Chapter 5

Biology and Management of the Rice White Tip Nematode *Aphelenchoides besseyi* (Christie, 1942)

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Abstract

Aphelenchoides besseyi Christie, 1942, is an important plant-parasitic nematode species that causes significant economic losses worldwide. It primarily infests rice (*Oryza sativa* L.), but also impacts a broad spectrum of hosts including ornamental plants, Strawberries, bean, and various other crops. Due to its ability to be transmitted through seeds and its high tolerance to environmental conditions, *A. besseyi* is considered a quarantine pest of major concern. In rice, it causes a physiological disorder known as "white tip disease," characterized by leaf whitening, stunted growth, and yield reduction in infected plants. Studies on the morphology, biology, damage mechanisms, and dispersal pathways of *A. besseyi* have revealed that the species is well adapted to both humid environments and dry seed conditions. This adaptability facilitates its long-distance dissemination. Due to the limited efficacy of chemical control methods, the adoption of biological control agents and cultivation of resistant varieties has gained greater significance for promoting environmental sustainability. This chapter presents an extensive summary of the taxonomy, morphological and molecular identification, life cycle, ecology, distribution, damage symptoms, and management strategies of *A. besseyi*.

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1. INTRODUCTION

Aphelenchoides besseyi (Christie, 1942), is an important nematode species exhibiting both free-living and phytoparasitic phases. This species is particularly notorious for the damage it inflicts on rice (*Oryza sativa* L.), where the characteristic white discoloration at leaf tips has led to its common designation in the literature as the "white tip nematode" (Franklin & Siddiqi, 1972).

A. besseyi has been reported from most rice growing regions across Asia, Africa, Europe, the North, and Pacific Islands, South and Central America. Yield losses in rice caused by this nematode differ significantly according to the cultivated variety, environmental conditions (temperature and humidity), agronomic practices, and seasonal fluctuations.

Because of its broad host spectrum and capacity to be transmitted through seed (Ou, 1985a), this nematode is recognized as a quarantine pest and is of major economic concern in global rice production. While it predominantly feeds ectoparasitically on rice and strawberry, endoparasitic development has also been observed in certain hosts (Hockland, 2004). Particularly in susceptible rice cultivars, its ectoparasitic feeding on stems, leaves, and bud meristems has been reported to cause severe yield reductions (Tulek & Çobanoğlu, 2010).

Average yield losses in infested fields range between 10–30%, but in heavily infected conditions losses may reach up to 70% in susceptible cultivars, while resistant cultivars may still suffer losses of up to 20% (Prot, 1992; Lin et al., 2004; Muthukrishnan et al., 1974; Tikhonova, 1966).

Unlike obligate parasites, *A. besseyi* is capable of surviving without a host by feeding on fungi in soil. Under drought conditions, it can persist in an anhydrobiotic state within seeds or plant debris. In dry tissues, particularly beneath the rice hulls, it can survive for up to three years (Tiwari & Khare, 2003) and adversely affect seed quality (Rajan & Mathur, 1990). This remarkable longevity represents a significant risk for both dissemination and quarantine concerns (Cralley & French, 1952).

Beyond rice, it is known as the causal agent of "summer dwarf" and "crimp disease" in strawberry (*Aphelenchoides fragaria*). More recently, it has also been recognized as the etiological agent of "black leaf spot disease" in common bean (*Phaseolus vulgaris* L., Fabaceae) (Chaves et al., 2013). Additionally, it has been found in the soil associated with imported penjing (bonsai) plants, likely associated with irrigation water originating from nematode-infested rice fields. Beneath the husks of rice grains, the nematode may remain viable for extended periods in a quiescent, drought-adapted form.

1.1. History

Although the damage caused by *A. besseyi* is currently recognized as "white tip" the identity and causal nature of this disease remained ambiguous for decades. The first systematic record in Japan was by Kakuta (1915), who reported "black grain damage" in the Kyushu region. This damage resembled the "head blight" observed in Italian millet, and both conditions were suspected to be nematode-induced. Later, Tanaka and Uchida (1941) described another rice disorder characterized by stunted growth in Hokkaido and also linked it to nematodes. The "heart blight" described by Yoshii (1946) was subsequently named Aphelenchoides oryzae by Yokoo (1948). Comparative analyses by Yoshii and Yamamoto (1950b) across different regions on rice and millet damage demonstrated that the causal agent was the same nematode species (*A. oryzae*).

Similar debates occurred in the United States. Jodon (1935) described leaf tip whitening in rice as "white tip," but attributed it to iron deficiency (Ou, 1972). Tullis and Cralley (1936) and Jones (1938) supported this view, while Martin (1939) and Martin & Alstatt (1940) attributed the symptoms to magnesium deficiency or imbalances in the magnesium-calcium ratio. In contrast, Takimoto (1943) highlighted striking similarities between Japanese rice disorders and U.S. "white tip" cases, and Cralley (1949) confirmed that the U.S. disorder was also nematode-induced.

Clarity was achieved through the work of Allen (1952), who demonstrated that the nematodes causing rice damage in both Japan and the U.S. were morphologically identical to *A. besseyi*, previously described by Christie (1942) from strawberry. Based on taxonomic priority, *A. besseyi* was accepted as the pest responsible for "white tip."

Subsequent surveys reported its widespread distribution across Asia, tropical America, and the former Soviet Union. In Africa, however, it went unreported for decades until surveys conducted between 1965–1970 revealed natural populations on local rice varieties (e.g., Diatang de Bignona) in Senegal, suggesting its earlier presence at low densities on the continent (Barrat et al., 1969).

1.2. Hosts and Distribution

A. besseyi has a broad distribution and occurs in the majority of rice growing areas (Ou, 1985b). The first symptoms of rice white tip nematode were observed by Kakuta in Kyushu, Japan, who described it as "black grain disease" (Kakuta, 1915).

