Heterodera filipjevi

Scientific Name
Heterodera filipjevi (Madzhidov) Stelter, 1984

Synonyms:
Bidera filipjevi

Common Name
Cereal cyst nematode, Filipjev's cereal cyst nematode, rye cyst nematode, Gotland strain of *H. avenae*, pathotype 3 of *H. avenae*, race 3 of *H. avenae*.

Type of Pest
Nematode

Taxonomic Position (Siddiqi, 2000)
Class: Secernentea, **Order:** Tylenchida, **Family:** Heteroderidae

Reason for Inclusion in Manual
Requested by the CAPS community; found in Oregon in March 2008 – National cyst nematode survey and small-grain commodity survey.

Pest Description
The cereal cyst nematodes consist of a complex group of closely related *Heterodera* species (*H. avenae*, *H. filipjevi, H. latipons*, and others), collectively known as the "*Heterodera avenae* group". There has been considerable disagreement with respect to the taxonomic classification of species in the *H. avenae* group. *Heterodera* species in the *H. avenae* group are distinguished from each other by small differences in morphology. Cereal roots infected by *H. filipjevi* show the same symptoms and lemon-shaped cysts as those infected by *H. avenae* (Fig. 1). Nematode taxonomists distinguish between these species using a combination of morphological and molecular analysis.

Figure 1. *Heterodera avenae* cysts attached to oat roots. Photo courtesy of R. Cook.

Heterodera avenae, together with other bifenestrate cyst nematodes having a short vulval slit, were placed in the genus *Bidera*, but Mulvey and Golden (1983) synomized *Bidera* with *Heterodera*. At first, this synonomy was not universally accepted (Baldwin and Mundo-Ocampo, 1991), but it was confirmed by recent molecular analyses (Subbotin et al., 2010).

Heterodera filipjevi is diagnosed by the following morphological measurements (Handoo, 2002): 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).

The second stage juveniles (Fig. 2) found in Oregon in 2008 (see Potential Distribution section) ranged from 530-570 µm in length, had a stylet (22.5-24.5 µm) with anchor-shaped basal knobs, and a tail (52.5-62.5 µm) with a hyaline tail terminal (30-38 µm) (Smiley et al., 2008). The lateral field had four lines of which the inner two were distinct.

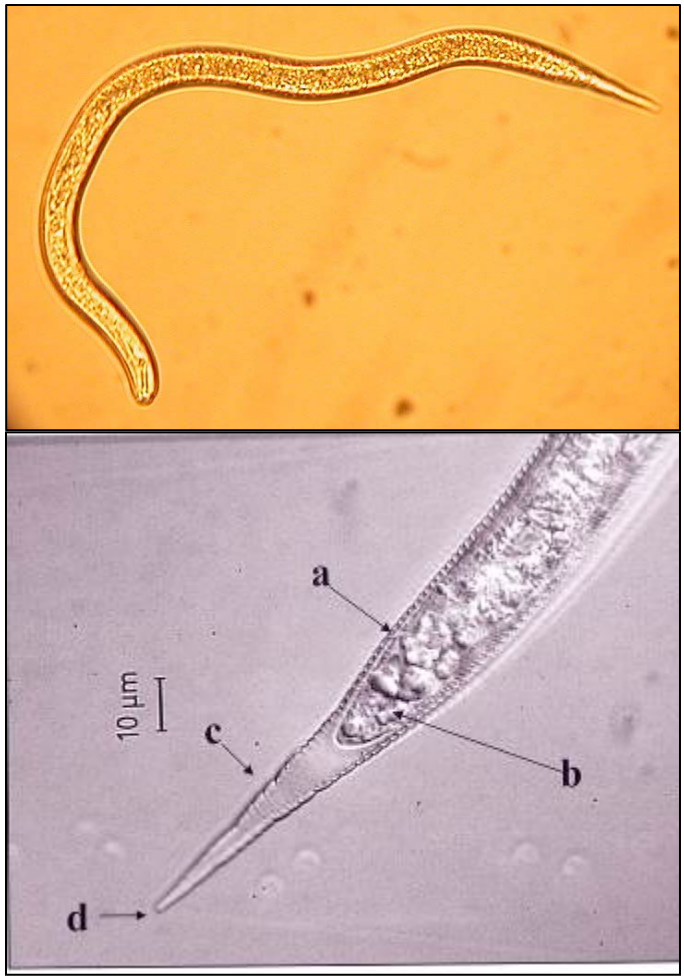

Figure 2. Top: *H. filipjevi* J2. Bottom: Tail of *H. filipjevi* second stage juvenile with anus (a), true tail (b), hyaline tail (c), and the rounded tail tip (d). Photos courtesy of R. Smiley, Oregon State University and R. Holgado, Norwegian Institute for Agricultural & Environmental Research, Norway, respectively.

