Journal of Nematology 34(3):250–262. 2002.

A Key and Compendium to Species of the *Heterodera avenae* Group (Nematoda: Heteroderidae)

Zafar A. Handoo[1]

Abstract: A key based on cyst and juvenile characters is given for identification of 12 valid *Heterodera* species in the *H. avenae* group. A compendium providing the most important diagnostic characters for use in identification of species is included as a supplement to the key. Cyst characters are most useful for separating species; these include shape, color, cyst wall pattern, fenestration, vulval slit length, and the posterior cone including presence or absence of bullae and underbridge. Also useful are those of second-stage juvenile characteristics including aspects of the stylet knobs, tail hyaline tail terminus, and lateral field. Photomicrographs of diagnostically important morphological features complement the compendium.

Key words: compendium, cyst, diagnostic compendium, *Heterodera avenae* group, identification, key, morphology, nematode taxonomy.

The cereal cyst nematode *Heterodera avenae* Wollenweber 1924 is a major pest of cereals throughout the world. The origin of this species appears to be in Europe, where it was first recorded on oats, then later on wheat and barley (Meagher, 1977) and maize (Swarup et al., 1964). Mulvey and Golden (1983) gave the first illustrated key to the 34 cyst-forming genera and species of Heteroderidae in the western hemisphere with species morphometrics and distribution and included four species in the *H. avenae* group. The taxonomy of the *H. avenae* group has been advanced by numerous review papers published by different workers (Ferris et al., 1989, 1994; Golden, 1986; Krall, 1977; Mulvey, 1972, 1973; Robinson et al., 1996; Rumpenhorst et al., 1996; Stone and Hill, 1982; Vovlas, 1985; Williams and Siddiqi, 1972; Wouts and Sturhan, 1995; Wouts et al., 1995).

H. avenae, together with other bifenestrate cyst nematodes having a short vulval slit, were placed in the genus *Bidera* (Krall and Krall, 1978), but Mulvey and Golden (1983) synonymized *Bidera* with *Heterodera.* Although Wouts (1985) retained *Bidera,* it was rejected by Stone (1986) and Luc et al. (1988). Baldwin and Mundo-Ocampo (1991) included nine species in the *H. avenae* group. In describing one new species of *Heterodera,* Wouts et al. (1995) gave a key to species of *H. avenae* group.

There are limitations to comparing measurements of species of the *avenae* group made by different investigators vs. a reevaluation where they are all made by one investigator (as in the present study). The limitations to the Wouts et al. (1995) key are overcome in the present manuscript. The previous key was dependent on ambiguous characters that are avoided or better defined in this new key, which incorporates a broader understanding of intraspecific variability than the past keys. Also, the presentation of a compendium of crucial diagnostic characters provides an important compilation for use in identification of species as a practical alternative and supplement to the key. Subbotin et al. (1996) gave morphological, morphometric, and biochemical characters of several populations of the *H. avenae* group from the former USSR and compared them with populations of *H. avenae* and an undescribed species of *H. avenae* group from Germany. The identification of members of the *H. avenae* group has been advanced through several biochemical and molecular studies (Bekal et al., 1997; Subbotin et al., 1998, 1999). The analysis of ribosomal DNA has become a popular tool for (sub) species identification of several nematode genera. ITS regions were found to be useful to differentiate species within the *H. avenae* group (Bekal et al., 1997; Ferris et al., 1994). Also, Subbotin et al. (1998) presented a comparative analysis of several populations of seven species of the *H. avenae* group and the morphometrics of juveniles, and their studies showed that rDNA-RFLPS can distinctly separate species and populations within the *H. avenae* group. However, carefully developed morphological identification is needed to support the exploration of other alternative systems. There is a need for a morphological basis for reciprocal illumination in determining the reliability of biochemical/molecular systems as a wider range of populations and species is tested.

The objectives of this study were to examine specimens and published data on *Heterodera* spp. (*H. avenae* group), define the valid and most significant differentiating characters, and prepare a new key and compendium containing morphometric and related details of all the life stages to facilitate easy identification of 12 valid *Heterodera* spp. of the *H. avenae* group.

Materials and Methods

Paratype specimens of six species (*H. avenae, H. bifenestra, H. hordecalis, H. iri, H. latipons,* and *H. mani*) were

Received for publication 17 July 2000.

[1] Microbiologist, USDA, ARS, Nematology Laboratory, Plant Sciences Institute, Beltsville Agricultural Research Center, Beltsville, MD 20705-2350.

Mention of a trade name, warranty, proprietary product, or vendor does not constitute a guarantee by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

The author thanks Donna M. S. Ellington, Support Scientist, Nematology Laboratory, USDA, ARS, Beltsville, MD, for technical assistance. I also thank D. Sturhan and W. Wouts for the loan, study, and deposition of paratype specimens of *Heterodera spinicauda* in the USDA Nematode Collection.

E-mail: handooz@ba.ars.usda.gov

This paper was edited by R. T. Robbins.

TABLE 1. Diagnostic data on mature female and vulva cone structures of *Heterodera* species (*H. avenae* group).

Species	Body			L/W ratio	Stylet length	DGO
	Length (without neck)	Neck length	Width			
H. arenaria	748 (480–940)	160 (100–200)	589 (380–840)	1.3	30 (28–31)	5 (4–5.2)
H. aucklandica	388 (360–415)	122 (90–150)	230 (175–300)	—	27 (25–30)	5 (3–8)
H. avenae	604 (504–780)	108 (95–120)	340 (350–500)	1.4 (1.2–1.6)	26–32	5.0
H. bifenestra	363 (278–440)	92 (44–137)	271 (205–348)	1.3 (1.1–1.6)	22 (20–23)	5 (3–7)
H. filipjevi	—	—	—	—	—	—
H. hordecalis	500 (350–731)	107 (76–136)	400 (220–561)	1.1 (1.1–1.6)	27 (25–30)	—
H. iri	676 (565–764)	125 (99–147)	548 (463–606)	1.3 (1.2–1.4)	28 (25–30)	8 (3–11)
H. latipons	525 (348–645)	83 (58–103)	414 (277–510)	—	25 (21–28)	4 (3–5)
H. mani	617 (485–721)	157 (146–164)	539 (418–679)	1.1 (1.0–1.3)	30 (24–34)	8 (5–9)
H. pratensis	430 (345–550)	127 (105–145)	343 (180–470)	1.7 (1.4–2.5)	29 (25–30.5)	4.3 (4–5.2)
H. spinicauda			Not described			
H. turcomanica			Not described			

obtained and examined from the USDA Nematode Collection, Beltsville, Maryland. Type specimens of one additional species (*H. spinicauda*) on *Agrostis stolonifera* and reed grass from Zuidland, Zeeland, The Netherlands, were provided for study by D. Sturhan (Germany) and W. Wouts (New Zealand). All specimens were either already mounted in glycerin or preserved in 3% formaldehyde + 2% glycerin solution in vials. Examinations were made with a compound light microscope and morphometric data obtained with an eyepiece micrometer. Light-microscopic images of fixed nematodes were taken with the Bioquant ver. 3.2 imaging system (Biometrics, Inc., Nashville, TN), and photographs were made with an automatic 35-mm camera, both attached to a Leitz DMRB Leica microscope. Original descriptions and any subsequent redescrip-

TABLE 2. Diagnostic data on cysts and vulval cone structures of *Heterodera* species (*H. avenae* group).