In China, *A. besseyi* (listed on the EPPO A2 list) was initially identified in Heilongjiang Province as the pathogen causing white tip disease in rice. During the summer of 2021, the nematode was detected in a rice field in Acheng district, and its identity was confirmed using molecular, morphological, and pathogenicity analyses (Hu et al., 2023).

In Brazil, *A. besseyi* (EPPO A2 List) was initially reported as the pathogen causing leaf spot disease on cowpea (*Vigna unguiculata*) under natural field conditions. During surveys conducted in May 2021 and June 2022, the nematode was detected in two locations within the Rio Largo municipality, Alagoas State, in northeastern Brazil. The species' identity was verified using morphological, morphometric, and molecular approaches (Noronha et al., 2023).

EPPO Region: Turkey, Italy (mainland), Georgia, Portugal (mainland), Hungary, Ukraine, Azerbaijan, Romania, Russian Federation (southern Russia), Uzbekistan, Bulgaria, Kyrgyzstan

Africa: Ghana, Zambia, Burundi, Mali, Comoros, Egypt, South Africa, Niger, Cameroon, Malawi, Togo, Benin, Gabon, Sierra Leone, Nigeria, Madagascar, Gambia, Central African Republic, Rwanda, Senegal, Tanzania, Côte d'Ivoire, Uganda, Guinea, Burkina Faso, Zimbabwe, Kenya, Democratic Republic of Congo, Congo, Chad

Asia: Vietnam, Japan (Honshu, Shikoku, Kyushu), Myanmar, Indonesia, Korea Republic, Malaysia (West), Afghanistan, India (Kerala, Punjab, Bihar, Gujarat, Meghalaya, Jharkand, Uttar Pradesh, Assam, Tripura, Haryana, West Bengal, Odisha, Madhya Pradesh, Delhi, Tamil Nadu, Maharashtra), Pakistan, Bangladesh, Sri Lanka, Iran, Tajikistan, Uzbekistan, Nepal, Kyrgyzstan, China (Guizhou, Liaoning, Hubei, Xinjiang, Zhejiang, Jilin, Henan, Fujian, Hebei, Sichuan, Guangxi, Jiangxi, Hunan, Shandong, Anhui, Ningxia, Shanxi, Guangdong, Jiangsu, Shaanxi, Heilongjiang), Thailand, Cambodia, Laos, Taiwan, Philippines.

North America: United States (California, Arkansas, Florida, Texas, Hawaii, Louisiana), Mexico

Central America & Caribbean: Panama, Dominican Republic, Cuba, El Salvador, Costa Rica, Guadeloupe, Dominica

South America: Ecuador, Brazil (Pará, São Paulo, Rio Grande do Sul, Alagoas, Tocantins, Sergipe, Paraná, Minas Gerais, Bahia, Santa Catarina, Maranhão, Rio Grande, Mato Grosso do Norte, Amapá)

Oceania: Fiji, Australia (Queensland, Northern Territory), Papua New Guinea, Cook Islands

In Turkey, *A. besseyi* was first reported in 1995 from İpsala (Edirne) and Gönen (Balıkesir) districts (Öztürk & Enneli, 1997). Later surveys revealed its presence in other rice growing regions (Black Sea and Central Anatolia), where it caused significant yield losses, reaching up to 57.9% on the susceptible "Halilbey" cultivar in the Marmara region (Tülek & Çobanoğlu, 2010; Çelik & Devran, 2019).

1.3. Biology

After sowing, dormant *A. besseyi* juveniles become activated by water and begin feeding on the sensitive primordium of germinating seeds. They initially feed as endoparasites within the coleoptile for 7–10 days and later live as ectoparasites on the innermost leaf sheath during subsequent developmental stages (Tsay et al., 1998). During tillering, nematodes migrate to the growing point, where they settle ectoparasitically on folded young leaves, moving upward with plant growth and feeding on vegetative tissues without penetrating them. Upon completion of tillering, nematode numbers increase rapidly, reaching the spikelet. They occur more abundantly on the outer surface of the spikelet and enter during flowering when glumes open (Yoshii & Yamamoto, 1950b). Nematodes invade the flowers before anthesis, when spikelets are still enclosed by the flag leaf sheath, and continue feeding endoparasitically in the ovary, anther, lemma, palea, and embryo (Huang & Huang, 1972). They may remain viable within seeds for up to four months (Goto & Fukatsu, 1952).

The life cycle of *A. besseyi* is temperature-dependent, completing in approximately 10 days at 21 °C. Development from egg to adult female takes 6.5–7 days: egg (0.5 d), second-stage juvenile (0.13 d), third stage (0.65 d), and fourth stage (0.9 d). Female maturation takes an additional 4.3–4.8 days (Sudakova & Stoyakov, 1967). Larvae require feeding for development; in distilled water they become inactive within 2–3 days. Under natural conditions, cycle duration varies: 3 days at 31.8 °C, 6 days at 25 °C, 9 days at 20.6 °C, and 29 days at 14.7 °C (Tikhonova, 1966).

Reproductive rate depends on the host plant and its resistance. After tillering, nematode reproduction accelerates, peaking during spikelet formation (Goto & Fukatsu, 1956). On cultures of Fusarium solani, life cycle duration was reported as 24 ± 4 days at 16 °C, 15 ± 2.9 days at 20 °C, 9 ± 2 days at 23 °C, 10 ± 2 days at 25 °C, and 8 ± 2 days at 30 °C, with 30 °C being optimal. Although oviposition, hatching, and molting occur at 35 °C, population growth ceases at this temperature (Huang et al., 1972).

The longevity of these nematodes is remarkable: they can persist for 2–3 years in rice grains (Todd & Atkins, 1958; Yoshii & Yamamoto, 1950a), and some studies report survival for up to 8 years (Zem & Mamteiro, 1977). Nematode recovery is higher from seeds with lower moisture content compared to those with higher moisture levels (Chaudhury & Chaudhury, 1996). Inoculated plants tend to produce a larger proportion of lighter seeds that float on water, while nematode mortality is greater in heavier seeds; additionally, the rate of seed swelling rises with nematode density in lighter seeds (Togashi & Hoshino, 2003). Nematodes also persist in rice stubble left in the field, contributing to interseasonal inoculum survival. Associated fungi such as *Fusarium* spp. and *Curvularia* spp. may serve as alternative hosts (Sivakumar, 1987).