The cysts were lemon-shaped, light brown in color, had a zigzag pattern on the cyst wall, and had a bifenestrate vulval cone with horseshoe-shaped semifenestra. The cysts were characterized by body length including neck 718-940 µm, body width 395-619 µm, l/w ratio of 1.1-2.2, neck length 75-140 µm and width 50-95 µm, fenestra length 50-65 µm and width 27-40 µm, heavy underbridge 60-80 µm, vulval slit 7.5-8.5 µm, and many bullae (Smiley et al., 2008).

Detailed descriptions for each life stage of *H. filipjevi* from Norway were provided by Holdago et al. (2004a, b). Additional morphological and molecular characteristics of this species were published by Subbotin et al. (2010).

Eggs: Cylindrical with rounded edges (Fig. 6) (Holdago et al., 2004b).

Second-stage juveniles (J2s): The second stage juvenile (Fig. 2) body length ranges from 455-557 µm, and the tail is tapering to a rounded tip. The length of the tail is 52-67 µm and its hyaline part measures 30-41 µm, corresponding to more than 50% of the total tail length. The head is offset and usually with three annules, and the distance from the head to the valves of the median bulb is 59-79 µm. The lateral fields have four lines, of which the inner two are more distinct, and the outer bands are heavily areolated (Fig 3). The stylet is robust with anchor-shaped basal knobs, and measures 22-25 µm in length (Fig. 3). The ratio of hyaline tail to the true tail is 1.2-1.7 (Holgado et al., 2004b).

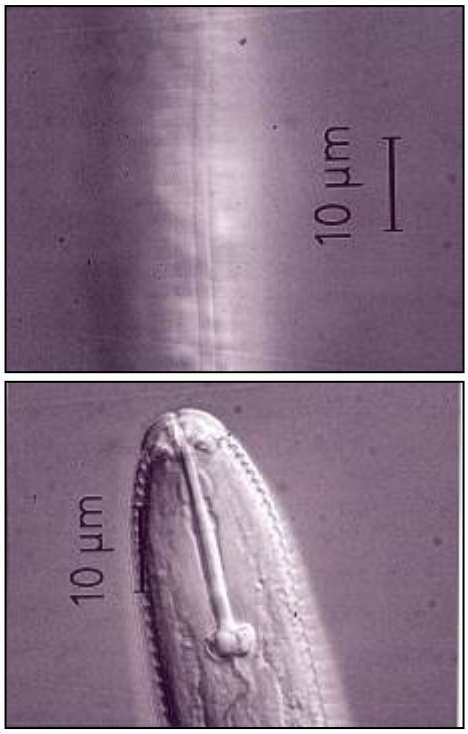

Figure 3. Top: The lateral field in the mid body region of *H. filipjevi* J2 has four lines with a heavy areolation on the outer bands. Note the two distinct inner lines. Bottom: The stylet of *H. filipjevi* J2 is robust, with anteriorly concave knobs. Photo courtesy of R. Holgado, Norwegian Institute for Agricultural & Environmental Research, Norway.

Cysts: Newly formed cysts are lemon-shaped, similar to *H. avenae*, *H. latipons*, and *H. hordecalis* (Fig. 4, 5) and partially covered with a white sub-crystalline layer. The cyst wall has ridges running in zigzag patterns, and irregularly arranged punctations and pores. The cyst is golden to light brown and is almost transparent, with the outline of individual eggs clearly visible (Fig. 6). The cyst is 455-874 µm in length and 253-747 µm in width. The vulval cone is bifenestrate with horseshoe-shaped semifenestra and has an underbridge. The vulval slit varies between 6.0 and 10.8 µm, and the width of the vulval bridge is 7.2-13.1 µm. The fenestral length ranges from 38.4 to 58.4 µm, and the length of the semifenestrae are 19.3-32.0 µm. The ratio between fenestral length and width was in the range of 1.7-2.8. The dimensions of the underbridge were 53-110 µm in length and 4.0-11.3 µm in width. The bullae are weak to medium, distinct, and mostly globular in shape with a pale to medium brown color. Their position and arrangement vary between focal planes (Holgado et al., 2004b).

Females: Gravid females are pearly-white and lemon-shaped, with protruding neck and vulva cone. The cuticle bears a zigzag pattern that runs concentrically around the neck and vulval regions. The head is offset, with a squarish and prominent labial disc. The female stylet has sloping knobs. Ovaries are paired and convoluted. The vulva is slit-like, protruding posteriorly. The anus is distinct (Holgado et al., 2004b).

