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Research article

The hidden burden: morphological, histological, and pathological features of *Paradujardinia halicoris* in dugongs (*Dugong dugon*) from the Andaman coast of Thailand

Peerapon Sornying[1], Domechai Kaewnoi[1], Narissara Keawchana[1], Piyarat Khumraksa[2], Sattaya Ruangpoon[2], Santi Ninwat[2], Pimwarang Sukkarun[3], Apinya Arnuphapprasert[3] and Watcharapol Suyapoh[1,4,*]

[1]*Department of Veterinary Science, Faculty of Veterinary Science, Prince of Songkla University, Songkhla 90110, Thailand.*
[2]*Marine and Coastal Resources Research Center (Lower Andaman Sea), Trang 92150, Thailand.*
[3]*Faculty of Veterinary Science, Rajamangala University of Technology Srivijaya, Na-khonsithammarat 80240 Thailand*
[4]*Dugong and Seagrass Research Station, Prince of Songkla University, Songkhla 90110, Thailand*

Abstract

Paradujardinia halicoris is a large gastrointestinal nematode that is commonly reported in dugongs (*Dugong dugon*). Although often considered non-pathogenic, heavy infections have been associated with significant gastrointestinal pathologies. However, detailed studies on the parasite's morphology, histology, and pathological effects remain limited, particularly in dugongs in Thai waters. This study aimed to investigate the prevalence, morphological features, and pathological impact of *P. halicoris* on stranded dugongs along the coast of Thailand. Between January 2019 and May 2025, 166 Dugong carcasses were necropsied following standardized postmortem protocols. The gross lesions and parasite burden were recorded for each case. The recovered nematodes were preserved and examined using stereomicroscopy, scanning electron microscopy (SEM), and histological techniques to characterize their external and internal morphology. Pathological lesions were evaluated for severity and anatomical distribution, and parasitic occurrence was analyzed in relation to the biological data. Overall, 62.0% (103/166) of necropsied dugongs were infected with gastrointestinal nematodes, with the highest prevalence observed in juveniles and sub-adults. *P. halicoris* was predominantly localized in the stomach but also extended into the intestines, with worm burdens ranging from 4 to 687 individuals. Gross lesions included mucosal erosion, ulceration, hemorrhage, abscess formation, and intestinal obstruction. SEM revealed detailed surface structures such as lip morphology, interlabia, amphids, and sex-specific features. Histological examination clearly demonstrated the internal structures including the esophagus, reproductive tract, musculature, and pseudocoelom. This study provides the first detailed account of *P. halicoris* pathology, host biology, and parasitic morphology in Thai dugongs, emphasizing the importance of parasitic surveillance for marine mammal health and conservation.

Keywords: Dugong, Gastrointestinal nematode, Nematode morphology, *Paradujardinia halicoris*, Pathology

*Corresponding author: Watcharapol Suyapoh. Department of Veterinary Science, Faculty of Veterinary Science, Prince of Songkla University, Songkhla 90110, Thailand. E-mail: watcharapol.s@psu.ac.th.

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INTRODUCTION

Dugong (*Dugong dugon*) is a herbivorous marine mammal and the sole extant species within the family Dugongidae, order Sirenia (Domning, 2009). It is distributed throughout tropical and subtropical coastal waters from East Africa to New Caledonia and latitudinally from Okinawa Island, Japan, to northern Australia, including the territorial waters of Thailand (Panyawai and Prathep, 2022). In Thailand, populations inhabiting the Gulf of Thailand have been reported to experience varying levels of inbreeding, which may warrant special conservation measures (Poommouang et al., 2022). The species is afforded the highest level of legal protection in Thailand and is recognized as a flagship species for marine biodiversity conservation and habitat protection (Kingdom of Thailand, 2019).

Recent investigations in Thai waters have revealed that natural causes, particularly infectious diseases including viral, bacterial, and parasitic infections are significant contributors to marine mammal strandings (Daochai et al., 2024; Sukkarun et al., 2025; Eiamcharoen et al., 2025). Among these, helminth infections remain one of the most neglected tropical diseases and pose substantial health threats to both terrestrial and aquatic fauna in tropical regions (Al-Amin and Wadhwa, 2023). Nematode infections, especially those caused by members of the Ascarididae family, can lead to notable pathogenic consequences, particularly under conditions of heavy parasitic burden (Wolstenholme et al., 2024). These nematodes exert pathogenicity through various mechanisms, including mechanical damage and release of excretory/secretory (E/S) products that modulate host immune responses (de Almeida Lopes et al., 2024).

In dugongs, the large ascarid nematode *Paradujardinia halicoris*—formerly known as *Ascaris halicoris* (Owen, 1833), *Dujardinia halicoris* (Owen, 1833) Baylis, 1920, and *Dujardinascaris halicoris* (Owen, 1833) Baylis, 1947, has been frequently reported (Anand et al., 2018; Rajesh et al., 2023). Although often considered non-pathogenic, this species has been associated with gastrointestinal lesions, including severe mucosal erosion, ulceration, hemorrhage, and transmural abscesses in some cases (Woolford et al., 2015). Although *P. halicoris* has been documented in stranded dugongs in Thailand (Waikagul et al., 1998), comprehensive data on its prevalence, pathological effects, and diagnostic characteristics within Thai populations are lacking. This deficiency has been highlighted as one of the key research gaps in Dugong knowledge in Thailand (Panyawai and Prathep, 2022).

Therefore, this study aimed to investigate the occurrence, morphological characteristics, and pathological impact of *P. halicoris* infection in dugongs stranded along the Thai coastline. This study provides foundational knowledge essential for understanding parasite-associated morbidity and supports ongoing conservation and health monitoring efforts for this vulnerable marine species.

MATERIALS AND METHODS

Ethical clearance and sample use authorization

All procedures involving the use of archived animal tissues were performed in compliance with institutional guidelines and relevant regulations. The experimental protocol was reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) of Prince of Songkla University (Approval No. MHESI 68014/1236). The committee classified the study as exempt under the criteria of Exempt Determination Research. Tissue samples were collected and used with official permission from the Department of Fisheries of Thailand (MOAC Document No. 0510.5/12652) issued in accordance with Section 73(1) of the Wildlife Preservation and Protection Act, B.E. 2562 (2019).