1.4. Symptoms and Economic Importance

The primary and diagnostic symptom of rice white tip nematode infection is the chlorosis observed in the apical 3–5 cm of leaves, which subsequently progresses to necrosis. Wrinkling and deformation also occur in the flag leaf surrounding the panicle, resulting in reduced panicle and grain size. These symptoms may be confused with calcium or magnesium deficiency. In rice, seeds are the primary inoculum source. Upon sowing, nematodes become active and migrate to the growing points of stems and leaves. In susceptible cultivars, *Aphelenchoides besseyi* feeds ectoparasitically not only on stems and leaves but also on meristematic tissues and floral organs (Yoshii & Yamamoto, 1950a).

Infected plants exhibit leaf tip whitening of tillers. Flowers may become sterile or produce shriveled, malformed grains with poor germination capacity (Tamura & Kegasawa, 1956). By feeding on stems, leaves, buds, and developing embryos, the nematode reduces plant vigor and height, leading to fewer and smaller panicles.

A. besseyi damages not only rice but also a wide range of hosts. In strawberry, it induces “summer dwarf” or “crimp disease,” characterized by leaf wrinkling, deformation, stunting, and reduced flowering. These symptoms have been reported in the Australia, United States, and more recently in Europe. Similar symptoms can be confused with damage caused by other Aphelenchoides species (foliar and bud nematodes). It also causes leaf drop in *Ficus elastica*, leaf lesions in *Polianthes tuberosa*, and fruit capsule rot and premature fruit drop in *Capsicum annuum*, often mimicking fungal diseases. Conversely, in the grass *Sporobolus poiretii*, the nematode has been reported to stimulate plant growth and flowering. Additionally, infestations have been documented in *Boehmeria nivea*, several ornamentals (e.g., *Chrysanthemum* spp., *Hibiscus* spp., *Saintpaulia ionantha*), and various grasses (*Panicum spp, Pennisetum* spp., *Setaria* spp.).

Economic losses vary with initial nematode population density, rice variety, environmental conditions, and cultivation practices. Yield reductions generally range from 30–50% (Swain, 1987). In greenhouse and micro-plot experiments conducted in Rasht (Guilan Province, Iran) during 2005–2006, losses due to *A. besseyi* were estimated, and both symptom severity and yield losses increased with nematode population density (Jamali et al., 2009). In Turkey, field studies revealed yield reductions of 28.11–57.91%, 1000-grain weight losses of 12.11–22.35%, and milling recovery losses of 12.78% in infested plots (Tulek et al., 2012).

2. METHODS FOR OBTAINING *Aphelenchoides besseyi*

2.1. Seed-Based Extraction

Aphelenchoides besseyi is disseminated worldwide primarily through seeds, especially rice seeds. Therefore, accurate and high-yield extraction from seed material is of critical importance in quarantine and survey studies. One of the most frequently employed methods described in the literature involves immersing dehusked seeds in shallow water (Uebayashi et al., 1971). Although effective, this method is labor-intensive. Alternatively, the Baermann funnel technique, applied after splitting and crushing seeds, is widely used (Nandakumar et al., 1975). Protocols have also been developed to achieve high recovery efficiency from individual seeds. For example, Hoshino and Togashi (1999) reported nearly 100% recovery of viable nematodes by placing longitudinally opened seeds inside pipette tips submerged in water-filled tubes. The ISTA (2017) guidelines recommend a minimum sample size of 1000 seeds with a maximum subsample size of 250 seeds, while EPPO (2013) standards specify that husks and hulls may also be used as alternative test material.

2.2. Extraction from Plant Tissues

For the extraction of nematodes from leaves, shoots, and other soft plant tissues, the Baermann funnel and its modifications are the most recommended methods. To detect low-level infestations, these methods should be applied for at least 48 hours (EPPO, 2013; Van Bezooijen, 2006). Additionally, blender-filtration and centrifugal-flotation techniques are also employed, particularly in samples containing large amounts of tissue, where they provide efficient results (Hooper, 1986). The literature emphasizes that method selection is critical depending on tissue type; for fresh leaves, the Baermann funnel is considered the most suitable for recovering active nematodes.

2.3. Extraction from Soil and Mixed Materials

For nematode isolation from soil and the rhizosphere, sieving, elutriation, and centrifugal-flotation methods are commonly applied (Coolen & D'Herde, 1972; Hooper, 1986). These procedures concentrate nematodes, allowing subsequent purification by Baermann funnel or other separation techniques. Such protocols are particularly important for evaluating persistent stages in soil.

2.4. Microscopic Examination and Slide Preparation

Extracts obtained from plant material and soil may contain all developmental stages, including adults and juveniles. Under a stereomicroscope, members of the order Aphelenchida can be recognized by the presence of a large, rounded median bulb. Most species are robust-bodied and sluggish in movement; in contrast, *A. besseyi* is slender, pale in color, and an efficient "swimmer," exhibiting characteristic sinuous movements in water (Tamura & Kegasawa, 1957; Tamura & Kegasawa, 1958; Hollis & Keoboonrueng, 1984).

Selected individuals from the extracts are transferred onto glass slides to prepare temporary mounts. Nematodes become immobilized when collected in a water drop and gently heated up to approximately 60 °C. Individuals of *A. besseyi* killed by mild heat appear straightened. Preparations may be sealed with wax or nematodes can first be placed in a fixative solution to produce permanent slides. Although temporary water mounts are often preferred for species identification, fixed specimens allow clearer observation of structures such as the stylet.

Morphological diagnosis particularly considers sexual dimorphism in body size: females measure 0.62–0.88 mm in length, while males range from 0.44–0.72 mm. The head region is offset, and the median bulb is large and oval-shaped. The tail tapers conically and terminates in a distinctive mucron with four projections, giving a star-like appearance. This mucron is regarded as a key diagnostic feature for differentiating *A. besseyi* (Nandakumar et al., 1975; EPPO, 2009; EPPO, 2013).