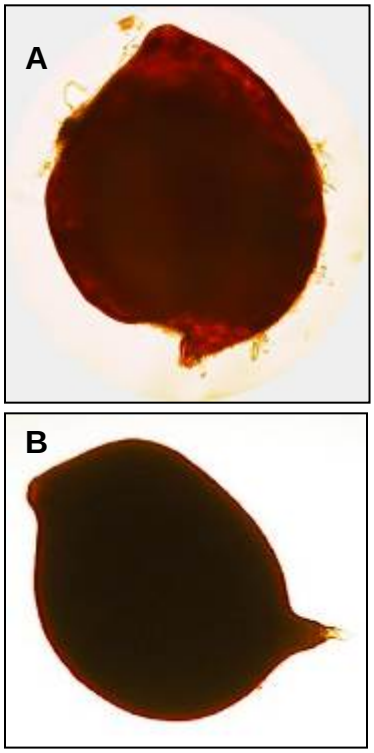

Figure 4. Cysts of A) *H. filipjevi B) H. avenae*. Photos courtesy of R. Smiley, Oregon State University.

Biology and Ecology

Like other cyst forming nematodes, *Heterodera filipjevi* has a sedentary endoparasitic habit. It has one generation per growing season and completes its life cycle in five to seven months (Hajihasani et al., 2010a; Seifi et al., 2013).

The life cycle of *H. filipjevi* is essentially the same as that for other species of *Heterodera*. Second-stage juveniles (J2s) emerge from the cyst (Fig. 7), are motile in soil, and penetrate host roots behind the root tip. They molt to become differentiated as male or female. Females establish a specialized feeding site (a syncytium) in the stele. Males exit the root, move through soil, and inseminate the immobile females. Adult females retain the eggs and, as egg masses develop, the females rupture the root cortex and protrude from the root surface, leaving the head and neck embedded. When the female dies at the time of root senescence, the cuticle turns brown and the body becomes a dry, leathery cyst filled with embryonated eggs. The cysts break off from the roots and become free in the soil, where they persist for many years and serve as the survival stage of the nematode. When conditions become favorable for hatching, which often coincides with the typical planting time for host cereals in a specific region, the eggs hatch inside the cyst to develop into the second juvenile (J2) stage. The J2s leave the intact cyst and become available in soil for invading roots of crops.

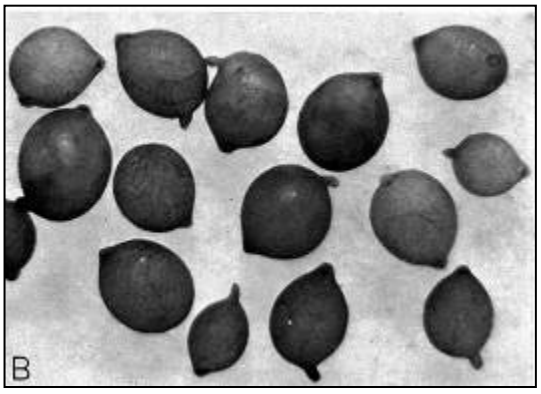

Figure 5. Lemon-shaped cysts of *H. hordecalis*. Photo courtesy of S. Andersson.

Information is not currently available on the persistence of cysts in the absence of host material. Information for *H. avenae* simply states that the eggs within the cysts remain viable in the soil for several years (Kort, 1972), and *H. filipjevi* will most likely be similar.

The greatest risk to cereal crops occurs when the presence of seedling plants coincides with the presence of high populations of infective juveniles in the soil. This occurs shortly after eggs hatch and motile J2s move out of the cyst though the vulval slit. The juveniles move into the soil where they may invade near the tips of young root segments. *H. avenae* eggs hatch in early spring in Oregon (Smiley et al., 2005). Populations of *H. avenae* juveniles in the soil increase rapidly 2 weeks after mean weekly air temperature stabilized between 2-4°C (36 and 40°F). Peak populations of juveniles occur following a spike in weekly mean air temperature to 16°C (60°F) in mid-April.

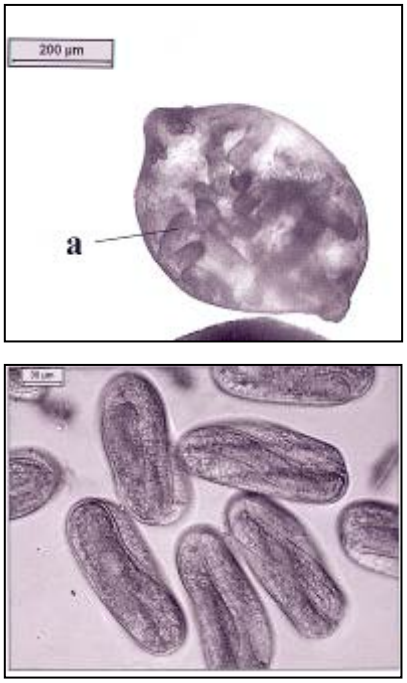

Figure 6. Top: The cyst wall of *H. filipjevi* is often transparent with the outline of eggs (a) clearly visible. Bottom: *H. filipjevi* eggs. Photos courtesy of R. Holgado, Norwegian Institute for Agricultural & Environmental Research, Norway.