Species	Body				Fenestra					Underbridge	
	Length (without neck)	Neck length	Width	L/W ratio	Length	Width	Vulva slit length	Vulva bridge width	Bullae	Length	Width
H. arenaria	799 (600–1,027)	—	602 (395–790)	1.3	47 (38–55)	22 (18–27)	9 (8–12)	8 (5–11)	present heavy	absent	
H. aucklandica	690 (565–800)	—	460 (215–550)	—	21 (16–26)	27 (24–32)	9 (7–12)	4 (4–7)	present heavy	absent	
H. avenae	710 (580–975)	—	510 (390–725)	1.3 (1.3–1.4)	48 (40–52)	21 (18–23)	9 (8–11)	6 (5–8)	present heavy	absent	
H. bifenestra	431 (311–572)	—	350 (205–509)	1.2 (1.0–1.5)	45 (39–58)	25 (20–32)	13 (10–16)	5–17	absent	absent	
H. filipjevi	690 (490–830)	—	490 (340–620)	—	52 (41–64)	28 (21–33)	7 (6–8)	8 (6–9)	present	82 (72–106)	17 (15–18)
H. hordecalis	563 (395–731)	101 (68–128)	437 (255–561)	1.3 (1.1–1.5)	55 (47–62)	22 (18–26)	20 (17–24)	27 (19–35)	absent	115 (85–143)	26 (22–34)
H. iri	675 (600–755)	119 (100–131)	520 (450–550)	1.3 (1.1–1.5)	42 (35–50)	24 (17–28)	11 (8–15)	—	present (fairly heavy)	35–50	10–16
H. latipons	525 (348–645)	83 (58–103)	414 (277–510)	—	67 (58–76)	21 (15–27)	7 (6–9)	33 (18–39)	absent	103 (80–125)	11 (7–14)
H. mani	590 (480–725)	139 (124–155)	494 (390–650)	1.2 (1.1–1.4)	52 (43–59)	27 (17–33)	6.5 (4–10)	7 (5–9)	present heavy	absent	
H. pratensis	675 (530–800)	—	570 (400–685)	1.2 (1.1–1.4)	20 (18–24)	24 (20–28)	11.2 (8.9–12.9)	6.9 (5–8.9)	present heavy	absent	
H. spinicauda	475 (340–590)	—	422 (270–540)	1.1 (1.1–1.2)	21 (17–29)	23 (18–29)	7 (5–9)	8 (5–11)	absent	76 (46–103)	17 (7–32)
H. turcomanica	557 (430–695)	—	363 (265–435)	—	71	18–25	9–14	35	present	—	14

TABLE 3. Diagnostic data on males of *Heterodera* species (*H. avenae* group).

Species	Body length	Body width	a	b	Spicule length	Gubernaculum length	Stylet length	DGO	Lateral lines
H. arenaria	1,604 (1,492–1,778)	32 (31–34)	46 (43–52)	11 (10–12)	40 (36–44)	10 (9–12)	33 (32–34)	5 (4–6)	4
H. aucklandica	1,120 (800–1,500)	29 (23–32)	39 (27–50)	—	39 (33–42)	14 (13–15)	29 (26–31)	6 (5–8)	4
H. avenae	1,400 (1,070–1,610)	—	51 (32–55)	9 (7–12)	36 (33–38)	10–12	28.5 (27–31)	3.6	4
H. bifenestra	770 (623–902)	22 (18–25)	35 (34–36)	4.7 (4.6–5)	29 (26–32)	10–12	23 (21–24)	3 (3–4)	4
H. filipjevi	—	—	—	—	—	—	—	—	—
H. hordecalis	1,112 (805–1,390)	29 (27–33)	39 (30–43)	6 (6–7)	37 (34–42)	11 (9–13)	27 (24–29)	—	4
H. iri	1,292 (1,060–1,450)	36 (33–40)	36 (32–36)	—	39 (36–43)	12 (11–14)	30 (28–33)	8 (6–10)	4
H. latipons	1,167 (960–1,406)	29 (25–33)	41 (32–51)	10 (9–11)	34 (32–36)	8	27 (22–29)	3–5	4
H. mani	1,388 (1,100–1,750)	29 (26–33)	49 (41–58)	—	39 (35–43)	12 (9–14)	26 (22–30)	6 (3–8)	4
H. pratensis	1,170 (1,050–1,330)	29 (28–30)	40 (37–47)	2.6 (2.1–3.2)	40 (38–44)	13 (12–14)	29 (26–31)	4.6 (4–5.2)	4
H. spinicauda	Males unknown								
H. turcomanica	Males unknown								

tions or other related data also were used to assess species that included other species of the group. The arrangement of the compendium included in Tables 1 through 4 is according to the Mulvey and Golden (1983) compendium format and contains updated morphometric data for the most important diagnostic characters of females, cysts, males, and second-stage juveniles of 12 valid species of the *Heterodera avenae* group. All measurements were made in micrometers (μm) unless otherwise stated.

SYSTEMATICS

Genus *Heterodera* Schmidt, 1871
Species of *Heterodera avenae* group
(Tables 1–4, Figs. 1–9)

H. arenaria Cooper, 1955
H. aucklandica Wouts, 1995
H. avenae Wollenweber, 1924
H. bifenestra Cooper, 1955

TABLE 4. Diagnostic data of second-stage juveniles of *Heterodera* species (*H. avenae* group).

Species	Body length	Body width	Stylet length	Lateral lines	Tail length	Hyaline terminal length	DGO	a
H. arenaria	639 (590–677)	—	29 (27–30)	4	79 (72–84)	51 (41–58)	6 (5–7)	28 (27–30)
H. aucklandica	508 (440–580)	20 (19–21)	25 (23–26)	4	76 (60–80)	46 (40–51)	8 (7–10)	25 (22–29)
H. avenae	577 (520–620)	20–24	27 (24–28)	4	68 (58–70)	41 (35–45)	5–6	25 (21–27)
H. bifenestra	452 (419–485)	20 (18–22)	23 (22–25)	3	78 (71–87)	46 (39–52)	—	—
H. filipjevi	551 (430–580)	23 (21–25)	27 (22–31)	3	51 (49–63)	35 (31–39)	—	24 (21–25)
H. hordecalis	436 (415–466)	19 (18–21)	23 (21–25)	4	52 (45–59)	34 (29–39)	—	23 (21–25)
H. iri	638 (573–695)	23 (19–32)	25 (23–28)	4	94 (83–103)	62 (51–75)	9 (8–10)	27 (22–30)
H. latipons	454 (401–478)	21 (19–22)	24 (23–25)	4	48 (42–54)	27 (20–31)	5 (4–5)	23 (20–25)
H. mani	578 (530–627)	22 (19–24)	24 (22–28)	4	67 (58–77)	40 (28–48)	6 (2–10)	27 (22–30)
H pratensis	535 (490–575)	21 (20–23)	24 (24–25)	4	67 (60–73)	42 (35–47)	5.1 (4.4–6.3)	25 (22–27)
H. spinicauda	445 (420–485)	19 (17–23)	23 (22–24)	4	64 (52–69)	34 (27–40)	4 (4–5)	23 (21–25)
H. turcomanica	Not described		23–25	—	35	—	—	—