Study area and sample collection

This study was conducted using dugong (*Dugong dugon*) carcasses that were stranded along the coastlines of four provinces bordering the Andaman Sea in southern Thailand Phang Nga, Trang, Satun, and Krabi from January 2019 to May 2025. All necropsies were performed by trained veterinarians from the Andaman Coastal Research Center (Lower Andaman Sea), Department of Marine and Coastal Resources (DMCR), following standardized marine mammal postmortem protocols. Dugong carcasses in an advanced state of decomposition were excluded from the study to ensure the reliability of the gross and histopathological observations.

For each suitable carcass, biological and ecological data were recorded by the DMCR team and subsequently shared with the researchers for further analysis. Collected data included the date of discovery and necropsy, observed stranding location, geographic coordinates (latitude and longitude), sex, body length, chest girth (m), body weight (kg), presence of parasites, anatomical location of parasite infestation, and number of parasites recovered. This comprehensive dataset enabled the evaluation of parasitic burden and associated pathology in relation to biological parameters such as age, sex, and body condition of the stranded dugongs.

The age of each dugong was estimated and categorized into five age classes based on body length and chest girth, following the criteria established by (Marsh, 1980). The categories included: newborn calves (NB), dependent calves (C), juveniles (J), sub-adults (SA), and adults (A). Specifically, individuals less than 1.25 m in length and with a chest girth less than 120 cm were classified as newborn calves. Dependent calves ranged from 1.25 to less than 1.80 m in length and from 120 to less than 145 cm in chest girth. Juveniles were 1.80 to less than 2.20 m in length, with chest girths of 145 to less than 165 cm. Sub-adults measured 2.20 to less than 2.60 m with chest girths of 165 to less than 185 cm. Adults were defined as individuals ≥2.60 m in length and 185 cm in chest girth.

Parasite collection and identification

All parasitic specimens recovered during necropsy were carefully collected from the gastrointestinal tracts of dugongs and immediately fixed in 10% neutral buffered formalin to preserve their morphological integrity. The samples were stored in a dark room at room temperature to prevent photodegradation. In this study, nematodes preserved from the parasite stock were used for morphological examination. A total of 20 nematode specimens consisting of 5 males and 15 females were randomly selected for detailed morphological analysis. These specimens were submitted to the Faculty of Veterinary Science, Prince of Songkla University, for species identification and further analysis.

To evaluate infection intensity, worm burden was classified following criteria adapted from Hall and Holland (2000), originally developed for Ascaris lumbricoides. Based on these guidelines, the infection levels of *P. halicoris* were defined as mild (1–50 worms), moderate (51–100 worms), and severe (>101 worms). This classification provides a standardized framework for quantifying parasitic burden across individuals.

Morphological characterization of the nematodes was performed using three complementary microscopy techniques: (1) stereomicroscopic examination, to observe gross morphological features such as body shape, size, and external structures; (2) scanning electron microscopy (SEM), to investigate fine surface details including lip structure, cuticular ornamentation, and reproductive openings; and (3) histological examination, using paraffin-embedded sections stained with hematoxylin and eosin (H&E), to assess internal anatomical features such as the digestive and reproductive systems. These combined approaches allowed for accurate morphological identification and differentiation between the sexes.

Stereomicroscopic examination

Prior to examination, preserved 10 specimens, consisting of 3 males and 7 females were gently rinsed in distilled water to remove residual fixative and surface debris. Stereomicroscopic examination was performed using a Nikon SMZ445 Model C-LEDS Zoom Stereo Microscope (Nikon, Japan). Each nematode was placed in a glass Petri dish containing a small volume of distilled water to enhance the visibility of surface structures. Specimens were oriented and observed under low magnification (ranging from 7.5× to 80×) to assess gross morphological features.

The key morphological characteristics used for preliminary identification included body shape and size, morphology of the anterior end (e.g., lips, tooth-like structures), posterior end structures (e.g., tail shape, spicules in males, and valva in females), and cuticular ornamentation (e.g., striations) (Waikagul et al., 1998). Images were captured at 20X magnification using a smartphone camera under controlled lighting conditions. The stereomicroscopic data were then compared with standard taxonomic keys and reference literature to determine the genus or species level.

Scanning electron microscopic examination

Representative nematode specimens preserved in 10% neutral buffered formalin were selected based on the key morphological features observed under stereomicroscopy. The preparation for scanning electron microscopy (SEM) followed the protocol described by Hashemnia et al. (2024). Briefly, the specimens were gradually dehydrated through a graded ethanol series (30%, 50%, 70%, 90%, and absolute ethanol), with each step lasting 15–30 minutes. Complete dehydration was essential to prevent structural distortion during critical point drying with liquid CO_2 using an Autosamdri-931 critical point dryer (Tousimis, USA.). Dried nematodes were mounted on aluminum stubs using double-sided conductive carbon adhesive tape. The mounted samples were coated with a fine conductive layer to prevent charging under the electron beam. Gold coating of 25 nm was performed using the SPI-Module line of modular sputter coaters and carbon coaters (SPI Supplies, USA). Surface ultrastructural features were examined using a field emission scanning electron microscope (FE-SEM; Apreo-thermoscientific, Netherlands) operating in the high vacuum mode. SEM imaging was performed at accelerating voltages ranging from 5 to 15 kV. Digital micrographs were acquired at various magnifications to document detailed cuticular features, including transverse striations, lateral alae, cephalic papillae, lip structures, amphids, and male copulatory structures such as spicules.