According to Sahin et al. (2010), under controlled conditions optimum hatching for *H. filipjevi* occurred at 10°C (50°F, 40.5%) and 18°C (64°F, 42.8%) after 15 days. Hatching occurred but was significantly lower at 7°C (45°F, 15.2%) and no hatch occurred at 0°C. Under field conditions, maximum hatch (~11%) occurred at soil temperatures of 4 and 9°C (40 and 48°F). Results in the field and laboratory did not correlate well, suggesting that factors other than temperature may be involved in the hatching of this species (*e.g.,* host root exudates). Using microplots incubated outdoors, Hajihasani et al. (2010a) found that winter wheat roots became invaded by *H. filipjevi* as early as late November when the soil temperature was about 10°C (50°F). Peak densities of the J2 stage in soil occurred during winter when the daily mean soil temperatures as low as 0 and 5°C (32 and 40°F).

Because of this ability to hatch rapidly at cool temperatures, field population densities of *Heterodera filipjevi* could easily be underestimated if based only on cyst extractions during the spring. Accurate assessments of pre-plant densities of *H. filipjevi* from late fall through summer also requires the quantification of infective juveniles in the soil (Holgado et al., 2005). Extraction of juveniles requires a different extraction method than is required to extract cysts.

Specialized virulence groups called pathotypes occur within species in the *H. avenae* complex and are roughly equivalent to the "race" concept used to define virulence groups for the pathogens that cause rust diseases. At least 12 pathotypes have been described for *H. avenae*. However, the Gotland strain (Ireholm, 1994), race 3, and pathotypes Ha23 and Ha33 of *H. avenae* (Andersen and Andersen, 1982) are now considered to have synonymy with *H. filipjevi* (see Smiley et al., 2011). Each pathotype is virulent to cereals unless a specific host resistance gene is present to nullify its virulence to that pathotype. A clear understanding of the pathotype identity is required before one or more genes for resistance can be selected and used to improve the performance of wheat, barley, and oats planted on infested land (Smiley and Nicol, 2009; Smiley et al., 2011). The pathotype of *H. filipjevi* in Oregon has not been determined.

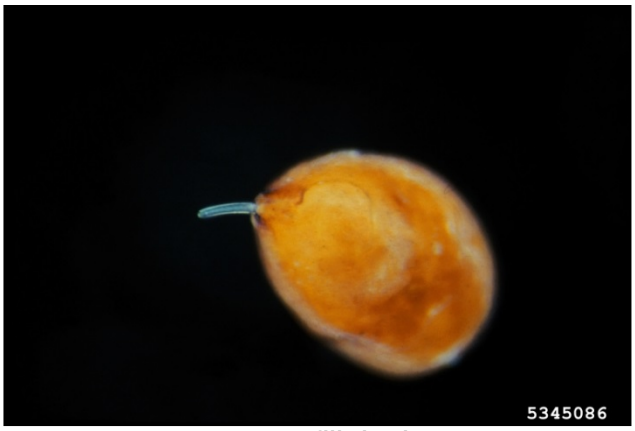

Figure 7. Juvenile *H. filipjevi* hatching from cyst. Photo courtesy of Bonsak Hammeraas, Bioforsk - Norwegian Institute for Agricultural and Environmental Research, Norway. www.bugwood.org

Symptoms/Signs

Symptoms are often due to mixed populations of cereal cyst nematodes or other soilborne pathogens and can mimic other problems such as nutrient deficiencies or drought stress.

In general, wheat plants become chlorotic and stunted due to the presence of cereal cyst nematodes. Growth may be patchy (Fig. 8). Barley roots exhibit no readily discernable symptoms. Leaf tips of plants affected by *H. avenae* often become discolored: reddish yellow on wheat, red on oats, and yellow on barley (Smiley and Nicol, 2009).