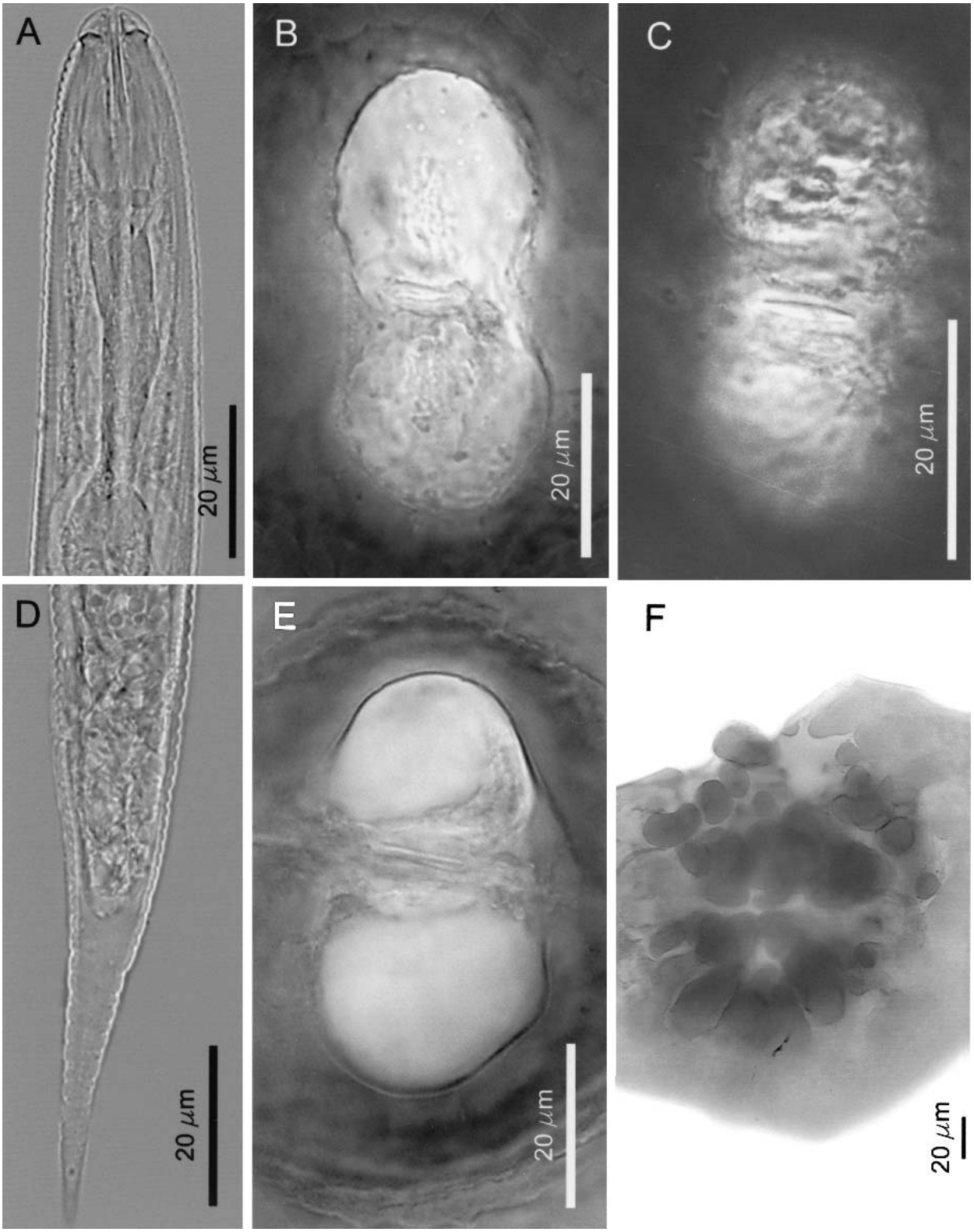

FIG. 1. Photomicrographs of *Heterodera avenae*. A,D) Head and tail of second-stage juveniles. B,C,E) Fenestra area of cysts showing vulva slit. F) Bullae.

H. filipjevi (Madzhidov, 1981) Stone, 1985
H. hordecalis Andersson, 1975
H. iri Mathews, 1971
H. latipons Franklin, 1969
H. mani Mathews, 1971
H. pratensis Gäbler, Sturhan, Subbotin and Rumpenhorst, 2000
H. spinicauda Wouts, Schoemaker, Sturhan and Burrows, 1995
H. turcomanica Kirjanova and Shagalina, 1965

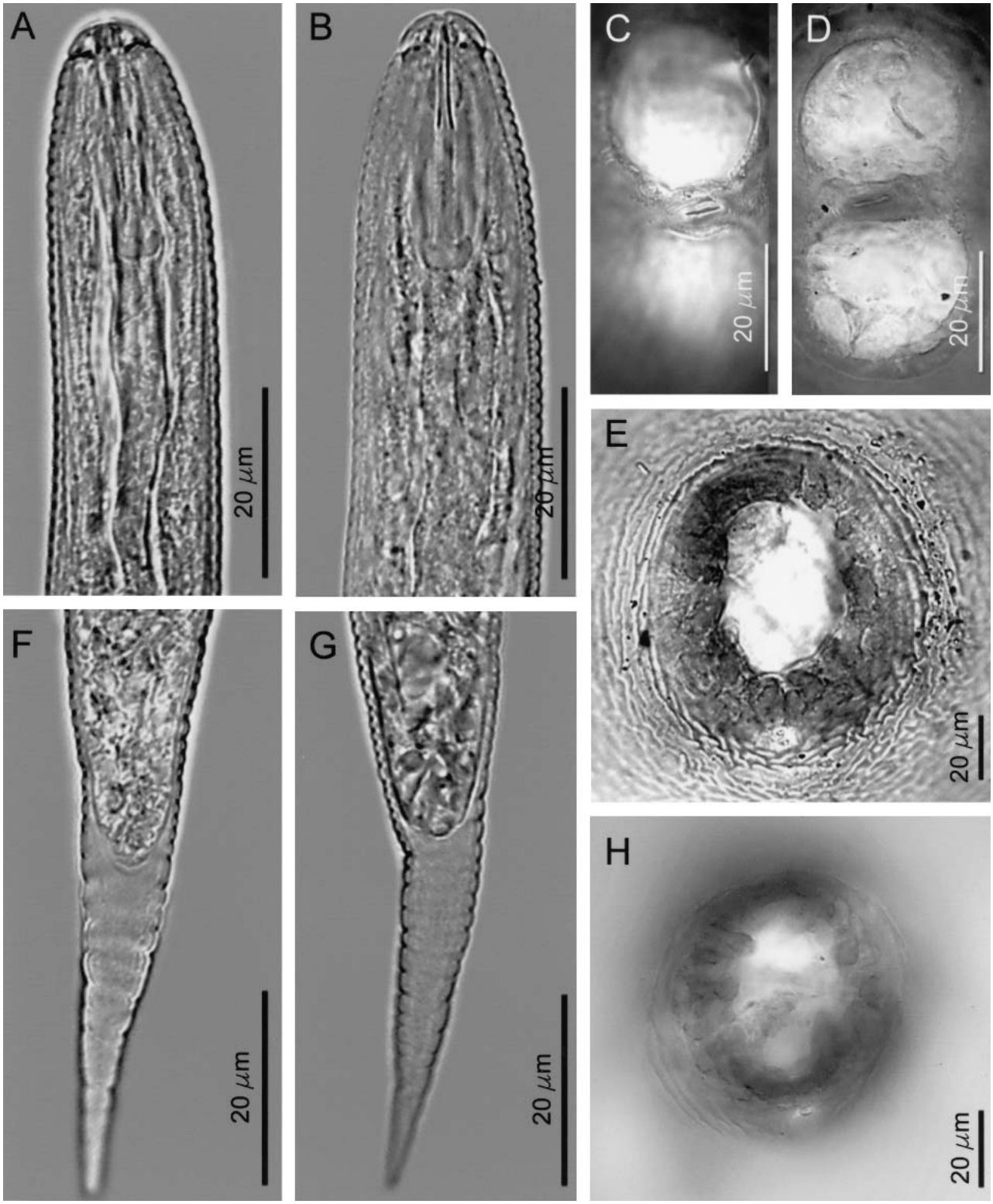

FIG. 2. Photomicrographs of *Heterodera mani*. A,B,F,G) Head and tail of second-stage juveniles. C,D) Fenestra area of cyst showing vulva slit. E,H) Bullae.