3. TAXONOMY AND IDENTIFICATION

3.1. Taxonomic Classification (Franklin and Siddiqi, 1972)

Kingdom: Animalia

Phylum: Nemata

Class: Secernentea

Order: Aphelenchida

Family: Aphelenchoididae

Genus: *Aphelenchoides* Fischer, 1894

Species: *Aphelenchoides besseyi* Christie, 1942

3.2. Identification

Name: *Aphelenchoides besseyi* Christie, 1942

Synonyms: *Aphelenchoides oryzae* Yokoo, 1948; *Asteroaphelenchoides besseyi* (Christie, 1942) Drozdovsky, 1967

Taxonomic position: Nematoda: Aphelenchida: Aphelenchina: Aphelenchoididae

Bayer computer code: APLOBE

Phytosanitary categorization: EPPO A2 list no. 122; EU Annex designation: II/A1 on rice and II/A2 on strawberry

3.3. Identification

Accurate identification of *A. besseyi* is essential for understanding its biology and for developing effective management strategies. The close morphological resemblance to other *Aphelenchoides* species, combined with its ability to induce variable symptoms in different hosts, represents a major challenge for diagnosis.

In general, species-level identification of *Aphelenchoides* nematodes relies on conventional microscopic techniques, based on the measurement of diagnostic morphological traits. However, as with most plant-parasitic nematodes, this approach provides reliable results only for adult individuals. For definitive species-level identification, detailed examination of morphological characters under high-powered microscopy (≥×1000 magnification with oil immersion) is required. Furthermore, differential interference contrast microscopy, and when accessible, scanning electron microscopy (SEM), offer critical assistance, particularly for the detailed assessment of lateral fields and tail morphology.

Nevertheless, diagnosis of *Aphelenchoides* species based solely on morphology is highly challenging. Therefore, several molecular diagnostic methods have been developed to support species identification (Ibrahim et al., 1994a, b). Molecular techniques allow detection at all life stages, including immature individuals, and yield reliable results in cases of low-level infestations or when atypical or damaged adults are present. Nonetheless, the specificity of current molecular assays is constrained, since the majority of tests have been developed and validated using a limited number of species and populations from narrow geographic areas.

When diagnosing *A. besseyi*, the potential occurrence of other *Aphelenchoides* species in soil, foliage, and rice husks must be considered (Table 1). Unfortunately, many of these species are morphologically difficult to distinguish, and inadequate species descriptions further complicate identification (Sanchez-Monge et al., 2015). For this reason, a combined approach employing both morphological and molecular methods is strongly recommended for accurate diagnosis of *A. besseyi*.

Table 1. A diagnostic key used to differentiate adult specimens of the genus Aphelenchoides from other nematode genera found in soil and plant tissues (Karssen & Groza, 2018).

1	Stylet present	2
	Stylet absent	NAS
2	Four-part pharynx with cylindrical procorpus, metacarpus with plates, slender isthmus and glandular basal bulb	3
	Two-part pharynx, anterior part slender, posterior part expanded, glandular and muscular	NAS
3	Dorsal pharyngeal gland outlet in metacorpus; metacorpus very large, often appears nearly as wide as the diameter of the body	4
	Dorsal pharyngeal gland outlet in procorpus behind stylet knobs; metacorpus moderate to reduced in size (less than three-fourths body width)	NAS
4	Pharyngeal glands lobe-like, long dorsal overlap of intestine	5
	Pharyngeal glands pyriform, not overlapping intestine; or pharyngeal glands lobe-like, ventral overlap of intestine	NAS
5	Lateral fields with four or fewer incisures*; stylet with basal knobs or swellings; female tail conoid, elongate conoid, convex conoid or subcylindrical to a pointed or narrowly rounded terminus; male spicules robust, thorn-shaped; adanal bursa absent	6
	Lateral fields with six or more incisures; stylet without basal knobs; female tail short, subcylindroid and with broadly rounded terminus; male spicules slender, tylenchoid; adanal bursa present	NAS
6	Tails of both sexes short, usually less than four times anal body width	7
	Tails of both sexes elongate to filiform, usually more than four times anal body width	NAS
7	Stylet slender, often about 10–12 μm and usually less than 20 μm; vulval flap absent; male without small bursa-like flap at tail tip	*Aphelenchoides*
	Not with the above combination of characters	NAS

NAS: not Aphelenchoides species.

**** Khan et al. (2012) reports populations having lateral fields with 6 incisures (additional information compared to the IPPC Diagnostic Protocol; IPPC, 2016).***

3.3.1. Description of *Aphelenchoides besseyi*

The morphological diagnosis of *Aphelenchoides besseyi* relies on conventional microscopic examination (Figure 1; 2). Reliable species-level identification is possible only in adult individuals, while juvenile stages are inadequate for accurate diagnosis. *A. besseyi* is distinguished by a prominent metacorpus (median bulb), with the esophageal gland overlap generally positioned dorsally. The dorsal esophageal gland opens into the esophageal lumen at the metacorpus level, just anterior to the pump chamber, whereas the subventral esophageal glands open posterior to the pump chamber into the lumen. This description is adapted from Hunt (1993).

Female

The female of *A. besseyi* has a slender body, usually straight or slightly curved ventrally when relaxed. The posterior part of the body tapers slightly anteriorly from the esophageal glands; the head region is about half the body width, rounded, and unstriated, with the lip base being wider than the body. The labial framework is six-rayed and weakly sclerotized; cheilorhabdions are slightly sclerotized. The lateral fields occupy about one-fourth of the body width and contain four incisures. The stylet is sharply pointed anteriorly, comprising about 45% of the total stylet length, and bears small basal swellings approximately 1.75 μm in diameter. The procorpus is cylindrical, 1.5–2 times as long as the width of the median bulb, and carries a refractive valvular structure just posterior to its midpoint. The esophageal glands overlap dorsally and subdorsally along the intestine for 4–8 body widths. The nerve ring is located about one body width posterior to the median bulb, and the excretory pore is usually situated near the anterior margin of the nerve ring. The hemizonid, distinct in specimens recovered from non-cultured seeds, lies 11–15 μm posterior to the excretory pore, while the hemizonion, positioned 20–30 μm behind the hemizonid, is usually difficult to observe. Cuticular striations are spaced at intervals of 0.9–1.1 μm at midbody.