Study the parasite histology

Histological examination of the internal morphology was performed on 10 preserved nematode specimens, comprising two males and eight females. Sample processing followed standard histological protocols as described by Suyapoh et al. (Suyapoh et al., 2025). Briefly, the specimens were fixed in 10% neutral buffered formalin to preserve the cellular architecture. After fixation, the tissues were dehydrated through a graded ethanol series, cleared in xylene to eliminate residual alcohol, and embedded in paraffin wax to maintain structural integrity. Paraffin-embedded samples were sectioned at 4 µm a thickness using a rotary microtome. Tissue sections were stained with hematoxylin and eosin (H&E) to evaluate their general morphology. The stained slides were mounted with coverslips for light microscopic examination. Morphological observations and measurements were conducted using a Nikon ECLIPSE Ni-U advanced upright microscope equipped with a high-resolution digital video camera (Nikon, Japan). Image capture and analysis were performed using the NIS-Elements Imaging Software (Nikon). Illustrations were generated from the captured micrographs and digitally processed to enhance the clarity and detail for taxonomic documentation.

Statistical Analysis

The prevalence of *P. halicoris* infection was calculated for each age class as the proportion of infected individuals out of the total examined, with 95% confidence intervals (CIs) estimated using the Clopper–Pearson exact method. Data on infection prevalence across age classes were analyzed using the Chi-squared test to assess whether age was associated with differences in *P. halicoris* infection rates. The test compared the number of infected and uninfected individuals within each age group. When the Chi-square test indicated statistical significance, pairwise post-hoc comparisons between age classes were conducted using Fisher's exact test, with Bonferroni correction applied to adjust for multiple testing. Statistical p-value of <0.05 was considered statistically significant. All statistical analyses were performed using SPSS version 23.0 (IBM Corp., Armonk, NY, USA).

RESULTS

Necropsied animals and biological data

Between January 2019 and May 2025, 166 dugongs (*Dugong dugon*) were necropsied at the Marine and Coastal Resources Research Center (Lower Andaman Sea), located in Trang Province, Thailand. Dugong carcasses in an advanced state of decomposition were excluded from the study to ensure the reliability of pathological assessments. Each individual was categorized by age class based on standard morphological criteria. Of the total examined dugongs, 14 were identified as new-born calves (NB), 12 as dependent calves (C), 30 as juveniles (J), 47 as sub-adults (SA), and 57 as adults (A). Additionally, six individuals could not be assigned to a specific age class due to insufficient morphological data and were therefore classified as unknown (Unk). This classification provided a comprehensive overview of the age structure of the examined dugong population.

Among the 166 dugongs examined, 103 individuals (62.0%) were infected with gastrointestinal nematodes. Infections were detected across all age classes, with prevalence rates of 28.6% (4/14; 95% CI: 8.4–58.1) in new-born calves, 50.0% (6/12; 95% CI: 21.1–78.9) in dependent calves, 80.0% (24/30; 95% CI: 61.4–92.3) in juveniles, 72.3% (34/47; 95% CI: 57.4–84.4) in sub-adults, and 61.4% (35/57; 95% CI: 47.6–74.0) in adults, while no infections were detected in six individuals of unknown age (95% CI: 0.0–45.9). A chi-square test revealed a statistically significant difference in infection prevalence among age classes ($\chi^2 = 23.44$, df = 5, $p < 0.001$), indicating that age is an important factor that influences susceptibility to gastrointestinal nematode infection. Overall, these findings demonstrated a high prevalence of infection in the population, particularly among juveniles and sub-adults. A summary of the infection status by age class is presented in Table 1.

Table 1 Age classification and gastrointestinal nematode infection status of necropsied dugongs (*Dugong dugon*) from the Lower Andaman Sea, Thailand (January 2019 – May 2025; n = 166).

Age class	Total examined	Infected (n)	Infected (%)	95% CI
New-born calf (NB)	14	4	28.6%	8.4 – 58.1%
Dependent calf (C)	12	6	50.0%	21.1 – 78.9%
Juvenile (J)	30	24	80.0%	61.4 – 92.3%
Sub-adult (SA)	47	34	72.3%	57.4 – 84.4%
Adult (A)	57	35	61.4%	47.6 – 74.0%
Unknown (Unk)	6	–	–	0.0 – 45.9%
Total	**166**	**103**	**62.0%**	

Necropsy revealed that gastrointestinal nematode infection in dugongs was associated with a wide range of pathological severities. Adult nematodes are primarily localized in the gastrointestinal tract but were also capable of migrating to other organs or orifices, leading to mechanical damage and luminal obstruction. Among the 103 infected dugongs, 60 (58.3%) harbored nematodes exclusively in the stomach, whereas only three (2.9%) had infections confined solely to the intestinal tract. Notably, 40 individuals (38.8%) exhibited widespread infestations involving multiple regions of the gastrointestinal system, including the stomach, small intestine, large intestine, and cecum (Figure 1ai-iv).

Parasite burden varied considerably among cases. The minimum number of nematodes recorded in a single individual was four, whereas the maximum number was 687 worms within the stomach. These findings indicate that the stomach is the most common site of nematode localization; however, extensive infections involving multiple regions of the gastrointestinal tract are relatively common.

Pathological lesions associated with nematode infection in dugongs ranged from mild to severe, depending on the intensity of infection. In cases of mild infection, significant pathological changes were not commonly observed. Worms were often seen loosely distributed within the ingesta, particularly in the stomach, without causing overt tissue damage. Some nematodes migrated in and out of the stomach and proximal duodenum through the pyloric orifice (Figure 1ai). In other instances, worms in the stomach without any associated mucosal damage, indicating impaction without overt pathology (Figure 1aii). This phenomenon may be associated with immune modulation during chronic infections, in which the host exhibits a subdued inflammatory response. Clinically, such cases may present with signs of stomach spasm or discomfort despite the absence of overt histopathological lesions. In contrast, moderate to severe infections were frequently associated with acute gastrointestinal lesions, including mucosal erosion, ulceration, congestion, and hemorrhage (Figure 1avi–vii). In cases of heavy or superinfection, large aggregates of worms formed compact, ball-like clusters that obstructed the intestinal lumen, resulting in segmental obstruction (Figure 1aiii–iv). The most frequently observed gastrointestinal complications include intestinal obstruction, volvulus, and intestinal perforation. In certain cases, the infection progressed to a transmural abscess formation within the intestinal wall (Figure 1av). In one particularly severe case, nematodes were found penetrated from the stomach into the peritoneal cavity, leading to diffuse peritonitis.