Key to the species of the *Heterodera avenae* group

1. Vulval slit long (17–24 μm) stylet knobs of second-stage juveniles deeply concave, often looking like hooks (Fig. 4A) -------- *H. hordecalis*

1a. Vulval slit short (4–16 μm); stylet knobs of second-stage juveniles not deeply concave (except *H. mani*) (Figs. 1A;5A,C) ---------- 2

2(1a). Cyst spherical, with very low vulval cone and distinct underbridge in the configuration of a ''bow tie'' (Fig. 3C,D,F); juvenile tail terminus sharply pointed (Fig. 3B) ---------- *H. spinicauda*

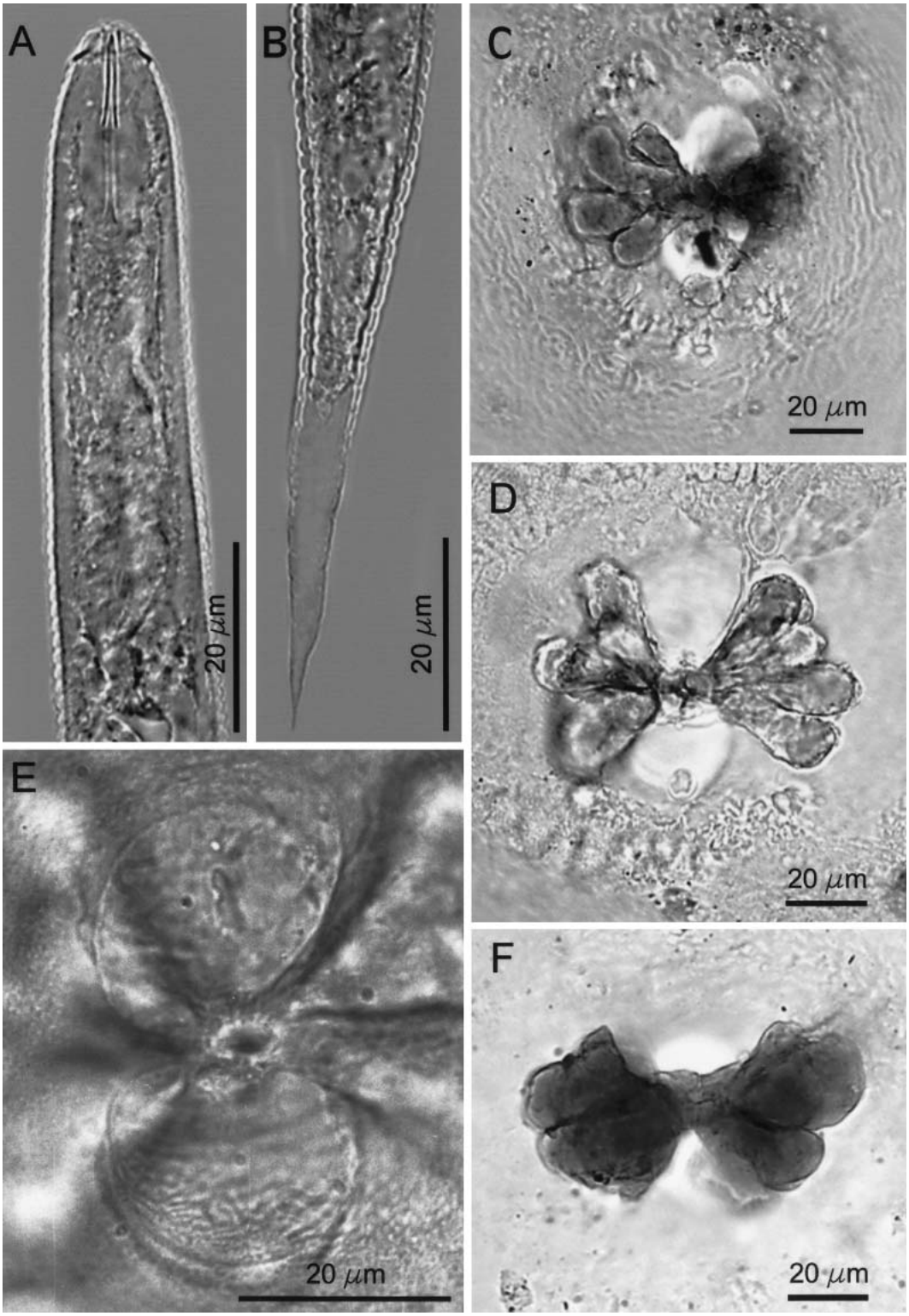

FIG. 3. Photomicrographs of *Heterodera spinicauda*. A,B) Head and tail of second-stage juveniles. C,D,F) Cyst vulval cone pattern with irregularly lobed ''bow-tie''-shaped underbridge. E) Cyst vulval cone area.

2a. Cyst lemon-shaped, with distinct vulval cone and no ''bow tie''-shaped underbridge; juvenile tail terminus not sharply pointed --------- 3

3(2a). Second-stage juveniles with 3 lines in the lateral field---------- 4

3a. Second-stage juveniles with 4 lines in the lateral field---------- 5

4(3). Cyst length shorter 431 μm (311–572); bullae and underbridge absent (Fig. 5E); vulval slit length 13 μm (10–16, Fig. 5E);

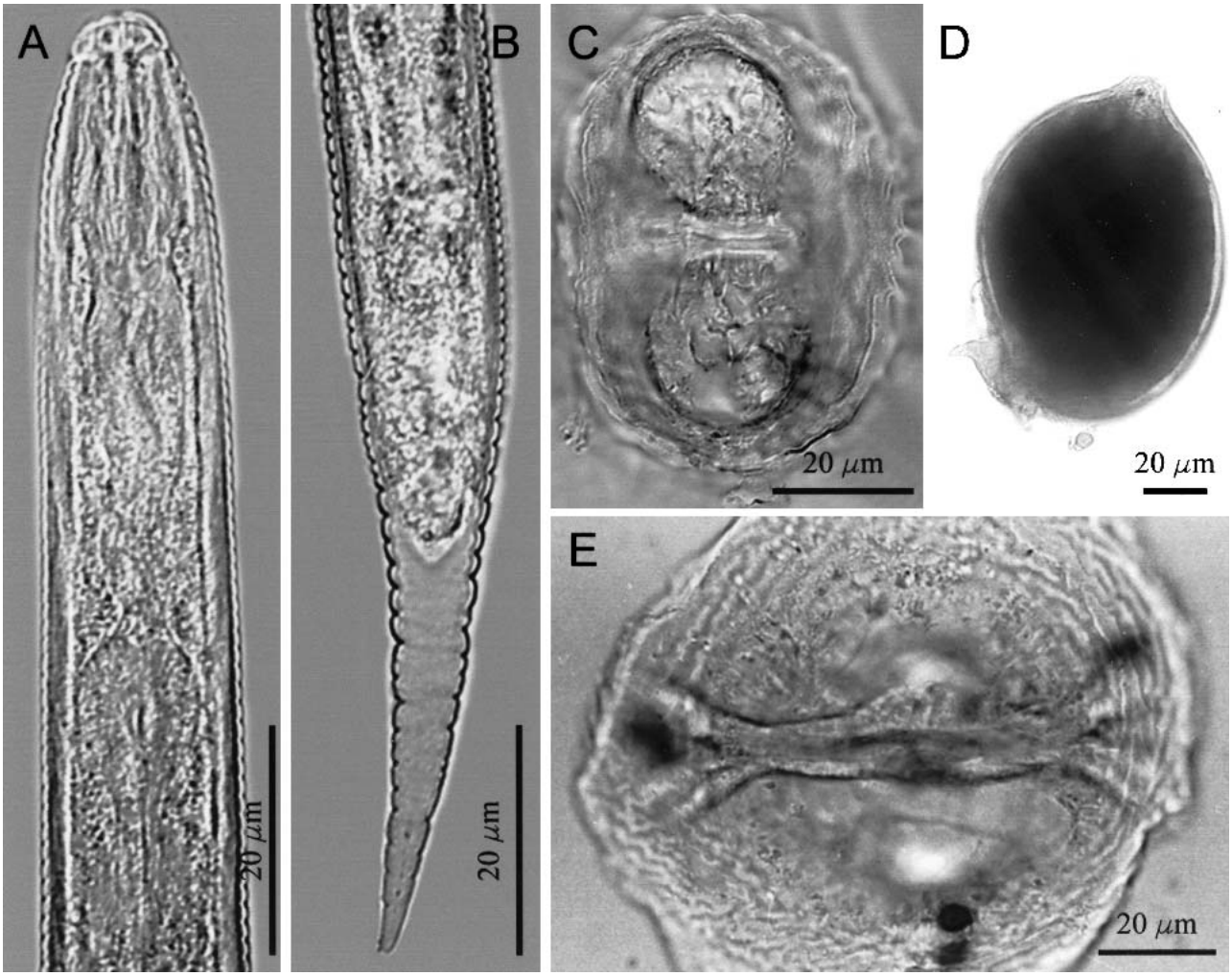

FIG. 4. Photomicrographs of *Heterodera hordecalis*. A,B) Head and tail of second-stage juveniles. C) Fenestra area showing vulval slit. D) Whole Cyst. E) Inside view of C showing underbridge and bullae.