Roots show abnormal branching or become

Figure 8. *H. filipjevi* damage on rye. Photo courtesy of Bonsak Hammeraas, Bioforsk- Norwegian Institute for Agricultural and Environmental Research, Norway. www.bugwood.org

bushy. In Oregon, patches of stunted seedlings (3-5 leaf stage) appeared in March. The stunted seedlings exhibited chlorotic or necrotic lower leaves, healthy younger leaves, few or no tillers, rotting of lower culms and crown, and light brown roots with little or no branching (Smiley et al., 2008). In Oregon, *H. filipjevi* was found co-occurring with the fungal pathogens *Pythium* spp. (Pythium root rot), *Gaeumannomyces graminis* var. *tritici* (take all of wheat), *Rhizoctonia solani* AG-8 (root rot, bare patch), and *Typhula incarnata* (snow mold) and the nematode species *Pratylenchus neglectus* (lesion nematode), and *Tylenchorhynchus* spp. (stunt nematodes). It is, therefore, difficult to determine which symptoms were caused by which pathogen.

Pest Importance

Recent studies have shown that *Heterodera filipjevi* infestation can be highly destructive to *Triticum* spp. (wheat) host crops. Preliminary yield loss studies by Nicol et al. (2006) indicate that *H. filipjevi* can cause yield reduction of up to 50% in *Triticum aestivum* in Turkey. Hajihasani et al. (2010b) studied effects of *H. filipjevi* infestation on the yield and growth parameters of winter wheat cv. Sardari in Iran. They concluded that an *H. filipjevi* population density of 20 eggs/J2s per gram of soil reduced grain yield by up to 48%.

H. filipjevi is recognized as a constraint to cereal production, particularly in temperate and semi-arid regions of the world where most cereal crops are produced (Nicol et al., 2004). In Norway, the occurrence of *H. filipjevi* caused damage to *Secale cereale* (winter rye) (Holgado et al., 2005), and this nematode is an important pest of cereals in both Sweden and Norway (Ireholm, 1994; Holgado et al., 2004ab, 2005).

The main hosts of *H. filipjevi* (wheat, rye, oat, and barley) are widely grown commodities in the United States. Planted acreage of these commodities in 2013 totaled over 63 million (USDA-ERS, 2013). Wheat was by far the most widely cultivated, encompassing 56 million of those acres. The total 2013 U.S. wheat harvest consisted of 2.13 billion bushels and had an estimated value of $14.9 billion (USDA-ERS, 2013). Approximately 51% of the wheat produced in the United States in 2013 was destined for export, comprising a total of 19.5% of the global export market for this commodity (USDA-ERS, 2013).

At the genus level, *Heterodera* is listed as a harmful organism in the following countries: Australia, Chile, Madagascar, Namibia, Nauru, South Africa, and Syria (USDA-PCIT, 2013). There may be trade implications with these countries if *H. filipjevi* is detected further or found to be established in the United States.

Known Hosts

Major hosts

Avena spp. (oat), *Elytrigia repens* (false wheat), *Hordeum* spp. (barley), *Secale* spp. (rye), *Triticum* spp. (wheat) (Damadzadeh and Ansaripour, 2001; NPAG, 2008; CABI, 2012).

Other Hosts
Elymus repens (quack grass) (CABI, 2012)

Experimental Hosts
Triticum discocoides (a tetraploid wheat), *T. durum* (a tetraploid wheat), *T. tauchi* (a diploid wheat), *T. monococcum* (a diploid wheat), *T. ovatum* (a tetraploid wheat), *T. tauchii* (a diploid wheat), *T. turgidum* (a tetraploid wheat), *T. umbellatum* (a diploid wheat), and *T. ventricosum* (a tetraploid wheat) were identified as hosts under laboratory conditions (Bekal et al., 1998).

Zea mays (corn) is considered resistant to *H. filipjevi*. The nematode is able to penetrate corn roots, but females fail to reproduce (Seifi et al., 2013). Corn has been used as a trap crop in India (Bajaj and Kanwar, 2005).

Known Vectors (or associated organisms)
Heterodera filipjevi is not known to be a vector and does not have any associated organisms. However, root damage by cereal cyst nematodes often favors greater colonization of roots by root-rotting fungal pathogens and by saprophytic bacteria, fungi, and non-plant-parasitic nematodes. These secondary organisms cause more intense rotting and discoloration than that caused by the plant-parasitic nematode itself.

Known Distribution
At present, the known distribution of *H. filipjevi* is as follows: **Asia:** China, India, Iran, Syria, and Turkey. **Europe:** Estonia, Germany, Norway, Russia, Serbia, Sweden, Tajikistan, Ukraine (Holgado et al., 2004a; Nicol et al., 2004; Tanha-Maafi et al., 2007; NPAG, 2008; CABI, 2012; Oro et al., 2012; Seifi et al., 2013).

H. filipjevi was first detected in the United States (Oregon) in March 2008 (Smiley et al., 2008). In 2014, *H. filipjevi* was discovered in a wheat field in Washington state (Smiley and Yan, 2015). It is currently unknown how this nematode arrived, where it came from, whether the infestation is established, or whether this species is more widely distributed in Oregon, Washington, or other states.