Parasite identifications

External morphology

Based on gross and stereomicroscopic examinations, the body of *P. halicoris* is elongated, cylindrical, and encased in a thick cuticle with prominent transverse striations extending along its entire length. In males, the body measured approximately 8.80 ± 0.29 cm in length and 2.59 ± 0.88 mm in width, whereas in females, it measured 12.38 ± 1.30 cm in length and 3.16 ± 1.23 mm in width (Figure 1bi). The anterior end featured a terminal mouth surrounded by three well-developed lips with distinct interlabia and a lack of teeth (Figures 1bii–iii). In males, the lips measured approximately 301.30 ± 7.35 μm in length and 371.70 ± 25.73 μm in height, while in females, the corresponding measurements were 268.65 ± 41.67 μm and 446.75 ± 70.71 μm, respectively. The male tail was compressed at the level of the cloacal aperture and tapered to a pointed tip with a slight ventral concavity. A pair of unsheathed spicules were present (Figure 1biv). In females, the vulva was located ventrally and appeared as a distinct slit-like opening (Figure 1bv).

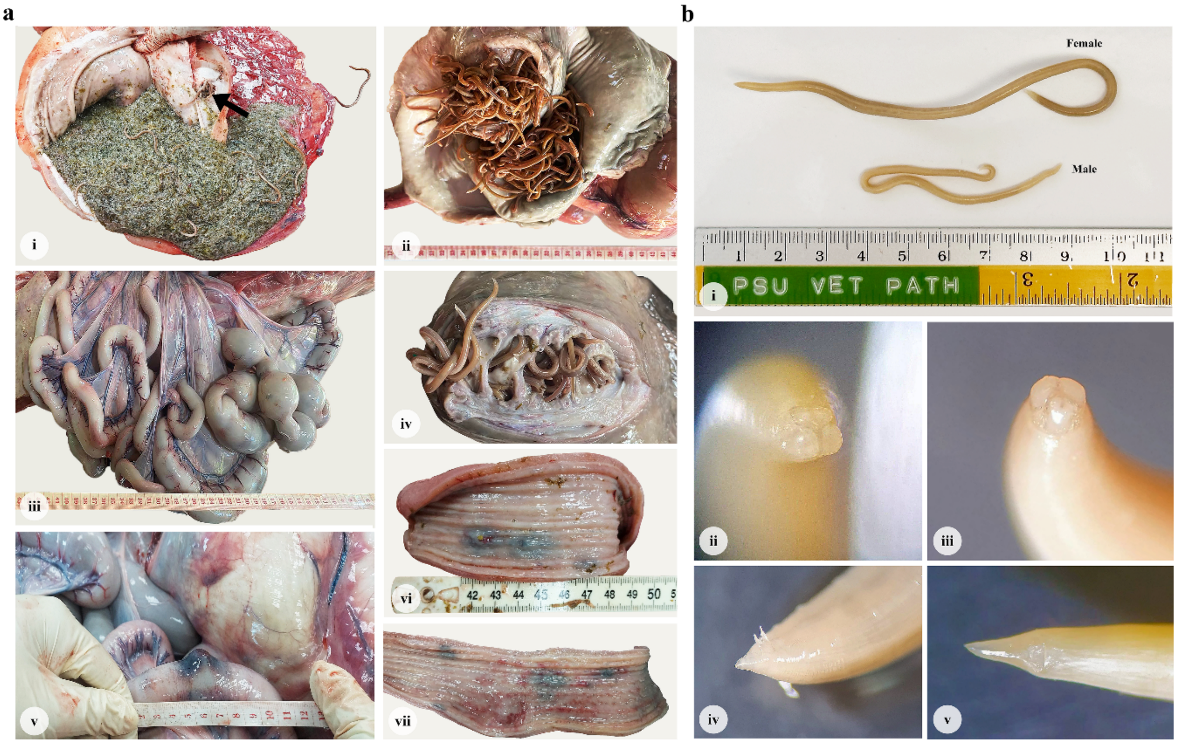

Figure 1 Pathological gross lesions associated with *Paradujardinia halicoris* infection and morphological characteristics of the nematode in dugongs from Thailand's Andaman Sea coast. (a) Pathological lesions in the gastrointestinal tract of dugongs associated with *P. halicoris* infection. (i) Light infection showing nematodes migrating between the stomach and proximal duodenum through the pyloric orifice (arrow). (ii) Accumulated nematodes in the stomach without overt mucosal damage. (iii–iv) Severe worm aggregation forming ball-like masses obstructing the intestinal lumen, resulting in segmental intestinal obstruction. (v) Thick-walled conical transmural abscess associated with chronic heavy infection. (vi–vii) Mucosal lesions including erosion, ulceration, congestion, and hemorrhage; (b) Gross examination and stereomicroscopic views of *P. halicoris*. (i) Comparative size of male and female worms showing marked sexual dimorphism; females are larger than males. (ii) En face view of the anterior end displaying three well-developed lips with interlabia. (iii) Lateral view of the anterior end showing lip arrangement and terminal mouth. (iv) Posterior end of a male showing a pointed tail with slight ventral concavity and paired unsheathed spicules. (v) Ventral view of a female tail exhibiting a slit-like vulvar opening.

Scanning electron microscopy (SEM)

Scanning electron microscopy (SEM) revealed that, in the en face view (Figure 2a), the dorsal lip (d.lip) appeared triangular, whereas the subventral lips (sv.lip) were oval. In both the lateral and anterolateral views (Figures 2b–c), the lips were observed to have slightly narrowed bases, which provided space for broad-based, triangular interlabia (t.ilb.) (Figure 2c). Dorsolateral papillae (dl.p.) and ventral papillae (v.p.) were clearly visualized using SEM (Figures 2b–c, white arrowheads). Additionally, a small, indistinct amphid (amp.) was located on the dorsolateral surface of the subventral lips (Figure 2c; black arrowhead). The lips were longer than they were wide and distinctly separated from the body by a marked constriction. The lips were interlocked via oral grooves, and two tooth-like projections (t.p.) were noted at the mid-lateral margins of the lips. A prominent structure was also observed at the base of the lip (Figure 2d, white arrow). The mouth opening was terminal and triangular (Figure 2d) and connected to the proximal esophageal opening (e.o.), which occasionally contained ingested material (igt.) (Figure 2e).

