

Morphological Characterization of the Infective Juvenile Stages of *Steinernema adamsi* Using Light and Scanning Electron Microscopy

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ABSTRACT

Entomopathogenic nematodes (EPNs) of the genus *Steinernema* are obligate insect parasites that inhabit soil ecosystems and form symbiotic associations with bacteria of the genus *Xenorhabdus*. Accurate identification of the nematodes is essential for their effective application in biological control programs. In the present study, we investigated the morphology of the infective juvenile (IJ) stage of *Steinernema adamsi*, a recently reported novel EPN species from Thailand, using compound light microscopy and scanning electron microscopy (SEM). The nematodes were previously identified by molecular analyses and were maintained in the laboratory through repeated infection cycles using *Galleria mellonella* as the insect host. Morphometric analysis showed that the IJs had a mean body length of 946.57 µm. SEM observations revealed that the lateral field of the IJ possesses eight distinct longitudinal ridges at the mid-body region. This study represents the first SEM-based description of the IJ stage of *S. adamsi*. The combined morphological observations presented here provide additional diagnostic information and contribute to more accurate identification of entomopathogenic nematodes.

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Authors' Contribution

JA designed the study, performed experiments, analyzed data, prepared figures and was involved with writing draft manuscripts. CS performed experiments and was involved with writing draft manuscripts. AD performed experiments and was involved with writing draft manuscripts. SP performed experiments and was involved with writing draft manuscripts. CH performed experiments and was involved with writing draft manuscripts. KJ performed experiments and was involved with writing draft manuscripts. AT performed experiments, provided materials and was involved with writing draft manuscripts. AV designed the study, performed experiments, analyzed data, managed projects and was involved with writing drafts and reviewing manuscripts. All authors read and approved of the final manuscript.

Key words

Biocontrol, Scanning electron microscope, *Steinernema*, Infective juvenile stage, Thailand, Morphology

INTRODUCTION

Entomopathogenic nematodes (EPNs) belonging to the genera *Heterorhabditis* and *Steinernema* are soil-dwelling nematodes that maintain mutualistic relationships with symbiotic bacteria, *Photorhabdus* and *Xenorhabdus*, respectively (Tarasco *et al.*, 2023; Liao *et al.*, 2025).

The efficacy of EPNs in controlling insect pests and insect vectors are influenced by both abiotic and biotic factors, with specific species characteristics playing a primary role (Lacey and Georgis, 2012; Thanwisai *et al.*, 2022; Shapiro-Ilan and Lewis, 2024; Pansri *et al.*, 2025). Consequently, accurate species identification is essential for effective biological control. However, the increasing number of described EPN species, together with morphological convergence among closely related taxa, complicates precise diagnosis (Půža and Machado, 2024). Resolving these taxonomic issues requires an integrative approach combining molecular data with multi-stage morphological analyses of infective juveniles (IJs), males, and females (Hominick *et al.*, 1997; Půža *et al.*, 2025). Among these developmental stages, IJs are particularly important for characterization. While conventional light microscopy (LM) remains efficient for observing overall body size,

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shape, and internal structures (such as the esophageal bulb), scanning electron microscopy (SEM) provides high-resolution information on external morphology. SEM reveals subtle diagnostic features, including cuticular patterns and cephalic amphid structures, which improve the accuracy of species delimitation.

Steinernema adamsi, a new entomopathogenic nematode from Thailand, was first described in 2024 by Baniya *et al.* This EPN was recovered from loam around the rhizosphere of a longan tree (*Dimocarpus* sp.) in Mueang Lamphun District, Thailand (Baniya *et al.*, 2024). Even though morphology of the IJs, male, and female of *S. adamsi* were described, limitation of the SEM on the IJs was lacking. Therefore, this study aims to investigate the morphology of IJs of *S. adamsi* by using compound microscopes and scanning electron microscopes. This will be baseline and useful for further identification of EPNs.