second-stage juvenile stylet length 23 μm (22–25) with recessed posteriorly directed knobs; tail length 78 μm (71–87); hyaline tail terminus length 46 μm (39–52) ---------- *H. bifenestra*

4a. Cyst length elongate 690 μm (490–830); bullae and underbridge present; vulval slit length 7 μm (6–8); second-stage juvenile stylet length 27 μm (22–31) with slightly concave anteriorly directed knobs; tail length 57 μm (49–63); hyaline tail terminus length 35 μm (31–39) ---------- *H. filipjevi*

5(3a). Vulval cone top deeply indented, appearing saddle-shaped (Fig. 5F); tail of second-stage juvenile short, mean length 35 μm ---------- *H. turcomanica*

5a. Vulval cone top smooth or rounded; tail of second-stage juvenile 48 μm or longer ------ 6

6(5a). Bullae strongly developed, many; second-stage juvenile average length of hyaline tail terminus more than 30 μm ---------- 7

6a. Bullae usually absent, but a few sometimes present at the level of the underbridge (Fig. 6D); second-stage juvenile average length of hyaline tail terminus less than 30 μm (Fig. 6B) ---------- *H. latipons*

7(6). Cysts mostly creamy brown to yellow (except dark brown in *H. arenaria*); underbridge present (except *H. arenaria*); mean second-stage juvenile tail length more than 75 μm; mean hyaline tail terminus more than 46 μm ---------- 8

7a. Cysts pale to medium brown or dark brown to black; underbridge absent (rarely present); second-stage juvenile mean tail length 69 μm or less; hyaline tail terminus mean about 45 μm or less ---------- 9

8(7). Second-stage juvenile tail 94 μm (83–103); hyaline tail terminus 62 μm (51–75) (Fig. 7B) ---------- *H. iri*

8a. Second-stage juvenile mean tail length less than 80 μm; hyaline tail terminus mean less than 51 μm ---------- 10

9(7a). Cysts dark brown to black; second-stage ju-

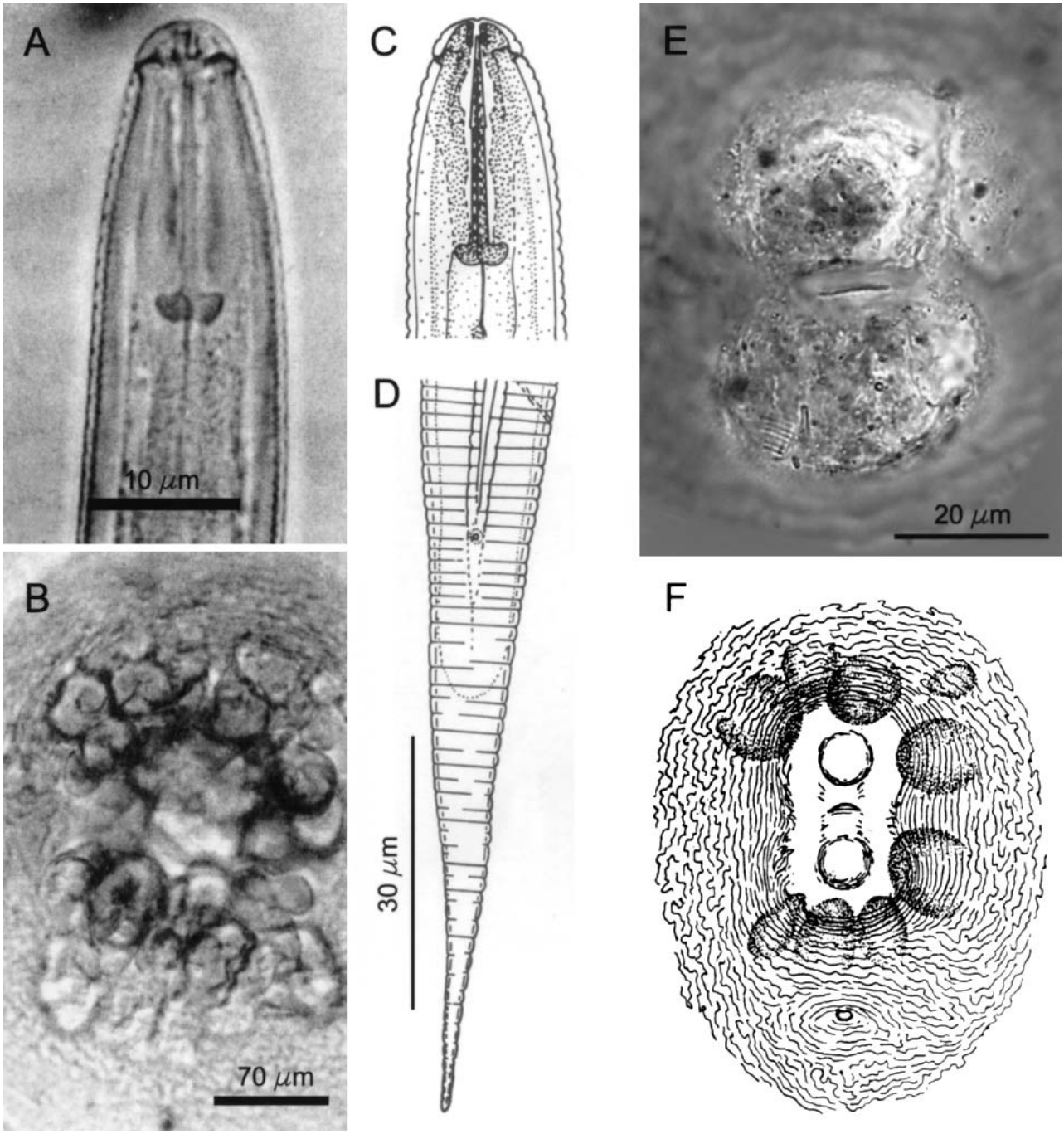

FIG. 5. A–D) Photomicrographs and drawings of *Heterodera aucklandica*. A,C,D) Head and tail of second-stage juveniles. B) Vulval cone of cyst showing bullae. (A–D after Wouts and Sturhan, 1995). E) Photomicrographs of fenestral region of *Heterodera bifenestra* cyst showing vulval slit. F) Drawing of *Heterodera turcomanica* anal-vulval plate of cyst. (After Kirjanova and Shangalina, 1965.)

venile stylet knobs shallowly concave anteriorly (Fig. 1A); vulval slit length long 9.6 µm (10–12, Fig. 1B,C,E); spicule short 33–38 µm with a bidentate terminus ---- *H. avenae*

9a. Cysts generally brown, spheroidal with small vulval cone; second-stage juvenile stylet knobs deeply concave, anteriorly anchor-shaped (Fig. 2A,B); vulval slit length short 6.5 µm (4–9, Fig. 2C,D); spicule long 35–43 µm with a bidentate terminus ---------- *H. mani*

9b. Cysts pale to medium brown or darker, lemon-shaped with low vulval cone, generally elongate but occasionally almost spherical (Fig. 8F); second-stage juvenile stylet knobs slightly concave or almost flat anteriorly, sloping slightly posteriorly (Fig. 8A); vulval slit length long 11 µm (8–13); spicule long 38–46 µm with tridentate terminus ---------- *H. pratensis*

