H. Oatridge of the Bureau of Entomology and Plant Quarantine, USDA, at the Oakland, California, port of entry, from soil (in ship's stores) with potatoes taken aboard at Callao, Peru. Slide T-202t, United States Department of Agriculture Nematode Collection, Beltsville, Maryland.

PARALECTOTYPES: Two cysts, larvae, and eggs: Same data and collection as lectotype. Slides T-989p-T-992p.

TYPE HABITAT AND HOST: Unknown. Thought possibly to be the roots of some solanaceous plant.

TYPE LOCALITY: Unknown. Thought to be some area in Peru.

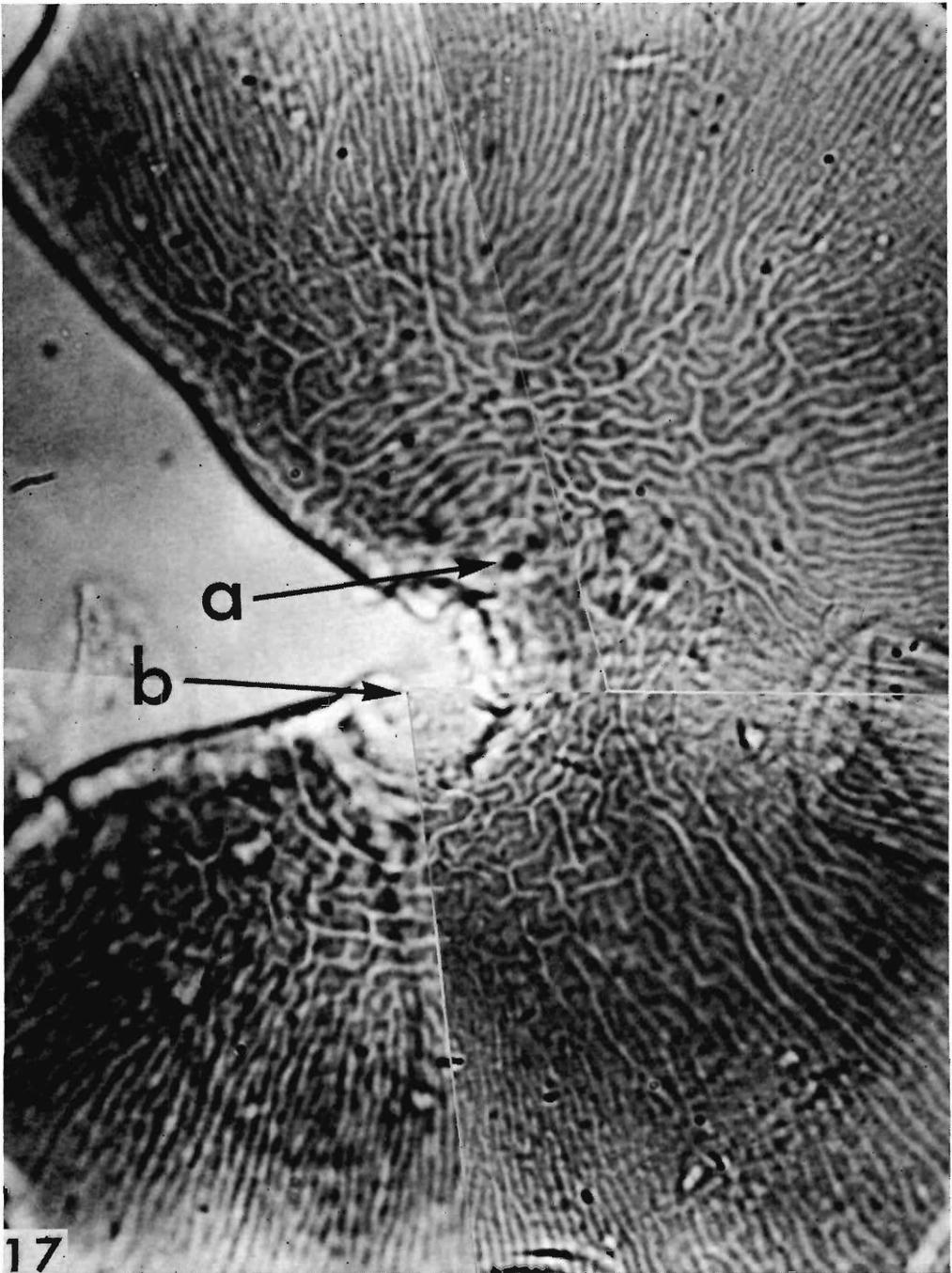
As far as known, this nematode has never been found since the initial collection was made although it is obviously a very distinctive species. Perhaps more specimens and a host can be found in the future by sampling various plants in and around potato fields in Peru.