MATERIALS AND METHODS

Infective juvenile stage of entomopathogenic nematodes

The EPN isolate used in this study was previously collected (Ardpairin *et al.*, 2023). EPNs were maintained in the laboratory of the Department of Microbiology and Parasitology, Faculty of Medical Science, Naresuan University by using *Galleria mellonella* larvae as bait (Ardpairin *et al.*, 2023). The experimental study involved with invertebrate animals were approved by the Animal Care and Use Committee at Naresuan University (NU-AI631005). The *S. adamsi* (eALN11.5_TH) was maintained by infecting *G. mellonella* in the laboratory. The EPNs were previously molecularly identified based on sequencing of the ITS and 28S rDNA (Ardpairin *et al.*, 2023; Baniya *et al.*, 2024). To propagate the IJs, EPN isolates were re-infected with *G. mellonella* larvae. The modified white trap was performed to isolate the fresh IJs which were then cleaned with several changes of distilled water. The cleaned IJs were kept in the refrigerator with 13–16 °C.

Light microscopic study

Temporary fresh mounts were prepared to examine the morphology of the IJ stage of EPNs. A few IJ stages of EPN were transferred on a drop of distilled water on clean glass slide and covered with a clean coverslip. The prepared slides were flamed heat from a few seconds to stop moving the IJs of the EPNs. Their length of each EPN species (n= 20) was measured under light microscope (Olympus BX51, Tokyo, Japan).

Scanning electron microscopic study

For SEM examination, the IJs were washed five times

in sterile phosphate-buffered saline (PBS) for 3 min to get rid of impurities. The nematodes were then fixed in 4% glutaraldehyde in PBS for 24 h at 20 °C. After fixation, the nematodes were washed three times in PBS for 15 min. For post-fixation, 1% osmium tetroxide was used to fix the nematodes for 2 h. Dehydration was done in a series of alcohols for 10 min (ethyl alcohol: 30, 50, 70, 90, and 100%). After that the alcohol was changed to amyl acetate (ethyl alcohol: amyl acetate, 25: 75, 50: 50, 75: 25, 100% amyl acetate), 10 min each turn. The samples were dried at the critical point (Polaron Range/CPD 7501, UK) and coated with a 30 nm layer of gold palladium (Polaron Range/SC 7620, UK). The samples were observed in scanning electron microscope (LEO/LEO1450VP, Oberkochen, Germany) at the voltage of 15 kV.

RESULTS

Morphometric analysis of the IJs of *S. adamsi* (eALN11.5_TH) was done using light microscopy (n = 20; Supplementary Table SI). The average body length was $946.57 \pm 57.97 \mu\text{m}$, ranging from 856.50 to 1052.10 μm . The 95% confidence interval (919.44–973.70 μm) indicated high phenotypic stability in size distribution. Observations under light microscopy revealed that live IJs were enclosed within a cuticular sheath (Fig. 1A–B). The heat-relaxed IJs exhibited a straight to slightly curved posture. The lip region appeared smooth with a closed mouth,

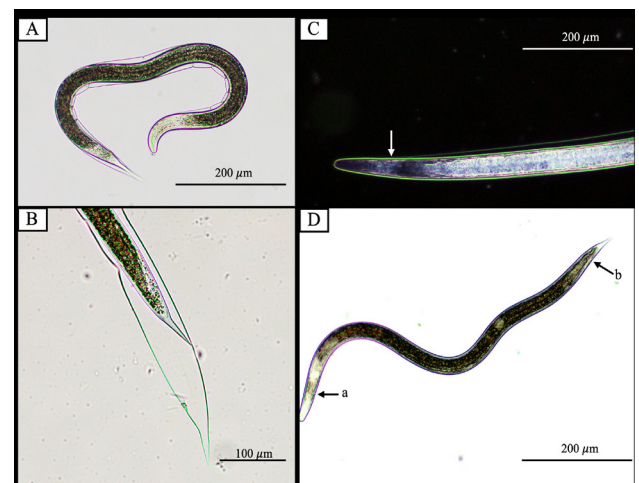


Fig. 1. Light microscopy (LM) micrographs of *Steinernema adamsi* (eALN11.5_TH) infective juveniles showing live individuals enclosed within a cuticular sheath (A); a conoid tail with a visible hyaline portion and pointed terminus (B); the mid-corpus region highlighting the excretory pore (white arrow) (C); and the posterior region illustrating the nerve ring (a) located above the basal bulb, a long straight rectum, and a distinct anus (b) (D).