10(8a). Body length of second-stage juveniles, fe-

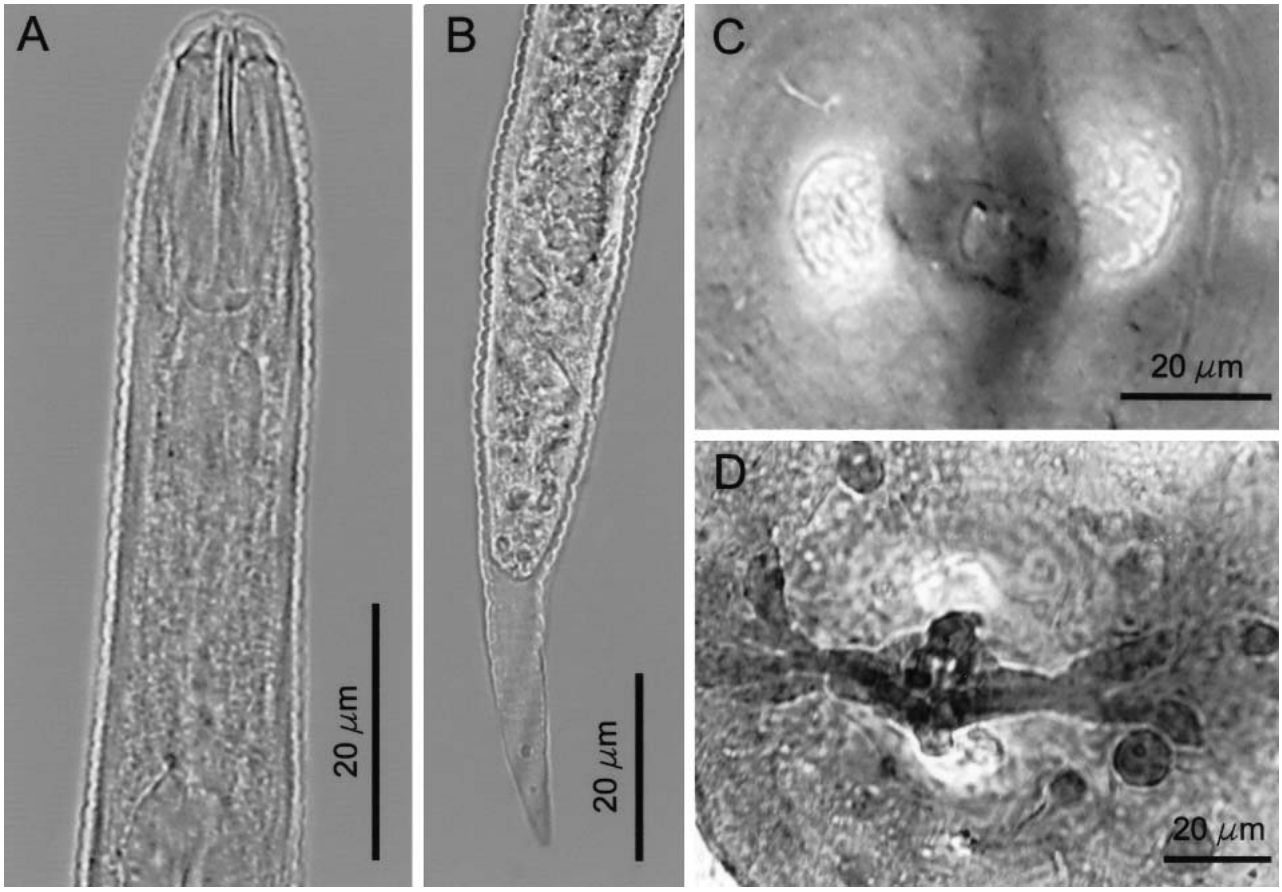

FIG. 6. Photomicrographs of *Heterodera latipons*. A,B) Head and tail of second-stage juveniles. C) Cyst fenestra area showing vulval slit. D) Inside view of C showing underbridge and occasionally scattered bullae.

males, and males longer (L = 639 μm (590–677) in juveniles, 748 μm (480–940) in females, and 1,604 μm (1,492–1,778) in males); stylet length of second-stage juveniles and males longer, measuring 29 μm (27–30, Fig. 9A, B) and 33 μm (32–34), respectively ---------- *H. arenaria*

10a. Body length of second-stage juveniles, females, and males shorter (L = 508 μm (440–580) in juveniles, 388 μm (360–415 in females, and 1,120 μm (800–1,500) in males); stylet length of second-stage juveniles and males shorter, measuring 25 μm (23–26, Fig. 5A, C) and 29 μm (26–31), respectively ---------- *H. aucklandica*

DISCUSSION

In the present paper, 12 species are included in the *Heterodera "avenae* group'' on the basis of commonly shared cyst terminal cone characters, particularly in having a short vulval slit and a bifenestration. Cyst terminal cone and second-stage juvenile morphology are also critical (Figs. 1–9).

The measurements of most of the examined specimens closely fit the original description and any subsequent redescriptions of species. Some of the variations noted in certain populations of species were incorporated into the morphometric compendium (Tables 1–4). This key is significant because it provides an all-inclusive guide to identifications and it works well with all described populations of the 12 valid *Heterodera* spp. in the *H. avenae* group, including the specimens of this group deposited in the USDA Nematode Collection (Handoo et al., 1998).

To take into account a wider perspective on the basic problems encountered in working with different populations within this *avenae* group, the author agrees with the usefulness of molecular data and suggests that, in cases of populations for which morphological data are equivocal, molecular data might prove useful.

LITERATURE CITED

Baldwin, J. G., and M. Mundo-Ocampo. 1991. Heteroderinae, cyst and non-cyst-forming nematodes. Pp. 275–362 *in* W. R. Nickle, ed. Manual of agricultural nematology. New York: Marcel Dekker.

Bekal, S. J., J. P. Gauthier, and R. Rivoal. 1997. Genetic diversity among a complex of cereal cyst nematodes inferred from RFLP analysis of the ribosomal internal transcribed spacer region. Genome 40: 479–486.