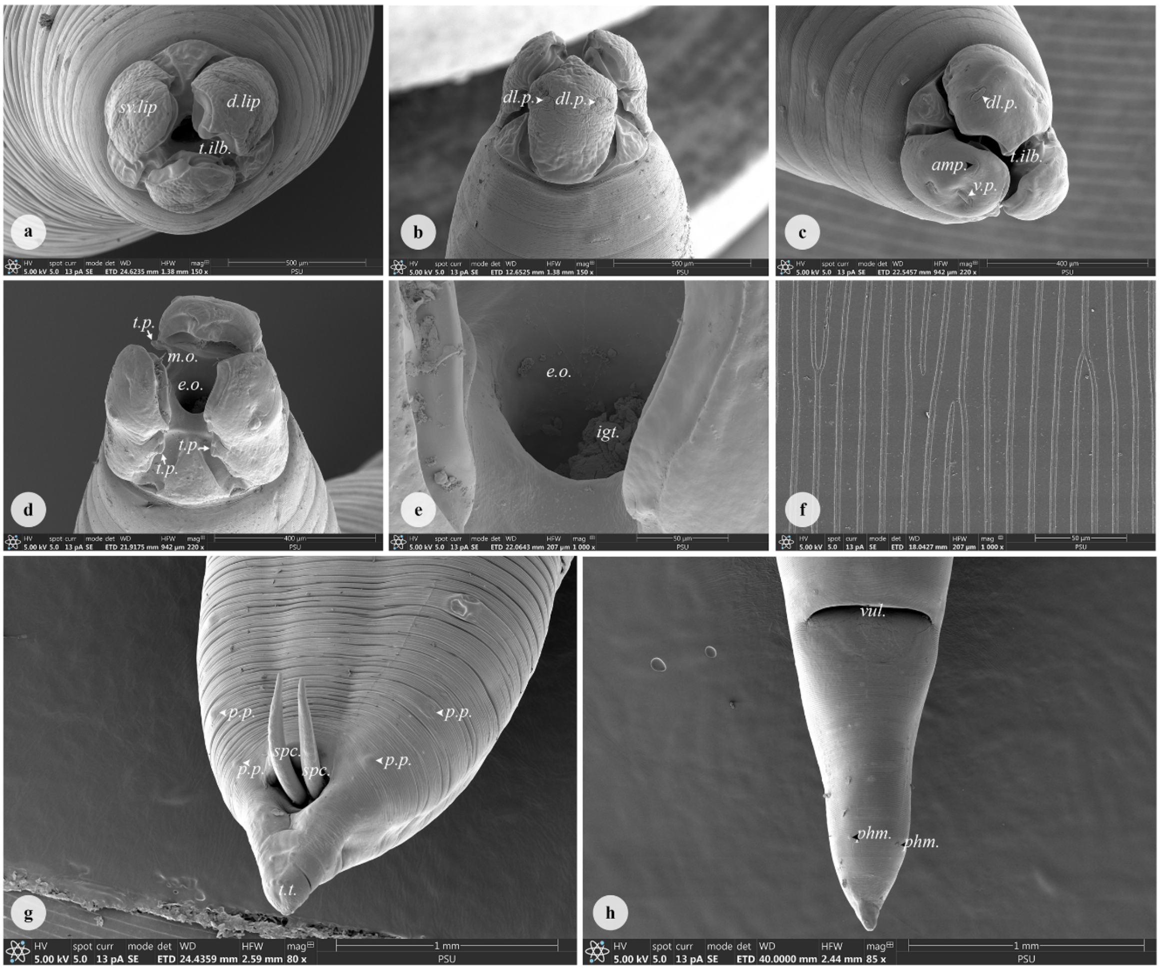

Figure 2 Scanning electron micrographs of *Paradujardinia halicoris* from dugongs (*Dugong dugon*) along Thailand's Andaman coast. (a) En face view of lips and interlabia. (b) Lateral view showing dorsolateral and ventral papillae. (c) Anterolateral view showing amphid and interlabia. (d) Oblique view of mouth with tooth-like projections and lip base structure. (e) Esophageal opening with ingested material. (f) Body surface with pseudosegmented cuticle. (g) Male tail showing spicules, ventrolateral and terminal papillae. (h) Female tail showing vulva and phasmids. Abbreviations: d.lip, dorsal lip; sv.lip, subventral lip; t.ilb, interlabia; dl.p., dorsolateral papillae; v.p., ventral papillae; amp., amphid; t.p., tooth-like projection; m.o., mouth opening; e.o., esophageal opening; igt., ingesta; spc., spicules; t.t., tail tip papillae; p.p., papillae; vul., vulva; phm., phasmids.

The body surface of *P. halicoris* was covered by a smooth, tough, and elastic cuticle exhibiting prominent transverse striations, which imparted a pseudosegmented appearance on the worm. These pseudosegmentations appeared either as single bands or branching structures (Figure 2f). The size and spacing of the pseudosegmented striations varied along the body; they were narrower in the anterior region and progressively widened toward the mid- and posterior regions.

In males, the tail appeared compressed at the level of the cloacal aperture and tapered to a pointed tip with slight ventral concavity. Two pairs of additional papillae were present on each side of the ventrolateral surface near the posterior margin of the cloacal aperture. Two smaller pairs of papillae were located near the tip of the tail (t.t.), and a pair of phasmids was observed at an intermediate position between the four posterior pairs of papillae (p.p.) (Figure 2g, white arrowhead). A pair of unsheathed spicules (spc.), each measuring 364.03 ± 88.37 μm in length, was also identified (Figure 2g). In females, the vulva (vul.) appeared as a slit-like opening located ventrally at approximately one-third of the body length from the anterior end (Figure 2h). The vulvar length was approximately 637.37 ± 93.43 μm. Pair of phasmids (phm.) was observed laterally on the posterior fifth of the tail, which was positioned distal to the anus (Figure 2h, black arrowhead).