which was confirmed by SEM observations revealing a completely sealed oral opening (Fig. 2A). The esophagus and intestine collapsed, with the intestinal lumen densely packed with fat globules (Fig. 1A). Key internal features included excretory pores (Fig. 1C) located near the mid-corpus region and a nerve ring situated slightly above the basal bulb (Fig. 1D). Although the lateral field pattern was clearly visible under LM, high-magnification SEM micrographs clearly revealed eight longitudinal lines in the lateral field (Fig. 2B). The posterior region featured a long, straight rectum and a distinct anus (Fig. 1D), which appeared as a closed transverse slit under SEM (Fig. 2C, D). The tail was conoid with a pointed terminus (Fig. 1B), and SEM analysis highlighted the gradual tapering toward a sharply pointed tip (Fig. 2C, D).

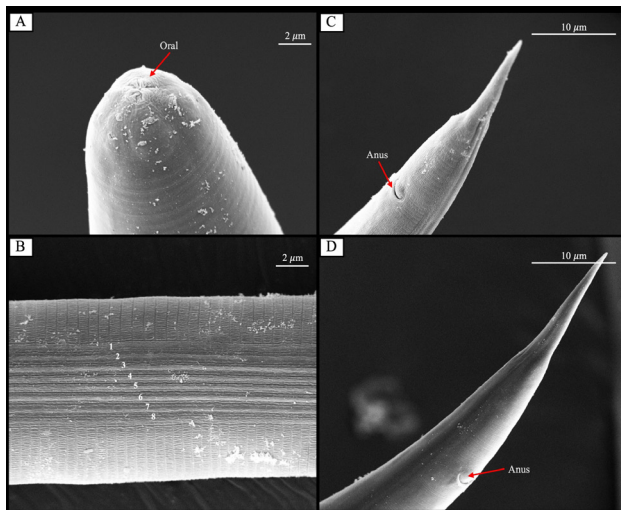


Fig. 2. Scanning electron microscopy (SEM) micrographs of *Steinernema adamsi* (eALN11.5_TH) infective juveniles revealing a smooth lip region with a completely sealed oral opening (red arrow) (A), the lateral field with eight distinct longitudinal lines at high magnification (B), and the posterior region highlighting the anus (red arrow) as a closed transverse slit with a gradually tapering tail to a sharply pointed tip (C–D).

DISCUSSION

Steinernema adamsi n. sp., a new entomopathogenic nematode from Thailand, belongs to the ‘Longicaudatum’ clade based on phylogenetic analyses. Its taxonomic identity is supported by ITS and 28S D2/D3 rDNA sequence data (Baniya *et al.*, 2024). In *Steinernema* taxonomy, IJs total body length (TBL) is an important diagnostic character that varies among phylogenetic groups. The IJs of *S. adamsi* (isolate eALN11.5_TH; mean length 946.57 µm) belong to the medium-to-long body

size range characteristic of species in the Longicaudatum clade. Compared with the long-bodied species of the ‘Glaseri’ group, the largest members of the genus with a mean TBL ≥ 1000 µm, including *S. khuongi* (mean 1066 µm), *S. glaseri* (mean 1,130 µm), and *S. cubanum* (mean 1283 µm) (Cimen *et al.*, 2015; Stock *et al.*, 2019), *S. adamsi* is noticeably shorter. In contrast, *S. adamsi* is clearly larger than members of the ‘Carpocapsae’ group, which are generally smaller in body size (often <600 µm) (Sharma *et al.*, 2022). In addition to body size and lateral field pattern, some *Steinernema* species possess distinctive morphological features that clearly separate them from other clades. For example, species of the ‘Bicornutum’ clade are characterized by unique cephalic “horn-like” structures (Sharma *et al.*, 2022). A representative species, *S. biddulphi* (mean IJ length 663 µm), possesses a lateral field with six ridges at the mid-body (Cimen *et al.*, 2016).