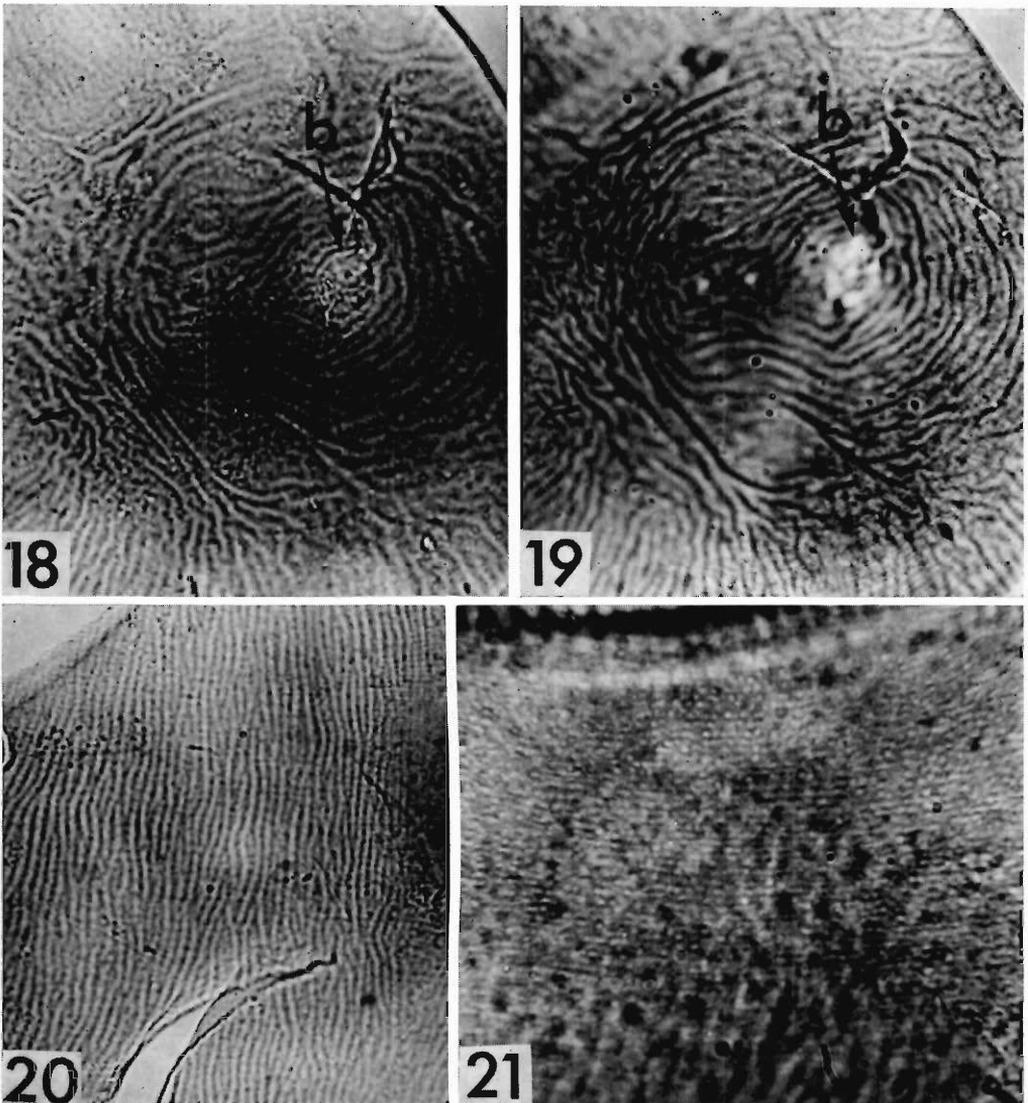
Mexican cyst nematode

As his doctorate thesis at the University of Wisconsin, Campos Vela (1967) made a very thorough study on the taxonomy, life cycle, and host range of a cyst nematode from Mexico which he named "*Heterodera mexicana* n. sp." in his thesis. As far as we know, there has not yet been a regular publication describing this proposed species. Consequently, in accordance with the present International Code of Zoological Nomenclature (especially Articles 7-9), this name is still unavailable (not properly published) as a specific name. When used as a specific name under these circumstances, as by Jones et al. (1970) and by Franklin (1971), it becomes a *nomen nudum* since it has never been published in the sense of the Code. Mayr (1969) discusses such a point clearly in his recent book (p. 347), and we agree that an unavailable name has no standing in zoological nomenclature and is best never recorded.

In describing *H. virginiae*, Miller and Gray (1968) correctly did not refer to the above nematode name as used in Campos Vela's thesis research. With both specimens and description of *H. virginiae* on hand, we soon had an opportunity also to examine material of the Mexican cyst nematode and Campos Vela's thesis. We were unable to find any consistent morphological differences of a specific nature between *H. virginiae* and the Mexican cyst specimens. Also, the measurements on most characters of specific value were identical, or nearly so, in both the thesis description of the Mexican cyst nematode and the published description of *H. virginiae*. As a matter of fact, Campos Vela pointed out (p. 43) that the morphological difference between his specimens and *H. virginiae* was the shape of the dorsal knob of the white female stylet. This character seemed to us to vary considerably between individual females and in the position of the specimen when viewed. This variable character, and the host differences indicated

Fig. 17. Composite photomicrograph of the posterior portion of a cyst of *H. leptonepia* (note pattern around fenestra and heavy striae leading anteriorly). "a" with arrow indicates anus. "b" with arrow indicates fenestra. →