Pathway
There are currently no restrictions on the import of *Avena sativa*, *Hordeum vulgare*, *or Secale cereale* seed material other than their required sampling as an FSA-A seed (USDA, 2013). Cyst nematodes can be transported on infested soil adhering to seed material (Greco et al., 1992, Riley et al., 2009). Since 2003, there have been shipments of *Avena* spp. (7), *Hordeum* spp. (31), and *Secale* spp. (1) from known host countries. There were also interceptions of *Avena* spp. (54) and *Hordeum* spp. (41) from known host countries (AQAS, 2013).

There are currently no restrictions on the import of *Triticum* spp. seed propagules from the following *H. filipjevi* host countries: Germany, Norway, Serbia, Sweden, Syria, and Ukraine (USDA, 2013). However, there have been no recorded shipments of *Triticum* spp. propagative material from those countries since 2003 (AQAS, 2013). There were 426 interceptions of *Triticum* spp. from known host countries, with the majority of those coming from China and India (AQAS, 2013).

In addition to transport on host material, *H. filipjevi* can be transferred to new areas via contaminated soil debris or plant material, primarily root tissue. Greco et al. (1992) suggest that increased traffic of machinery and personnel between the United States and the Middle East could increase the likelihood of accidental introduction of cyst nematodes which are present in this region. This suggestion was put forward referring to the 1991 Persian Gulf conflict, but it is just as relevant now in light of the United States presence in the Middle East.

Potential Distribution within the United States

On March 3, 2008, a nematode sample collected in northeastern Oregon from wheat was confirmed by the USDA-ARS Nematology Laboratory in Beltsville, MD as *Heterodera filipjevi* (Smiley et al., 2008). This was the first report of the *H. filipjevi* in the United States (NPAG, 2008). In 2014, *H. filipjevi* was discovered in a wheat field in Washington State (Smiley and Yan, 2015).

Biological information for this pest is not currently available to determine the potential distribution of this nematode within the United States. However, once a cyst nematode is introduced into a country, it is very difficult to minimize spread without extensive quarantine measures and expensive eradication strategies. Cyst nematodes are efficiently disseminated by all means of soil movement, including minute amounts of soil that contaminate equipment, by animals and plant products, and in soil that is moved by water and wind (NPAG, 2008). *Heterodera avenae*, for example, was first detected in the United States on oat in 1974 in Oregon. This species is now reported as being present in seven states in the West: California, Colorado, Idaho, Montana, Oregon, Utah, and Washington (Smiley, 2009). Since *H. filipjevi* can hatch at temperatures at or below those of *H. avenae,* areas of the United States that currently have *H. avenae* and grow barley, wheat, rye, or oats are at risk.

Survey

CAPS-Approved Method*:

Use soil sampling, collection of host roots, or of a combination of both methods.

Soil sample: Send sample to a nematode diagnostic lab where nematodes will be extracted from the soil and identified to the species level (preferred method). Laboratory methods that are acceptable for cyst extraction include sugar centrifugation, USDA cyst extractor, Fenwick can sieving, wet sieving, and elutriation. Cobb's sieving technique has been used regularly to extract second stage juveniles from the soil.

Collect host roots: Send sample to nematode diagnostic lab where nematodes will be extracted and identified.

*For the most up-to-date methods for survey and identification, see Approved Methods on the CAPS Resource and Collaboration Site, at http://caps.ceris.purdue.edu/.