Internal morphology

Histological examination of *P. halicoris* revealed distinct anatomical features in different body regions. In the anterior body sections, the internal structure included prominent lips (lip). bearing cuticular tooth-like projections (c.t.p.) and a centrally located foregut or esophagus (eso.) (Figure 3a–b). The oral opening was surrounded by a cuticle-lined buccal cavity (c.b.c.), which connected posteriorly to a simple muscular esophagus (Figure 3b).

Posterior body sections revealed that the intestine (int.), which was lined with uninucleate columnar epithelial cells, and terminated at the anal opening (an.op.) (Figure 3c). All internal organs were suspended within the pseudocoelomic cavity (pseu.c.) (Figure 3c). In the female specimens, the mid-body region exhibited both intestinal and reproductive structures, including the uteri (ut.) was filled with eggs (Figure 3d). Multiple organs were simultaneously visible in some sections, including the intestine (int.), uterus, ovary (ov.), and oviducts (ovi.) (Figure 3e). The vagina (va.) appeared as a slit-like opening located on the ventral surface was connected to the uterine tract (Figure 3f, black arrowhead). Occasionally, egg-containing embryos were observed in the vulva (Figure 3f).

Cuticle (cu.) exhibited regional variation in thickness, being especially thick in the mid to posterior body regions (Figure 3g–i). It was ornamented using transverse folds (fo.), and was most prominent in the posterior part of the body (Figure 3i). The surface of these folds displayed cuticular annulations (cu.annu.) (Figure 3h–i). The buccal cavity and the anterior esophagus were also lined with a thickened cuticle (Figure 3b). Beneath the cuticle was a hypodermal layer, which projected laterally into the pseudocoelom-forming lateral chords (l.c.) (Figure 3e, j). These lateral extensions of the hypodermis also housed clusters of nuclei, as the nuclei were otherwise sparse in the hypodermis. The dorsal and ventral nerve cords are associated with the hypodermis, with the ventral cord being larger. Together with the lateral chords, these structures divided the somatic musculature into quadrants.

Somatic muscle cells (m.) comprised a peripheral cytoplasmic portion and a contractile core. In hematoxylin and eosin (H&E) stained sections, the cytoplasmic region appeared pale (clear to light pink or grey), while the contractile region stained intensely red. These contractile portions consisted of parallel-arranged fibers (Figure 3h) and displayed a coelomyarian muscle pattern (coe.my.), characterized by muscle cells that project into the pseudocoelom in a radial cylindrical fashion (Figure 3j).

The digestive tract of *P. halicoris* comprises the mouth, buccal cavity, esophagus, intestine, and anus. The esophagus was uniform in diameter and had a cuticle-lined lumen in the anterior portion (Figure 3a). The anterior esophagus is muscular and often contains ducts leading to the esophageal glands (eso.gl.) (Figure 3b). The intestine, originating from the esophagus, was lined with cuboidal to columnar epithelial cells (Figure 3k).

The female reproductive system is didelphic and comprises of two reproductive tracts. Each ovary was a long, thread-like structure composed of a single layer of cuboidal epithelial cells, externally lined by a basement membrane. A cytoplasmic rachis occupied the central axis of each ovary and was surrounded by developing ova (Figure 3l). The ovaries lacked central lumen. The oviducts arising from the ovaries were emptied into the uteri, which contained developing eggs or embryos (Figure 3g). These are eventually released into the external environment through the vagina.