Ferris, V. R., J. Faghihi, A. Ireholm, and J. M. Ferris. 1989. Two-

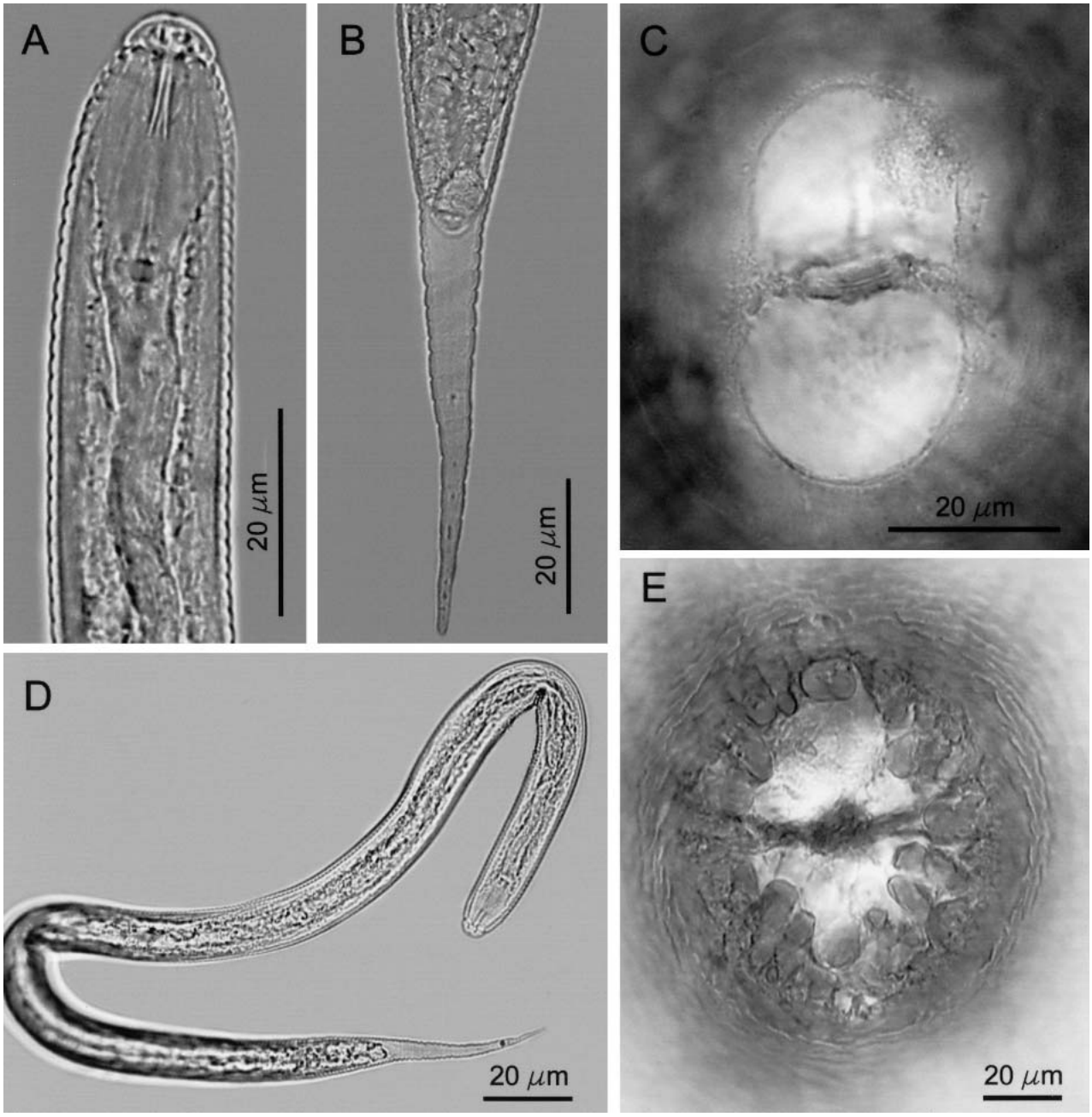

FIG. 7. Photomicrographs of *Heterodera iri*. A,B,D) Head, tail, and whole second-stage juveniles, respectively. C) Cyst fenestra area showing vulval slit. E) Inside view of C showing underbridge and bullae.

dimensional protein patterns of cereal cyst nematodes. Phytopathology 79:927–933.

Ferris, V. R., J. M. Ferris, J. Faghihi, and A. Ireholm. 1994. Comparisons of isolates of *Heterodera avenae* using 2-D PAGE protein patterns and ribosomal DNA. Journal of Nematology 26:144–151.

Gäbler, C., D. Sturhan, S. A. Subbotin, and H. J. Rumpenhorst. 2000. *Heterodera pratensis* sp. n., a new cyst nematode of the *H. avenae* complex (Nematoda: Heteroderidae). Russian Journal of Nematology 8:115–126.

Golden, A. M. 1986. Morphology and identification of cyst nematodes. Pp. 23–45 *in* F. Lamberti and C. E. Taylor, eds. Cyst nematodes. New York: Plenum Press.

Handoo, Z. A., A. M. Golden, and D. M. S. Ellington. 1998. Type specimens on deposit in the U.S. Department of Agriculture Nematode Collection, Beltsville, Maryland. Journal of Nematology 30:108–158.

Kirjanova, E. S., and L. M. Shagalina. 1965. Turkmenian cyst-forming nematode, *Heterodera turcomanica* Kirjanova et Schagalina sp.nov. (Nematoda: Heteroderidae). Izvestia of Academy of Science TurkmenianSSR, Seria Biologicheskih Nauk, 6:73–75.

Krall, E. 1977. Compendium of cyst nematodes in the USSR Nematologica 23:311–332.

Krall, E. L., and H. A. Krall, 1978. Systematic changes of phytonematodes of the family Heteroderidae based on tropic specialization of these parasites and their evolutionary connection with agricultural plants. In Fitogel'mintologicheskie issledovaniya, pp. 39–56. Moscow, USSR: Nauka. (In Russian.)

Luc, M., A. R. Maggenti, and R. Fortuner. 1988. A reappraisal of Tylenchina (Nemata). 9. The family Heteroderidae Filipjev & Schuurmans Stekhoven, 1941. Revue de Nématologie 11:159–176.

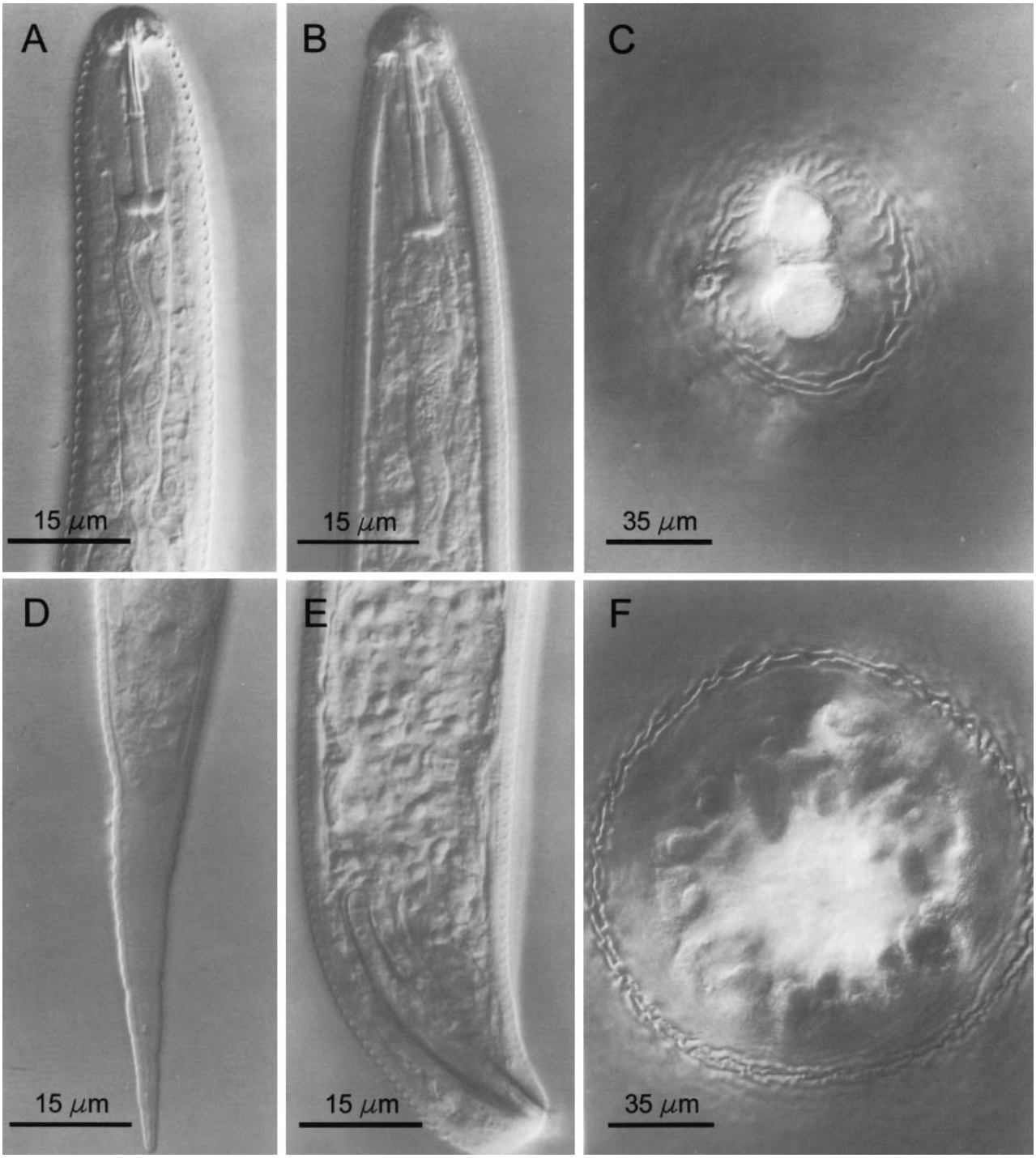

FIG. 8. Photomicrographs of *Heterodera pratensis*. A,D) Head and tail of second-stage juveniles. B,E) Male, anterior and posterior end. C,F) Cyst fenestra area and bullae in vulval cone. (After Gäbler et al., 2000, Courtesy Russian Journal of Nematology.)