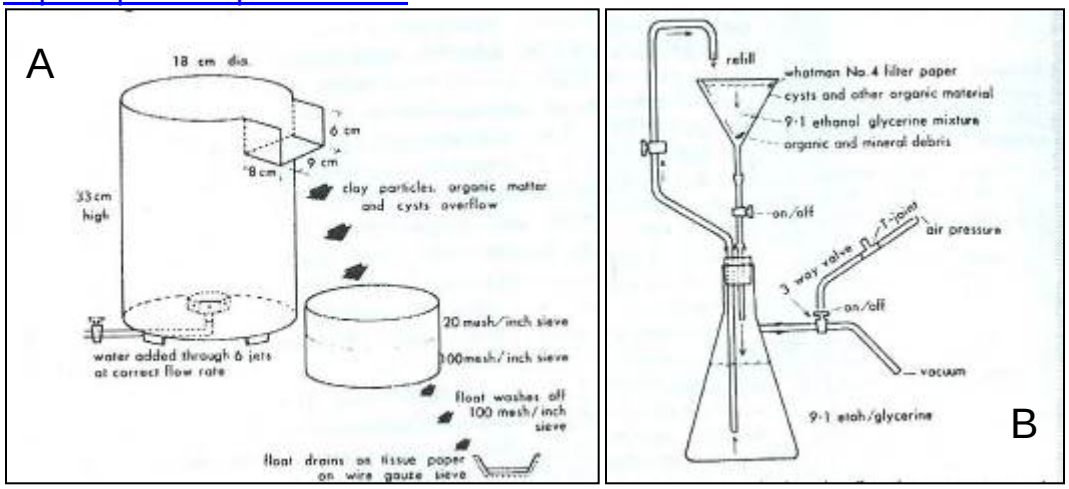

Figure 10 A) Modified Fenwick can used to separate nematode cysts and organic debris from soil sample B) Ethanol-glycerine flotation apparatus for separation of nematode cysts from sample organic matter. Reproduced from Caswell et al., 1985.

Literature-Based Methods:

Soil Sampling: Cereal cyst nematodes are extracted from soil, identified, and counted. A composite soil sample is collected from a sampling unit such as an entire field, a specific area of a field, or an experimental plot. Multiple (15 to 20) cores of soil are collected from the upper 8 to 12 inches of soil and combined for each composite sample. A subsample is removed from the larger sample and air-dried.

Cysts can be extracted from the subsample using a Fenwick can method (20 mesh screen over a 60 mesh screen) (Damadzadeh and Ansaripour, 2001), a modified Baermann funnel technique (Rumpenhorst et al., 2006), or a modified Fenwick can elutriation method (Fig. 10a), with further separation of cysts from the plant debris by flotation in an ethanol and glycerin solution (Fig. 10b) (Caswell et al., 1985; Ingham,1994). Cysts are then picked from the remaining debris and identified. Cysts can be crushed to determine the number of eggs plus juveniles, which can then be adjusted to reflect the nematode density per pound of oven-dry soil.

Survey for *Heterodera filipjevi* should crossover easily and inexpensively if a state already has equipment to survey for potato cyst nematodes, because the Fenwick can method used to survey for *Globodera pallida and G. rostochiensis* should also work for the extraction of *H. filipjevi* cysts.

There are a variety of additional methods available for cyst extraction from soil. Soil can also be processed using Cobb's decanting and sieving technique (10 mesh- 2mm, 50 mesh-300 µm, 150 mesh-106 µm, 400 mesh-38 µm, and 500 mesh-25 µm screens used by Kanwar et al., 2004) and a 60 mesh sieve placed over a 300 mesh sieve used by Bajaj and Kanwar (2005) to determine the presence of males, white females, and cysts. Subbotin et al. (2003) used sieving-decanting and centrifugation-flotation methods to isolate cysts from soil. Holgado et al. (2004b) air dried soil samples, passed the samples through a 5 mm sieve, and extracted cysts using a fluidizing column. Smiley (2012) also used a fluidizing column to extract cysts. Abidou et al. (2005) processed soil samples through a Kort elutriator.

Motile nematodes (*e.g.* juveniles) can be extracted using the Whitehead tray method (Smiley et al., 2008).

Key Diagnostics

CAPS-Approved Method*:

Confirmation of *Heterodera filipjevi* is by morphological identification. Keys are available for identification by morphological characteristics of the cyst, second-stage juvenile, male, and female. Handoo (2002) provides a key to the species within the *H. avenae* group, as well as a thorough review of morphological studies to date.

Literature-Based Methods:

Most diagnoses are made via morphological characteristics. Keys are available for identification by morphological characteristics of the cyst, second stage juvenile, male, and female (Handoo, 2002). The vulval cone of *H. filipjevi* is bifenestrate and the semifenestrae are horseshoe-shaped (Fig. 11). The *H. filipjevi* vulval cone has a distinct underbridge (Fig. 11).

However, because of the increasing number of species in the *H. avenae* complex, identification based on morphology is becoming more difficult (Subbotin et al., 2003).