The vulva is transverse, with slightly elevated lips. The spermatheca is elongate-oval, conspicuous, and may reach a length about eight times its width when fully distended; it is typically filled with sperm, containing a central nucleus surrounded by a ring of black granules. The ovary is relatively short and does not extend anteriorly to the esophageal glands; oocytes are arranged in 2–4 rows. The post-vulval uterine sac is narrow, delicate, and difficult to discern; it does not contain sperm and measures 2.5–3.5 body widths long, being less than one-third of the distance from vulva to anus. In cultured nematodes, it is more conspicuous and rounded. The tail is conoid, straight, narrowing posteriorly to a finely rounded terminus. Its length is 3.5–5 anal body diameters. At the tail tip, a mucron with three to four projections of variable shape is present, usually forming a star-like (stellate) appearance.

Male

Males of *A. besseyi* are nearly as numerous as females. In relaxed individuals, the posterior body end is curved ventrally through about 180°. The lip region, stylet, and esophagus are similar to those of the female. The tail is conical and terminates in a mucron bearing 2–4 pointed projections. Three pairs of ventro-submedian papillae are present: the first pair is adanal, the second located slightly posterior to mid-tail, and the third is subterminal. The spicules exhibit typical generic characteristics; however, the proximal end lacks a dorsal prominence (apex) and possesses only a moderately developed ventral rostrum. Dorsal spicules measure 18–21 μm in length (average 19.2 μm). The testis is single and elongate. The tail terminus bears four variable mucronate projections.

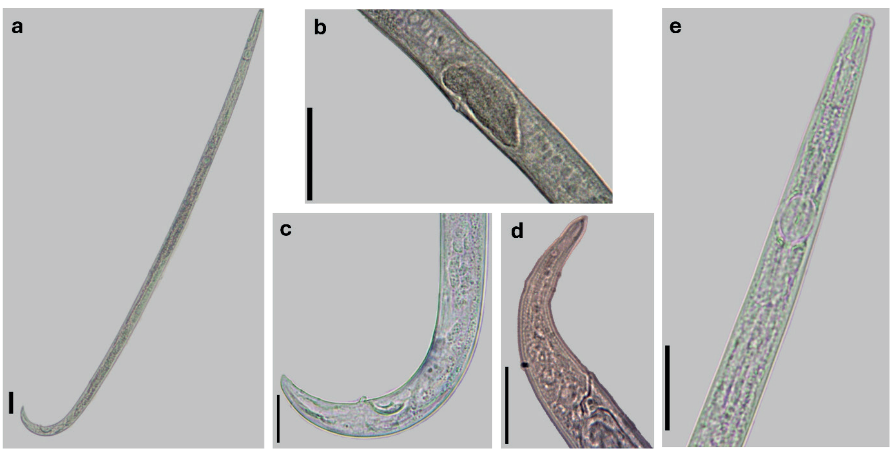

Figure 1. a. General morphology of the Aphelenchoides besseyi, b. Vulva, c. tail of male, d. tail of female and e. anterior.