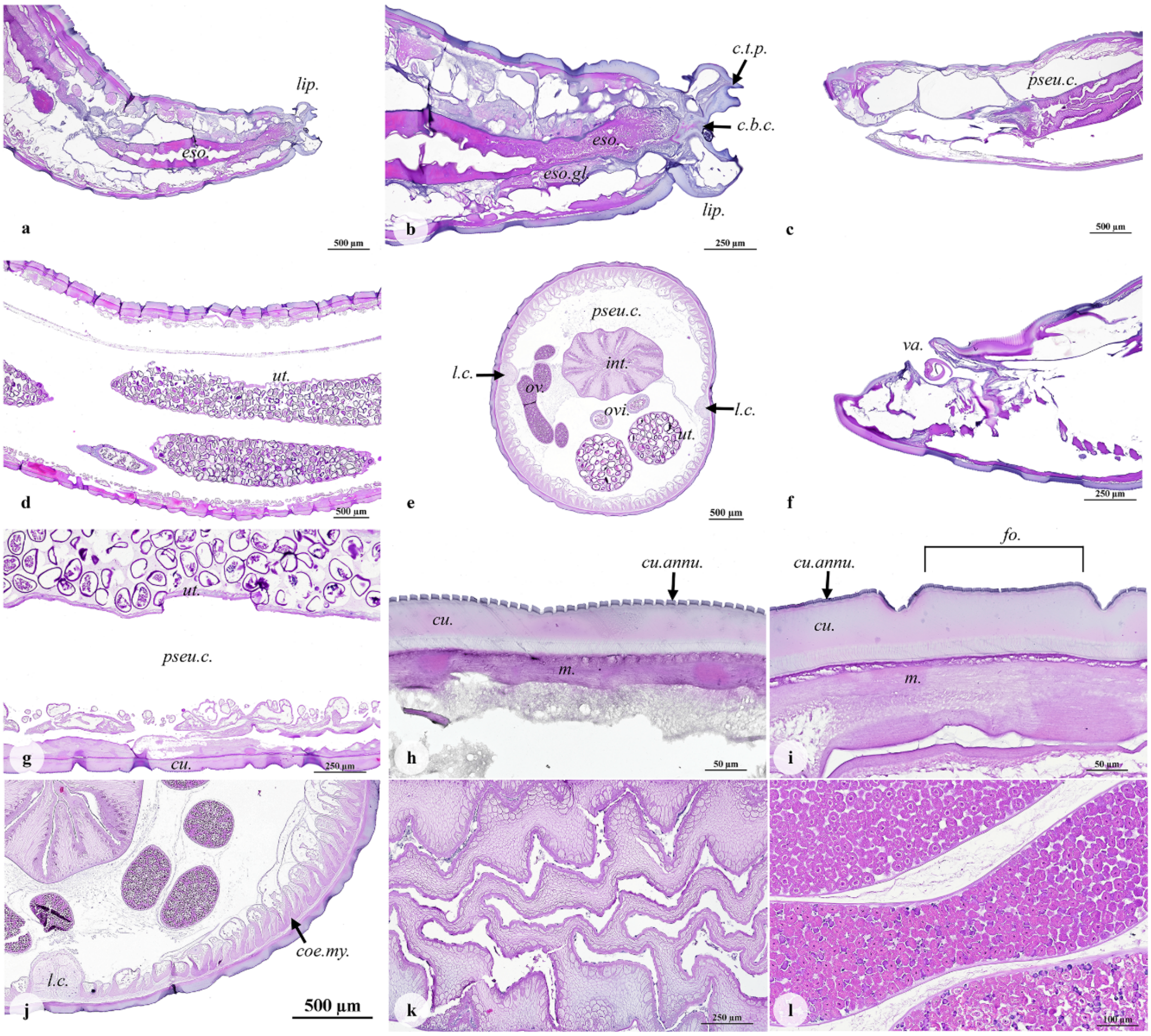

Figure 3 Histological sections showing the internal morphology of *Paradujardinia halicoris*. (a) Anterior region showing lips (lip.) with cuticular tooth-like projections (c.t.p.) and centrally located esophagus (eso.), (b) Buccal cavity (c.b.c.) connected to the muscular esophagus (eso.), with thick cuticular lining and esophageal glands (eso.gl.), (c) Posterior region showing the intestine (int.), anal opening (an.op.), and pseudocoelom (pseu.c.), (d) Middle body of a female showing uteri (ut.) filled with eggs, (e) Transverse section displaying multiple organs including intestine (int.), uterus, ovary (ov.), oviduct (ovi.), and lateral chord (l.c.), (f) Ventral view of the vagina (va.) and vulva containing embryonated egg, (g) Mid-body region showing thick cuticle (cu.) and developing eggs in uterus (ut.), (h) Cuticle with surface annulations (cu.annu.), (i) Posterior fold (fo.) of cuticle with surface annulations (cu.annu.) in the posterior region, (j) Lateral chord (l.c.) and coelomyarian muscle (coe.my.), (k) Intestinal epithelium composed of cuboidal to columnar cells, (l) Ovary showing cuboidal epithelium and central cytoplasmic rachis surrounded by developing ova. (a-l = H&E, a, c, d, e, j, original magnification ×4, scale bar = 500 µm; b, f, g, k, original magnification ×10, scale bar = 250 µm;l, original magnification ×20, scale bar = 100 µm; h, i, original magnification ×40, scale bar = 50 µm;).

DISCUSSION

Dugong (*Dugong dugon*) is an endangered marine mammal species and is designated as a protected animal under Thai law due to its conservation importance and declining population (Government, 2019). In recent years, dugong mortality in Thailand has increasingly been associated with both anthropogenic threats and natural causes, particularly infectious diseases (Daochai et Al., 2024). These infections may be caused by a wide range of pathogens, including bacteria, viruses, and parasitic helminths (Waltzek et al., 2012; Sukkarun et al., 2025). While most parasitic infections in marine mammals are considered to have low pathogenicity (Beck and Forrester, 1988), certain helminths with high a prevalence have been implicated in significant morbidity, strandings, and even mortality events (O'Shea et al., 1991; Aznar et al., 2001; Balbuena and Simpkin, 2014; Woolford et al., 2015).

Among parasitic helminths, nematodes are frequently found in dugongs, with *P. halicoris* being one of the most commonly reported gastrointestinal helminths (Owen et al., 2012; Woolford et al., 2015; Rajesh et al., 2023). The present study reaffirms the morphological characteristics previously described for this species *P. halicoris* is an ascaridoid nematode with a cylindrical body, striated cuticle, and terminal mouth with three toothless lips. It shows sexual dimorphism and has typical ascarid digestive and reproductive structures, confirming its adaptation to dugong parasitism (Waikagul et al., 1998; Anand et al., 2018). Our findings support these morphological observations and provide novel insights. Notably, we observed that the transverse striations of the cuticle occasionally displayed bifurcating or branching patterns, resembling fingerprint-like markings. This feature has not been previously reported and may represent individual-specific cuticular ornamentation, which is potentially useful for detailed taxonomic or population-level studies. However, further molecular confirmation, including gene sequencing and phylogenetic analysis, should be conducted to provide more definitive identification.

To date, no prior studies have described the histological features of *P. halicoris* in detail. Our histological analysis reveals that this species shares many fundamental anatomical characteristics with other ascaridoid nematodes, such as *Ascaris suum* and *Ascaris lumbricoides*, a well-studied terrestrial counterpart (Lőw et al., 2016; Yeremiev et al., 2017). When comparing both species, *P. halicoris* and *A. lumbricoides* possess a multilayered body wall composed of a thick cuticle, underlying hypodermis, and coelomyarian-type musculature, which is a common nematode feature (Hendrix, 2001). The pseudocoelomic cavity contains internal organs, including the digestive and reproductive systems (Lőw et al., 2016). The cuticle of *P. halicoris* varies in thickness along the body and is ornamented with transverse folds and annulations, especially in the posterior region, whereas A. lumbricoides is known for its radial striations and layered spiral fibers (Yeremiev et al., 2017). In both species, the hypodermis projects into the pseudocoelom as lateral chords containing nuclei, which is a common characteristic among nematodes. The digestive tract of both species follows the classical nematode pattern, beginning at the mouth and continuing through the buccal cavity, muscular esophagus, simple intestine, and anal opening (Gardiner et al., 1999). In *P. halicoris*, the esophagus is lined with a cuticle and associated with visible glandular ducts features that are also observed, though less prominently, in *A. lumbricoides*. Both species exhibit a didelphic reproductive system in females; however, *P. halicoris* displays distinct histological features, such as ovaries with a central cytoplasmic rachis surrounded by developing ova and lacking a central lumen—unlike *A. lumbricoides*, which typically displays a more tubular ovarian architecture (Yeremiev et al., 2017). The vagina of *P. halicoris* appears as a slit-like ventral opening, occasionally observed in embryonated eggs near the vulva. Despite their shared ascaridoid lineage, key differences exist in the anterior morphology. *P. halicoris* possesses cuticular tooth-like projections surrounding the buccal cavity, which are absent in *A. lumbricoides*, and exhibits more elaborate posterior cuticular ornamentation. These distinctions highlight species-specific structural adaptations that are likely reflective of their differing host environments—marine versus terrestrial—and may have diagnostic relevance when examining nematode infections under light microscopy.