According to recent taxonomic updates, the Longicaudatum clade currently includes *S. longicaudatum*, *S. guangdongense*, *S. hermaphroditum*, *S. lamjungense*, *S. pui*, *S. taiwanensis* (Půža and Machado, 2024), and *S. adamsi* (Baniya *et al.*, 2024). Morphometric analysis of the IJs in this study revealed that *S. adamsi* has a mean body length of 946 µm (range: 856.5–1052.1 µm), which is intermediate among members of the Longicaudatum clade (Table I). It is notably shorter than *S. longicaudatum* (mean IJ length 1043 µm), *S. pui* (mean IJ length 1004 µm), *S. taiwanensis* (mean IJ length 1012 µm), and *S. guangdongense* (mean IJ length 1055 µm) (Stock *et al.*, 2001; Qiu *et al.*, 2004, 2011; Tseng *et al.*, 2018). However, the body size of *S. adamsi* overlaps with the reported ranges of *S. hermaphroditum* (mean IJ length 928.5 µm) (Stock *et al.*, 2004) and *S. lamjungense* (mean IJ length 832 µm) (Khatri-Chhetri *et al.*, 2011). In addition, its symbiotic bacteria were proposed as a novel species as *Candidatus Xenorhabdus lamphunensis* (Heppert *et al.*, 2024). Moreover, *S. adamsi* showed potential to control the larvae of *Helicoverpa zea* in both laboratory and field conditions (Glover *et al.*, 2025).

The original description of *S. adamsi* was based on integrative taxonomic approaches, including whole-genome data and LM observations (Baniya *et al.*, 2024), but SEM observations were not reported. In the present study, SEM examination showed that *S. adamsi* (eALN11.5_TH) possesses eight equidistant longitudinal ridges at the mid-body, consistent with the lateral field pattern reported for other species of the Longicaudatum clade (Stock *et al.*, 2001, 2004; Khatri-Chhetri *et al.*, 2011; Qiu *et al.*, 2011; Tseng *et al.*, 2018).

Morphologically, the IJ of *S. adamsi* (eALN11.5_TH) is characterized by a rounded cephalic region continuous with the body contour and a tightly closed oral aperture.

Table I. Comparative SEM characteristics of infective juveniles of *Steinernema adamsi* and closely related species.

Species	IJ length (µm)	Lateral field ridges	Tail shape	Distinguishing SEM traits
<i>S. pui</i> (Qiu <i>et al.</i> , 2011)	900–1120	8 ridges at mid-body, reducing to 5 and 2 posteriorly	Short, attenuate; hyaline region ~46%	Rounded, slightly truncated head; distinct slit-shaped amphids
<i>S. taiwanensis</i> (Tseng <i>et al.</i> , 2018)	983–1045	Ridge formula: 2–6–7–8–2	Elongate, no dorsal constriction; hyaline region ~54%	Smooth labial region; amphids inconspicuous
<i>S. hermaphroditum</i> (Stock <i>et al.</i> , 2004)	700–1100	8 equidistant longitudinal ridges	Conoid, pointed tip; hyaline region ~50%	Head tapering from pharynx; dorsally displaced bacterial pouch
<i>S. lamjungense</i> (Khatri-Chhetri <i>et al.</i> , 2011)	690–950	Ridge formula: 2–6–7–8–3–2	Attenuate, blunt tip; hyaline region >50%; slight dorsal constriction	Distinct cuticular annulations; slightly offset head; prominent slit-shaped amphids; pore-like phasmid
<i>S. longicaudum</i> (Stock <i>et al.</i> , 2001)	929–1170	8 equidistant longitudinal ridges	Subconoid, finely pointed tip; hyaline region ~50%	Finely annulated cuticle; rounded head continuous with body; phasmids at 30–40% of tail length
<i>S. guangdongense</i> (Qiu <i>et al.</i> , 2004)	987–1145	Ridge formula: 2–7–8–7–4–2	Attenuate, gradual taper; dorsal constriction; hyaline region ~57.5%	Prominent transverse striations; rounded head continuous with body; amphids inconspicuous
<i>S. adamsi</i>	856–1052	8 equidistant longitudinal ridges	Conoid, pointed tip	Distinct cuticular annulations; rounded head continuous with body; tightly closed oral aperture