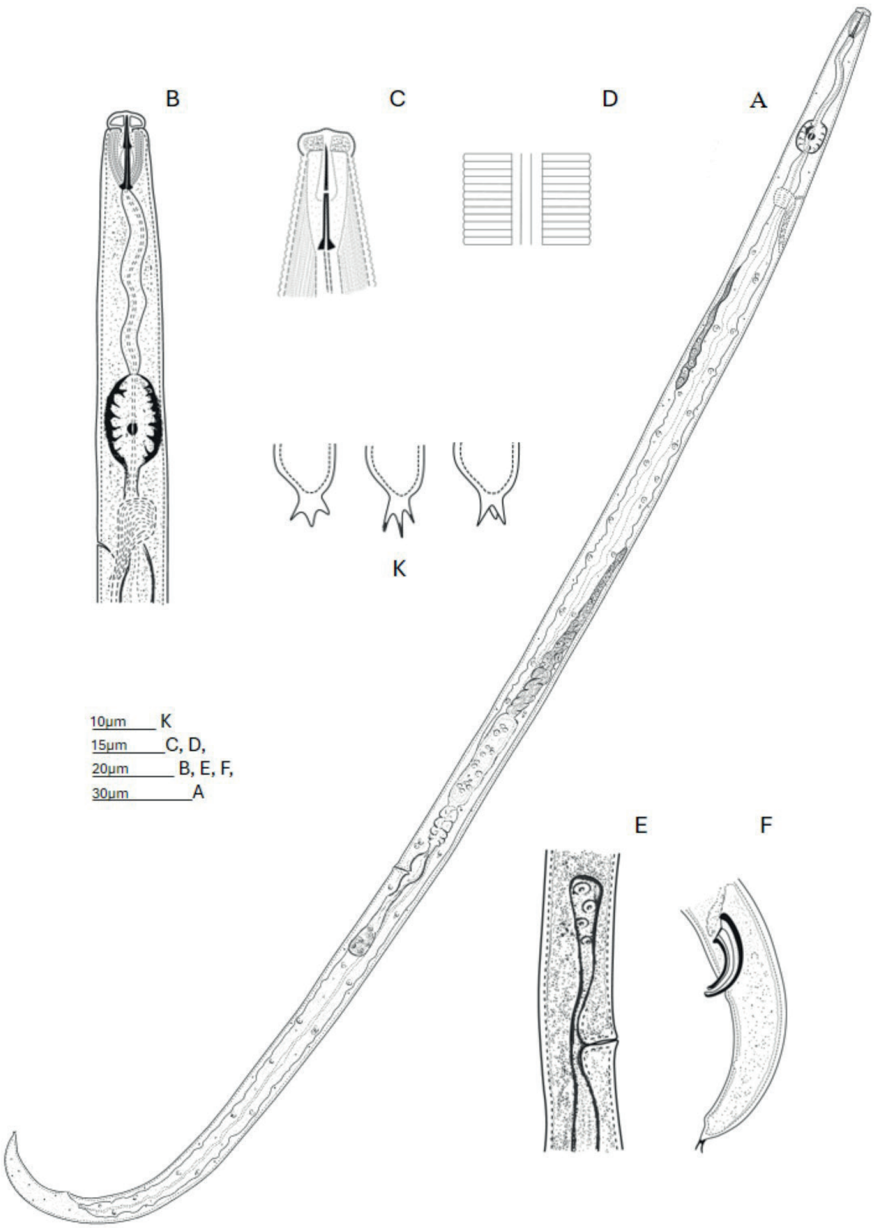

Figure 2. General morphology of the Aphelenchoides besseyi. A. Female; B. Anterior end of male showing the median bulb of the esophagus, nerve ring, and position of the excretory pore; C. Head region of female; D. Lateral field; E. Post-vulval uterine sac of female; F. Tail terminus of male; G. Variations in mucro shape (star-like tail tip) of female.

3.3.2. Molecular Diagnosis

Identification of *Aphelenchoides besseyi* based solely on morphological traits is often difficult because:

- Morphometric variations may occur among individuals,
- Confusion with closely related species (*A. fragariae*, *A. ritzemabosi*) is common,
- Morphological identification is unreliable in juvenile stages.

For these reasons, molecular methods are employed as supportive and confirmatory tools alongside morphology.

PCR Assays

In molecular analyses, DNA is typically extracted from single individuals, followed by PCR-based assays for species-level identification (Sakai, 2010). The most commonly targeted gene regions include:

- **28S rRNA D2–D3 expansion domains:** Subbotin et al. (2006) demonstrated that the D2A/D3B primer set can reliably distinguish *A. besseyi*.
- **18S rRNA and ITS regions:** Chizhov et al. (2006) and Khan et al. (2012) reported the utility of sequences from these regions for the diagnosis of *A. besseyi*.

DNA Barcoding

DNA barcoding is increasingly used for species identification through comparative sequence analysis and is widely applied to distinguish *A. besseyi* from other *Aphelenchoides* species. The most frequently employed barcoding loci include COI, 18S rRNA, and 28S rRNA regions. Sequences generated by these assays are deposited in public databases such as GenBank and Q-bank as reference data (EPPO, 2016).

Phylogenetic trees and network analyses provide insights into the genetic relatedness of populations collected from different geographical regions and allow assessment of intraspecific variation (Ye et al., 2007; Oliveira et al., 2019). Among these, COI-based DNA barcoding is currently regarded as one of the most reliable molecular tools for identifying *A. besseyi*. However, simultaneous use of multiple loci improves both specificity and accuracy of species diagnosis.

Molecular diagnostics of *A. besseyi* is critically important for:

- Differentiation from morphologically similar species (*A. ritzemabosi*, *A. fragariae*),
- Elucidation of genetic diversity among populations from different regions,
- Rapid and reliable detection in quarantine and phytosanitary programs.

Accurate identification of *A. besseyi* requires an integrative approach combining morphology and molecular tools. While morphological study of adults remains fundamental, morphometric variability among populations and similarity to related species may lead to misidentifications (Christie, 1942; Khan et al., 2012; Sanchez-Monge et al., 2015). Molecular assays targeting gene regions such as ITS-rDNA, the D2–D3 domains of 28S rRNA, and mitochondrial COI enhance specificity and reliability of species recognition (Subbotin et al., 2006; Oliveira et al., 2019). Integration of both morphological and molecular approaches not only strengthens diagnostic accuracy but also enables comprehensive understanding of genetic diversity, phylogenetic relationships, and dispersal dynamics of the species (Ye et al., 2007; EPPO, 2016).

4. HOST RANGE

The principal hosts at risk are rice and strawberry. *Aphelenchoides besseyi* has also been recorded on other crop plants (e.g., *Capsicum annuum* var. *longum*, *Gossypium hirsutum*, *Zea mays*), ornamentals (e.g., *Agave amica*, *Ficus elastica*, chrysanthemums), and turf grasses (e.g., *Panicum*, *Setaria*) (Table 2).

Soybean (Glycine max) has been identified as a host of A. besseyi under laboratory conditions (Oliveira et al., 2019) and has also been reported in natural field infestations (Meyer et al., 2017). However, reports differ regarding host susceptibility and the severity of subsequent damage. In addition, seeds of *Fraxinus americana* imported from the United States have been detected carrying infestations of *A. besseyi* (Gokte et al., 1989).