Photomicrographs of cysts of *H. leptonepia*. Fig. 18—Posterior portion with focus at outer surface. Fig. 19—Same as Fig. 18 but with deeper focus to under surface. Fig. 20—Portion of cyst near midbody showing heavy longitudinal striae. Fig. 21—Latitudinal rows of punctation shown at high magnification. "b" with arrow indicates fenestra.

by Campos Vela, do not seem to justify specific status for this nematode. In the absence of a full published description giving clearer and more reliable characters, we prefer to consider the Mexican cyst nematode as conspecific with

H. virginiae. In the meantime, should some identity of the population of the cyst nematode from Mexico be needed, perhaps the term, Mexican race (or race 1) of *H. virginiae* would be appropriate.

**Key to the *Heterodera* species of the
rostochiensis group (round cysts)**

1. Cysts with large fenestra and very small anus 2
Cysts with conspicuous fenestra and anus, both about equal in size *H. punctata*
2. Cysts with excretory pore near base of neck; vulva slit* generally straight, less than 25 μ in length 3
Cysts with excretory pore at mid-neck; vulva slit bow-shaped, about 35 μ in length *H. millefolii***
3. Cyst wall pattern with rugose striae at midbody primarily extending latitudinally; larvae with "a" = about 18–25; stylet 20 or more μ in length; outlet of dorsal esophageal gland about $\frac{1}{3}$ or less of stylet length 4
Cyst wall pattern with prominent striae extending longitudinally from fenestral area to near base of neck; larvae with "a" = 39; stylet 18 μ long; and outlet of dorsal esophageal gland about $\frac{2}{3}$ of stylet length *H. leptonepia*
4. Cysts with B/A ratio (Granek's ratio) averaging 2.8 or less; outlet of dorsal esophageal gland of males averaging about 3.5 μ from base of stylet 5
Cysts with B/A ratio averaging 4.5; outlet of dorsal esophageal gland of males approximately 6.4 μ from base of stylet *H. rostochiensis*
5. Cysts with B/A ratio averaging 2.8; cyst wall pattern in fenestral area mazelike *H. virginiae*
Cysts with B/A ratio averaging 1.5; cyst wall pattern in fenestral area appearing as wavy but rather continuous lines encircling the fenestra *H. tabacum*

As with other keys, this one is presented to aid in identification, perhaps eliminating some species from further consideration while pointing to one or more others for more careful examination. In any case, it is always advisable to refer to a particular species de-

* Exact nature of vulva and slit in *H. leptonepia* is not known but statement probably applies.

** *Heterodera millefolii* was described by Kirjanova and Krall on the basis of one female only. A more complete description involving the various other stages is needed in order to know better the characters of this species.

scription before making a final decision on the identity of the nematode.

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Enzyme Histochemistry of the Holdfast Organ and Forebody Gland Cells of *Alaria marcianae* (La Rue, 1917) (Trematoda: Diplostomatidae)¹

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ABSTRACT: Histochemical staining tests for hydrolytic enzymes in adult *Alaria marcianae* (La Rue, 1917) revealed B-glucuronidase, aryl sulfatase B, and leucine aminopeptidase in the holdfast organ gland cells, chymotrypsinlike enzymes in the tegumental surface layer of the holdfast organ, and a cathepsinlike indoxyl C-esterase in the anterior mass of holdfast organ gland cells, forebody gland cells, and certain anterior forebody tegumentary cells; gamma glutamyl transpeptidase and trypsinlike enzymes were not present. Strong protease and hyaluronidase activity was indicated by substrate film methods in areas corresponding to the holdfast organ, the forebody gland cells and ducts, and the anterior forebody tegumentary cells. The results support the view that the gland cells associated with the holdfast organ and lappets secrete hydrolases for extracorporeal digestion and indicate a similar function for certain forebody tegumentary cells. Lysosomal enzymes apparently are not involved in extracorporeal digestion.

Recent studies on adult strigeoids indicate that at least one function of the holdfast organ and forebody gland cells is the synthesis and release of hydrolytic enzymes for extracorporeal digestion (Lee, 1962; Erasmus and Öhman, 1963, 1965; Öhman, 1965, 1966a, b; Bogitsh, 1966a, b; Erasmus, 1968, 1969a, b, c, 1970). In strigeoids which lack lappets and/or forebody gland cells other specialized cells (lappet cells, "subcuticular cells") apparently serve a similar function (Öhman, 1966a; Bogitsh, 1966a; Bogitsh and Aldridge, 1967; Erasmus, 1969a). Information on these enzymes has

been derived from histochemical staining techniques and in vitro methods involving enzyme secretion.

The subject of the present study is the diplostomatid strigeoid, *Alaria marcianae* (La Rue, 1917). In a preliminary study of this parasite, Johnson, Bhatti, and Kanemoto (1971) reported acid phosphatase and nonspecific esterases in the tegumental surface layer and gland cells of the holdfast organ and nonspecific esterases in the forebody gland cells and ducts. The purpose of this study was to investigate further the nature of the hydrolases in these cells.

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