Meagher, J. W. 1977. World dissemination of the cereal-cyst nematode (*Heterodera avenae*) and its potential as a pathogen of wheat. Journal of Nematology 9:9–15.

Mulvey, R. H. 1972. Identification of *Heterodera* cysts by terminal and cone top structures. Canadian Journal of Zoology 50:1277–1292.

Mulvey, R. H. 1973. Morphology of the terminal areas of white females and cysts of the genus *Heterodera* (s.g., *Globodera*). Journal of Nematology 5:303–311.

Mulvey, R. H., and A. M. Golden. 1983. An illustrated key to the cyst-forming genera and species of Heteroderidae in the western hemisphere with species morphometrics and distribution. Journal of Nematology 15:1–59.

Robinson, A. J., A. R. Stone, D. J. Hooper, and J. A. Row. 1996. A redescription of *Heterodera arenaria* Cooper, 1955, a cyst nematode from marram grass. Fundamental and Applied Nematology 19:109–117.

Rumpenhorst, H. J., D. Sturhan, and S. A. Subbotin. 1996. Studies on the *Heterodera avenae* complex. Russian Journal of Nematology 4:95–96.

Stone, A. R. 1986. Taxonomy and phylogeny of cyst nematodes. Pp. 119–131 *in* F. Lamberti and C. E. Taylor, eds. Cyst nematodes. New York: Plenum Press.

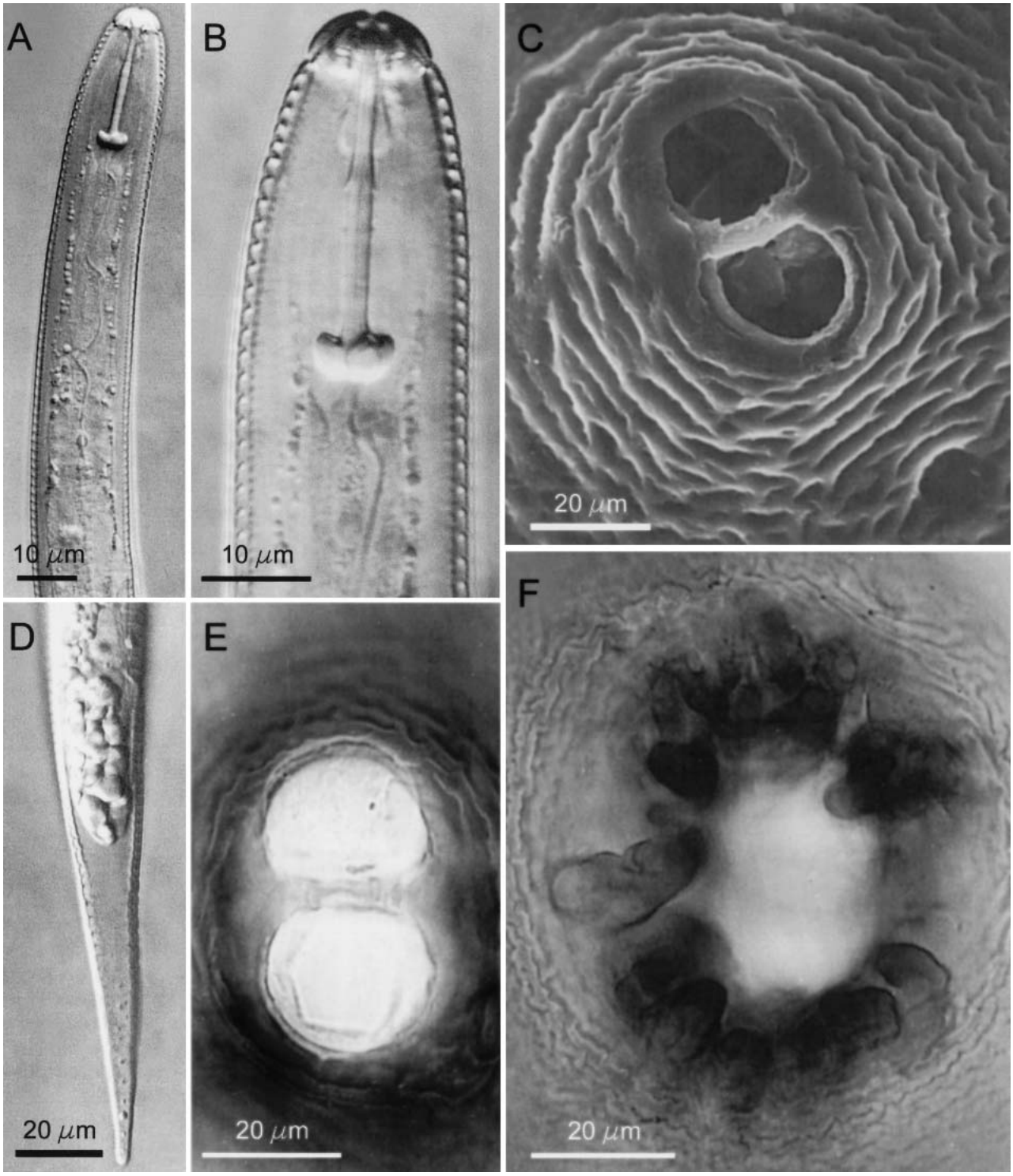

FIG. 9. Photomicrographs of *Heterodera arenaria*. A,B,D) Esophageal region, head and tail of second-stage juvenile, respectively. C,E) Fenestration pattern of mature cyst. F) Bullae in cyst cone. (After Robinson et al., 1996, Courtesy Fundamental and Applied Nematology.)

Stone, A. R., and A. J. Hill. 1982. Some problems posed by the *Heterodera avenae* complex. Bulletin OEPP 12:317–320.

Subbotin, S. A., H. J. Rumpenhorsst, and D. Sturhan. 1996. Morphological and electrophoretic studies on populations of the *Heterodera avenae* complex from the former USSR. Russian Journal of Nematology 4:29–38.

Subbotin, S. A., I. A. Waeyenberge, I. A. Molokanova, and M. Moens. 1998. rDNA-RFLP of species from the *Heterodera avenae* group. Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen Universiteit Gent: 1485–1489.

Subbotin, S. A., L. Waeyenberge, I. A. Molokanova, and M. Moens. 1999. Identification of *Heterodera avenae* group species by morphometric and rDNA-RFLPs. Nematology 1:195–207.

Swarup, G., S. K. Prasad, and D. J. Raski. 1964. Some *Heterodera* species from India. Plant Disease Reporter 48:235.

Vovlas, N. 1985. Morphology and histopathology of the cereal cyst

nematode (*Heterodera avenae* Woll.) attacking wheat, oats, and barley in Italy. Nematologica Mediterranea 13:87–96.

Williams, T. D., and M. R. Siddiqi. 1972. *Heterodera avenae,* C. I. H. descriptions of plant-parasitic nematodes, Set 1, No. 2, St. Albans. Herts, England.

Wouts, W. M. 1985. Phylogenetic classification of the family Heteroderidae (Nematoda: Tylenchida). Systematic Parasitology 7:295–328.

Wouts, W. M., A. Schoemaker, D. Sturhan, and P. R. Burrows. 1995. *Heterodera spinicauda* sp. n. (Nematoda: Heteroderidae) from mud flats in The Netherlands, with a key to the species of the *H. avenae* group. Nematologica 41:575–583.

Wouts, W. M., and D. Sturhan. 1995. *Heterodera aucklandica* sp. n. (Nematoda: Heteroderidae) from a New Zealand native grass, with notes on the species of the *H. avenae* group. New Zealand Journal of Zoology 22:199–207.