Table 2. Host list of Aphelenchoides besseyi

Host List	Reference
Abelmoschus esculentus (L.) Moench	Samina & Iqbal (2019)
Agave amica (Medik.) Thiede & Govaerts	Bala et al. (2019) Khan et al. (2012)
Allium cepa L.	Bridge et al. (2005)
Asplenium nidus L.	Tsay et al. (1998) Wu et al. (2016)
Avena sativa L.	Nemaplex (2021)
Boehmeria nivea (L.) Gaudich.	Fortuner (1970)
Capsicum annuum L.	Bridge et al. (2005) Hockland & Eng (1997)
Chrysanthemum sp. L.	Khan et al. (2012)
Chrysanthemum indicum L.	Wheeler & Crow (2019)
Chrysanthemum maximum Ramond.	Goodey et al. (1965)
Chrysanthemum X morifolium Ramat	Goodey et al. (1965)
Coleus blumei Benth.	Goodey et al. (1965)
Colocasia esculenta (L.) Schott	Bridge et al. (2005)
Cyperus iria L.	Goodey et al. (1965)
Dahlia pinnata Cav.	Goodey et al. (1965)
Digitaria sanguinalis Scop.	Goodey et al. (1965)
Dioscorea cayenensis Lam.	Noronha et al. (2020)
Dioscorea trifida L. f.	Bridge et al. (2005)
Erechtites praealta Raf.	Goodey et al. (1965)
Ficus elastica Roxb. ex Hornem	Marlatt (1966) Marlatt (1975)
Fragaria glandiglora Ehrn.	Jen et al. (2012)
Fragaria x ananassa Duchesne ex Rozier	Oliveira et al. (2019)
Fragaria vesca L.	Fernandez et al. (1998)
Fraxinus americana L.	Gokte et al. (1989)
Gerbera jamesonii Bolus ex. Hooker	Oliveira et al. (2019)
Gladiolus sp. L.	Khan et al. (2012)
Glycine hispida L.	Gokte et al. (1992)
Glycine max (L.) Merr.	Calandrelli et al. (2022) Meyer et al. (2017) Oliveira et al. (2019)
Gossypium hirsutum L.	Favoreto et al. (2018a) Favoreto et al. (2018b)
Hibiscus sabdariffa L.	Karssen & Groza (2018)
Hydrangea macrophylla Ser.	Goodey et al. (1965)
Impatiens balsamina L.	Goodey et al. (1965) Khan et al. (2012)
Ipomoea batatas L.	Bridge et al. (2005)

Continued from Table 2	
Nicotiana tabacum L.	Favoreto et al. (2024)
Oryza sativa L.	Tulek (2016) Çelik et al. (2020)
Panicum sp.	Karssen & Groza (2018)
Panicum miliaceum L.	Gokte & Mathur (1993)
Pennisetum sp.	Karssen & Groza (2018)
Phaseolus vulgaris L.	Chaves et al. (2013)
Pluchea odorata L.	Goodey et al. (1965)
Polianthes tuberosa L.	Khan et al. (2012)
Saccharum officinarum L.	Fernandez et al. (1998)
Saintpaulia ionantha Wendl.	Karssen & Groza (2018)
Setaria italica Beauvois.	Gokte & Mathur (1993)
Sporobolus poiretti Hitch.	Karssen & Groza (2018)
Sorghum halepense Pers.	Khan et al. (2012)
Stylosanthes hamata (L.) Taub.	Gokte et al. (1992) Khan et al. (2012)
Tagetes sp. L.	Goodey et al. (1965)
Tithonia diversifolia A. Gray	Goodey et al. (1965)
Torenia fournieri Linden	Goodey et al. (1965)
Vanda sp. v. X	Goodey et al. (1965)
Vigna unguiculata (L.) Walp.	Favoreto et al. (2022) Noronha et al. (2023)
Zea mays L.	Bridge et al. (2005) Khan et al. (2012)
Zinnia elegans Jacq.	Goodey et al. (1965)

5. MANAGEMENT

According to the European and Mediterranean Plant Protection Organization (EPPO), the rice white tip nematode has been included in the A2 list of quarantine pests since 1981.

5.1. Cultural Practices

Cultural measures represent an effective strategy in reducing populations of *Aphelenchoides besseyi*. The use of nematode-free seed and cultivation in nematode-free fields verified by soil analysis can prevent infestations (Taylor, 1969; Huelma et al., 1994). Practices such as planting clean seed and reclaiming infested areas can limit disease spread (El-Saadony et al., 2021). In addition, the use of resistant cultivars and crop rotation play significant roles in suppressing nematode populations (Hagag et al., 2024).

Rice cultivars vary considerably in their susceptibility to *A. besseyi* (Cralley & French, 1952; Atkins & Todd, 1959).

Utilizing certified nematode-free planting material is an effective strategy to prevent the spread of plant-parasitic nematodes (PPNs), including *A. besseyi* (Coyne et al., 2013). When rice is sown dry and fields are flooded after seedlings reach 7.5–10 cm in height, white tip symptoms occur in approximately 60% of cases. Flooding during germination results in milder disease expression. In contrast, direct sowing under flooded conditions kills most nematodes within one week, with only 0.5% of plants affected; this practice suppresses nematode populations for several years (Cralley, 1956). Similarly, early planting has been reported as an effective measure in the U.S. (Cralley, 1949).

5.2. Hot-water treatment Control

Pre-sowing hot-water treatment of infected seeds is an important physical control method against *A. besseyi*. It reduces nematode populations and prevents their dissemination (Atkins & Todd, 1959). Hot-water treatment is considered an effective approach, with several protocols proposed. Soaking seeds in cold water for 16–20 h followed by immersion in hot water at 50–52 °C for 5–10 min proved effective (Yoshii & Yamamoto, 1950c). Treatments at 60 °C for 20 min, however, delayed germination (Yoshii & Yamamoto, 1951).

For large seed lots lacking specialized equipment, 24 h pre-soaking is recommended, whereas for small samples direct hot-water immersion at 55–61 °C for 10–15 min is effective (Atkins & Todd, 1959). Gamma irradiation has also been investigated, with doses of 5–35 Gray reducing infection rates from 61% to 4% and increasing yield (Aleksondrova, 1985). The International Rice Research Institute (IRRI) recommends immersion of infested seeds in hot water at 52–57 °C for 15 min to eliminate *A. besseyi* (Mew & Misra, 1994).

Treatment temperature and duration must be carefully optimized, as both nematode mortality and seed germination capacity are directly affected (Hagag et al., 2024). Hot-water treatment is therefore regarded as an environmentally friendly, chemical-free physical control method.

5.3. Chemical Control

Various chemical methods have been studied and applied for decades in the control of *A. besseyi*. Nematicides such as fenamiphos, an acetylcholinesterase inhibitor, have been widely used, though their effectiveness depends on application method and environmental conditions (El-Saadony et al., 2021). Following restrictions on methyl bromide use, research into alternative nematicides has expanded (El-Saadony et al., 2021).