As *P. halicoris* infection has consistently been identified in necropsied dugongs, our study revealed a notably high prevalence of infection across all age classes. Specifically, 62.0% (103/166) of the examined individuals were infected, a markedly higher proportion compared to previous reports. For instance, only 1 of 32 stranded dugongs examined in Queensland, Australia, was found to be infected (Owen et al., 2012), and a prevalence of 3 out of 6 was reported in individuals from the central Torres Strait region (Woolford et al., 2015). The highest infection rates were observed in juveniles (80.0%) and sub-adults (72.3%), followed by adults (61.4%), dependent calves (50.0%), and new-born calves (28.6%). Similar to other herbivore, this age-related trend suggests that increased exposure to infective stages and accumulation of parasite burden may be associated with age and the onset of independent foraging behavior (Albery et al., 2024). These findings are consistent with those of previous studies that identified juveniles and sub-adults as the primary age groups harboring nematode infections (Owen et al., 2012; Woolford et al., 2015; Norina et al., 2018). The underlying causes contributing to the high prevalence of *P. halicoris* remain unclear. However, similar age-related patterns have been reported in gastrointestinal nematode infections among ruminants, where younger animals exhibit higher susceptibility (Ashraf et al., 2017). It has been proposed that older individuals develop partial immunity or age-related resistance, resulting in lower parasite burden (Colombo and Grencis, 2020). Factors such as immunological status, habitat differences, and environmental conditions may also influence the risk of infection (Regassa et al., 2006). Of particular interest is the detection of *P. halicoris* in newborn calves, which raises the possibility of its vertical transmission. We hypothesized that transplacental infection may occur, analogous to the mechanisms described in other ascaridoid nematodes such as *Toxocara vitulorum* (Ahmed et al., 2016) and *Neoascaris vitulorum* (Rao et al, 2000) in suckling calves, and *Toxocara canis* in dogs (Mubarak et al., 2023). This hypothesis is supported by previous reports of *P. halicoris* infections in pregnant dugongs, suggesting its potential for in utero transmission (Woolford et al., 2015). Nevertheless, it should be acknowledged that the estimated prevalence and severity of infection in this study may be limited in representing the overall dugong population in the wild, but rather reflect the condition of stranded individuals, thereby introducing a potential sampling bias.

Previous pathological reports of *P. halicoris* infection in dugongs have documented a broad spectrum of host responses ranging from subclinical cases with no apparent lesions (Woolford et al., 2015) to severe pathological changes directly associated with mortality (Norina et al., 2018). In our study, several key lesions consistent with earlier findings were observed, including gastrointestinal inflammation and localized tissue damage corresponding to areas of parasite attachment. Notably, we documented one severe case wherein extensive nematode infection resulted in intestinal wall perforation and subsequent peritonitis, strongly implicating *P. halicoris* as a primary or contributing cause of death. The variability in clinical severity observed among infected dugongs may be influenced by multiple factors, including the anatomical site of infection, parasite load, parasite activity, metabolic byproducts of helminths, and the host's immune and inflammatory responses (Wakelin, 1996). Helminth-induced pathology is known to occur through five primary mechanisms: (a) direct mechanical damage caused by parasite migration and feeding activity; (b) immunopathological responses mediated by Th2 cytokine activation, resulting in chronic inflammation, granuloma formation, and irreversible tissue remodeling; (c) toxic effects of parasite-derived secretory or excretory molecules; (d) facilitation of secondary infections through disruption of the local microbial environment; and (e) chronic verminous inflammation that promotes oxidative stress and exacerbates tissue injury (Wynn and Allen, 2010; Smout et al., 2011; Abd Ellah, 2013; Suyapoh et al., 2021a, 2021b). Specifically within the Ascarididae family, studies on *Ascaris suum* have demonstrated that excretory-secretory (ES) products released by the worms play critical roles in host–parasite interactions, contributing to tissue inflammation, immunomodulation, and immune evasion (Dailey and Stroud, 1978; Jaber et al., 2013; Suárez-González et al., 2024). These insights may be extrapolated to *P. halicoris*, given its phylogenetic proximity and similar gastrointestinal localization, suggesting that both mechanical and immunological mechanisms likely underpin the pathogenesis observed in dugong hosts.

CONCLUSION

This study revealed a high prevalence of *P. halicoris* infection in dugongs, particularly among juveniles and sub-adults. Alongside the confirmation of typical ascaridoid morphology, we report novel cuticular features and a fatal case of severe infection. These findings underscore the urgent need for further research on the parasite life cycle, transmission dynamics, risk factors, pathogenic mechanisms, and molecular characterization. Such studies are essential for advancing our understanding of *P. halicoris* and for guiding effective health monitoring and conservation strategies for dugong populations.

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AUTHOR CONTRIBUTIONS

Peerapon Sornying: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Writing – original draft (supporting).
Domechai Kaewnoi: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead).
Narissara Keawchana: Methodology (supporting); Writing – review & editing (supporting).
Piyarat Khumraksa: Data curation (supporting); Formal analysis (lead); Methodology (equal); Resources (equal).
Sattaya Ruangpoon: Data curation (supporting); Formal analysis (lead); Methodology (equal); Resources (equal).
Santi Ninwat: Resources (lead). Pimwarang Sukkarun: Methodology (supporting).
Apinya Arnuphapprasert: Methodology (supporting).
Watcharapol Suyapoh: Conceptualization (lead); Data curation (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (supporting); Project administration (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review & editing (lead).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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