The body shows distinct cuticular annulations, and the mid-body lateral field consists of eight evenly spaced longitudinal ridges. The tail is conoid, gradually tapering to a pointed terminus. However, the IJs of species within the *Steinernema* Longicaudatum clade exhibit highly conserved external morphology (Table I). They share many common SEM features, including a rounded cephalic region, a distinctly annulated cuticle, a lateral field with eight longitudinal ridges at the mid-body, and a conoid to attenuate tail. Nevertheless, high-resolution SEM observations show that the transition patterns of these ridges toward the anterior and posterior ends differ among species. For example, the lateral field formulas are 2–7–8–7–4–2 in *S. guangdongense*, 2–6–7–8–2 in *S. taiwanensis*, and 2–6–7–8–3–2 in *S. lamjungense*. On the other hand, *S. pui*, *S. hermaphroditum*, *S. longicaudum*, and *S. adamsi* (eALN11.5_TH) maintain simpler arrangements where the mid-body region is consistently characterized by eight equidistant longitudinal ridges. Furthermore, the caudal morphology and hyaline occupancy of the IJs provide important information to identify the species within this clade. In terms of hyaline proportions, *S. guangdongense* shows the longest zone at 57.5%, followed by *S. taiwanensis* (54%) while *S. hermaphroditum* and *S. longicaudum* share an intermediate occupancy of approximately 50%. Conversely, *S. pui* and *S. adamsi* (eALN11.5_TH) exhibit the shortest hyaline zones, both occupying around 46% of the tail length (Stock *et al.*, 2001, 2004; Khatri-Chhetri *et al.*, 2011; Qiu *et al.*, 2004, 2011;

Tseng *et al.*, 2018; Baniya *et al.*, 2024). These findings indicate that within this closely related clade, relying on a single morphological character is insufficient for species identification. Instead, the differentiation of these species requires an integrated diagnostic approach that combines SEM-based ridge transition variations with specific morphometric proportions, such as hyaline occupancy.

In summary, the morphometric and SEM data presented here provide preliminary baseline information for *S. adamsi* (eALN11.5_TH) within the Longicaudatum clade. However, these findings indicate that considering only the mid-lateral lateral features is insufficient to reliably distinguish these species. Therefore, additional morphological characteristics and developmental stages, including mature males and females, must be considered.

DECLARATIONS

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IRB approval and Ethical statement

Experiments related with insects were approved by the Animal Care and Use Committee at Naresuan University (NU-AI631005) while the experiments related with the biological specimens and safety were approved by the Naresuan University Institutional Biosafety Committee (NUIBC MI 63-11-52).

Supplementary material

There is supplementary material associated with this article. Access the material online at: <https://dx.doi.org/10.17582/journal.pjz/20260327111816>

Generative AI and AI assisted technology statement

The authors declare that no generative AI and AI assisted technology was used in the creation of this manuscript.

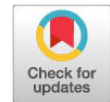
Statement of conflict of interest

The authors have declared no conflict of interest.

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Supplementary Materials

Morphological Characterization of the Infective Juvenile Stages of *Steinernema adamsi* Using Light and Scanning Electron Microscopy

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Supplementary Table SI. Body length measurements of infective juveniles (IJs) of *Steinernema adamsi* (eALN11.5_TH) based on light microscopy observations (n = 20).

No.	Length of the infective juvenile stage (μm)
1	898.5
2	988.2
3	965.2
4	897.3
5	1023.7
6	887.2
7	975
8	964.6
9	856.5
10	889.5
11	997.8
12	1052.1
13	1003.5
14	875.4
15	885.9
16	964.8
17	871
18	978.8
19	988.9
20	967.5
Average	946.57
S.D.	57.97237182
95% CI	27.13190519

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