Seed, soil, foliar applications, and fumigation have all been tested. For example, soaking rice seed in 1% potassium chloride or 1% sodium chloride solutions for 20 h followed by sun-drying at 40–41 °C for 6 h eliminated 95–97.6% of nematodes (Sivakumar, 1987). Fungicides and nematicides such as BMC (Methyl-N2-benzimidazolyl carbamate), thiabendazole, benomyl, carbofuran, fenitrothion, and oxamyl have shown successful results in seed treatments (Da Silva, 1992; Fortuner & Williams, 1975; Gregon & Prot, 1993; Tsay et al., 1998).

Soil treatments with fensulfothion (5 kg ha^{-1}) and diazinon (15 kg ha^{-1}) significantly reduced spread of *A. besseyi*. Foliar sprays of 0.5% dibetafluroethyl-p-nitrophenyl phosphate also proved highly effective (Sudakova & Stoyakov, 1971).

In foliar treatments applied before flowering, carbendazim was most effective in producing nematode-free seed. Fenitrothion reduced the number of sterile tillers, while phosphamidon increased grain weight and yield, reducing empty grains (Tiwari, 2000). Applications during the flag-leaf stage showed parathion, etaphos, isofenphos, carbosulfan, and monocrotophos to be effective (Kumar & Shivkumar, 1998). Post-planting applications of ethoprop and carbofuran resulted in 19% yield increases and effective control (Lee et al., 1976).

Fumigation with methyl bromide (100 g m^{-3} for 30 min) killed both nematodes and egg sacs (Tsay et al., 1995). In Zenith rice, 6 h fumigation with methyl bromide at 1.25 lb/1000 ft^3 completely eradicated seedborne nematodes without affecting germination (Tullis, 1951). However, direct nematicide application on seeds was found to have limited efficacy (Hoshino & Togashi, 2000). Seed treatment with benomyl or benomyl spraying 1–15 days after transplanting significantly reduced damage from *A. besseyi* (Gergon & Prot, 1993).

5.4. Biological Control

Biological control agents offer promising alternatives for managing *A. besseyi*. Both bacterial and fungal antagonists have been shown to suppress nematode populations. Examples include *Xenorhabdus bovienii*, *Bacillus thuringiensis*, *Purpureocillium lilacinum*, *Volutella citrinella*, and *Pseudomonas fluorescens*, which have demonstrated efficacy against *A. besseyi* (Pathak & Khan, 2010; Tulek et al., 2018; Zhang et al., 2021; Pires et al., 2022).

Although studies remain limited, some report promising results. Tulek et al. (2018) demonstrated that separate applications of *X. bovienii* and *P. lilacinum* suppressed white tip nematode populations, with combined application achieving greater success. Similarly, Zhang et al. (2021) reported that the fungus *Volutella citronella* GUCC2219 showed 59.45% predation in vitro, killing all nematodes within 72 h.

Between 2018 and 2022, research emphasized bacterial and fungal biological control agents (BCAs) and their potential to suppress major plant-parasitic nematodes (PPNs) including *A. besseyi*, *Ditylenchus dipsaci*, *Bursaphelenchus xylophilus*, *Meloidogyne* spp., *Globodera* spp., *Nacobbus aberrans*, *Heterodera* spp., *Rotylenchulus reniformis*, *Pratylenchus* spp., *Radopholus similis*, and *Xiphinema index* (Jones et al., 2013; Kantor et al., 2022). These studies highlight the importance of encouraging further research and screening of BCAs for future PPN management strategies.

5.5. Host Plant Resistance

The use of resistant rice cultivars against *A. besseyi* represents an environmentally friendly and sustainable management option. Resistant varieties offer both economic and ecological advantages compared to chemical control (Sasser, 1989; Reversat et al., 2003; Starr & Roberts, 2004). Resistance varies among genotypes, making the identification of resistant and tolerant cultivars critical for breeding programs (Tulek et al., 2015).

Studies conducted in the U.S. as early as 1949 demonstrated differential susceptibility of rice cultivars to *A. besseyi* (Cralley & Adair, 1949; Peng & Moens, 2003). Arkansas Fortuna, Rexoro, Nira 43, and Bluebonnet were identified as resistant, significantly reducing white tip incidence. In Japan, resistance from the Asa-Hi cultivar was incorporated into other varieties as a valuable breeding source (Nishizawa, 1953).

More recent evaluations revealed broad resistance spectra. For example, among 14 Iranian genotypes, four were highly resistant, four moderately resistant, three moderately susceptible, and three highly susceptible (Jamali & Mousanejad, 2011). In a separate study involving 1003 cultivars from diverse ecological and geographical backgrounds, three were found to be immune, 10 highly resistant, 164 moderately resistant, and 826 susceptible or highly susceptible (Margarita et al., 1994).

Similar findings were reported globally. In the U.S., cultivars such as Arkansas Fortuna, Asahi, Bluebonnet, Hill Long Grain, Century 231, Rexoro, Nira, and Texas Patna were resistant, while Century Patna 231, Century 52, and Rexark were highly resistant (Cralley & Adair, 1949; Atkins & Todd, 1959). In Japan, Tosan 38 was highly resistant, Norin 43 and Norin 8 resistant, and Natsushimo and Norin-Mochi 5 very resistant (Goto & Fukatsu, 1956). In India, Chinoor and Gumartia were nearly immune, while Surmartia was tolerant (Dastur, 1936). In Italy, Carnaroli and Pierrot were highly resistant, while Rinaldo Bersani was resistant (Orsenigo, 1954).

Overall, identification and deployment of resistant rice cultivars are fundamental to reducing *A. besseyi* populations and minimizing the need for chemical interventions. Thus, resistant varieties constitute a key component of integrated management strategies, particularly in regions where the nematode is widespread.

5.6. Integrated Management Approaches

Integrated management strategies combining cultural, chemical, and biological measures provide effective control of *A. besseyi*. This approach exploits the synergistic effects of multiple methods to sustainably suppress nematode populations (Abd-Elgawad et al., 2025). Moreover, integrated management helps minimize environmental impacts and reduces the risk of resistance development.

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