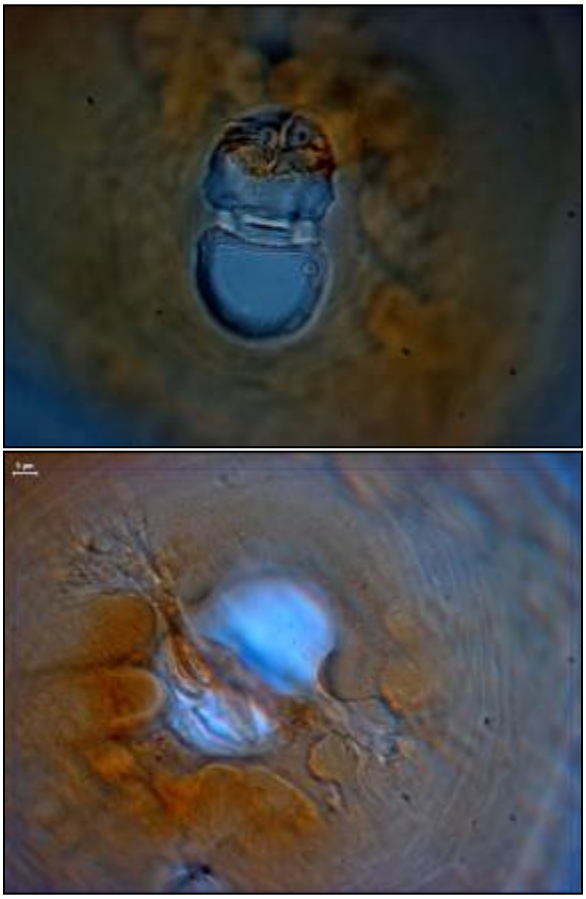

Figure 11. Top: Bifenestrate vulval cone of *H. filipjevi* with horseshoe-shaped semifenestrae Bottom: underbridge. Photos courtesy of R. Holgado, Norwegian Institute for Agricultural & Environmental Research, Norway.

For precise identification, other methods are used such as (1) protein electrophoresis, (2) isozymes/ isoelectrofocusing (Andres et al., 2001), and (3) molecular biology techniques, such as polymerase chain reaction (PCR), restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), and sequences of internal transcribed spacer ribosomal DNA (ITS-rDNA) (Bekal et al., 1997; Ferris et al., 1999; Andres et al., 2001; Nicol, 2002; Tanha-Maafi et al., 2003; Rivoal et al., 2003; Subbotin et al., 1999; Subbotin et al., 2001; Subbotin et al., 2003; Madani et al., 2004; Abidou et al., 2005; Yan and Smiley, 2010), and species-specific PCR (Peng et al., 2013; Toumi et al., 2013; Yan et al., 2013).

H. avenae, *H. filipjevi*, and *H. latipons* were also differentiated by electrophoresis on cellulose acetate plates using the enzymes esterase and malate dehydrogenase and aliquots of 25 females (Mokabli et al., 2001).

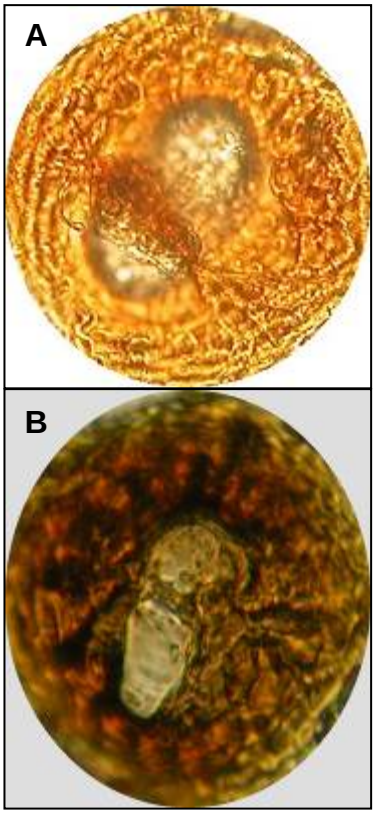

Figure 12. Vulval cones of A) *H. filipjevi* and *B) H. avenae*. Photos courtesy of R. Smiley, Oregon State University.

Easily Confused Species

Heterodera filipjevi has been confused with several other cyst nematode species that parasitize cereals, including (but not limited to) *H. avenae, H. bifenestra, H. hordecalis, H. latipons*, *H. mani, H. pakistanensis, H. tucomanica,* and *H. zeae* (Kort, 1972; Nicol, 2002).

H. filipjevi and *H. avenae* can be separated on the basis of morphology of the cyst (Fig. 4, 6) and the vulval cone (Fig. 11, 12) (Holgado et al., 2004b). *H. filipjevi* has a well-developed underbridge, whereas the underbridge in *H. avenae* is weakly developed or absent. Bullae (blister-like prominences near the vulval fenestra) in *H. filipjevi* are weak to medium, distinct, mostly globular, and pale to medium brown in color, whereas they are a strong, dark brown, numerous, clearly distinct, and variable in shape in *H. avenae*. The cyst wall of *H. filipjevi* is light in color, but those of *H. avenae* are dark brown. Eggs of *H. filipjevi* are easily observed through the cyst wall, unlike those of *H. avenae* (Fig. 6) (Holgado et al., 2004b).

H. latipons cysts differ from those of *H. filipjevi*, because they lack bullae which are present on those of *H. filipjevi* (Greco et al., 2002).

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Updates:

December, 2014: Added Washington State to the known distribution.

August, 2016: Removed outdated maps.