

First Record of Zoonotic Trematodes in *Sermyla riquetii* (Grateloup, 1840) from Thailand: Morphological and Genetic Characterization

PIYAWAN THONGCHOT¹, NUANPAN VEERAVECHSUKIJ^{1*}, CHANYANUCH JANMANEE¹, JIRAYUS KOMSUWAN¹, WIVITCHUTA DECHRUKSA¹, KITJA APIRAKSENA^{1,2}, NATTAPHONG YINGYODKUL¹, MATTHIAS GLAUBRECHT³ AND DUANGDUEN KRAILAS¹

¹ Parasitology and Medical Malacology Research Unit, Department of Biology, Faculty of Science, Silpakorn University, Nakhon Pathom 73000, THAILAND

² Demonstration School of Silpakorn University, Faculty of Education, Silpakorn University, Nakhon Pathom 73000, THAILAND

³ Department of Biodiversity of Animals, Universität Hamburg, and Leibniz Institute for the Analysis of Biodiversity Change (LIB), Zoological Museum, Martin-Luther-King-Platz 3, 20146 Hamburg, GERMANY

*Corresponding authors. Nuanpan Veeravechsukij (nuanpanve@gmail.com, veeravechsukij_n@su.ac.th)

Received: 21 July 2025; Accepted: 4 May 2026; Date of Publication: 30 June 2026

ABSTRACT. — *Sermyla riquetii*, a thiarid gastropod, serves as an intermediate host for various trematodes in brackish and coastal habitats. This study examined 6,137 *S. riquetii* specimens from 29 sites across 16 Thai provinces to identify larval trematodes using morphological and molecular approaches. Cercariae were detected in 35 snails (0.57%) and assigned to three morphological types: (i) pleurolophocercous (including *Centrocestus formosanus* and *Stellantchasmus falcatus*), (ii) parapleurolophocercous (*Procerovum cheni*), and (iii) furcocercous (*Transversotrema laruei*). The pleurolophocercous type was the most prevalent. Phylogenetic analysis of the ITS2 region confirmed the identities of *C. formosanus*, *S. falcatus*, and *P. cheni*, which clustered with corresponding GenBank sequences. Molecular data could not differentiate between pleurolophocercous and parapleurolophocercous types. This is the first report of *S. riquetii* as a host for *C. formosanus* and *P. cheni* in Thailand. The findings provide important baseline data on trematode-snail associations and support the potential role of *S. riquetii* in the transmission of zoonotic trematodes. This study contributes to the understanding of parasite biodiversity in tropical estuarine ecosystems and highlights the need for monitoring snail populations in disease risk assessments.

KEYWORDS: *Sermyla riquetii*, thiarid snail, trematode larvae, brackish water, Thailand

INTRODUCTION

Gastropods are critical intermediate hosts for various trematode species, which can significantly impact human health through infections by intestinal flukes, liver flukes, lung flukes, and blood flukes. Trematode infections pose public health challenges and contribute to socioeconomic issues, particularly in tropical and subtropical regions (Prasopdee et al., 2015; Martin and Cabrera, 2018; Apiraksena et al., 2020; Bawm et al., 2022; Tookhy et al., 2022). In Southeast Asia, over 50 species of food-borne intestinal flukes have been identified in humans, with the largest groups belonging to the families of Heterophyidae and Echinostomatidae. Of particular concern is the liver fluke *Opisthorchis viverrini*, which causes opisthorchiasis and leads to bile duct inflammation with serious complications, such as cholangitis, cholecystitis, liver cirrhosis, and cholangiocarcinoma. Approximately 20 million people worldwide have been infected with the lung fluke *Paragonimus* spp. Infection by food-borne trematodes in humans is primarily linked to the consumption of undercooked or raw second intermediate hosts, a behavior common in endemic areas and closely associated with traditional food practices (Chai et al., 2005; Chai et al., 2009; Chai, 2013a, 2013b;

Prueksapanich et al., 2018; Suwannatrai et al., 2018; Salim et al., 2021; Chai and Jung, 2022). In addition, snail-borne schistosomiasis remains a major parasitic disease of global public health importance, urging snail control agencies to limit its transmission. A comprehensive knowledge of the biology of food-borne or snail-borne trematodes and their vectors is essential to address the spread of these diseases (Clausen et al., 2012; Lu et al., 2018).

In Thailand, trematode infections have been reported in snails from the Bithyniidae, Planorbidae, Viviparidae, and Thiaridae, with the latter showing high susceptibility to cercarial infections. Species such as *Melanoides tuberculata* and *Tarebia granifera* serve as first intermediate hosts for intestinal flukes (Krailas et al., 2014; Veeravechsukij et al., 2018). Various thiarid snails, including *M. tuberculata*, *M. jugicostis*, *T. granifera*, *Mieniplotia scabra*, *Stenomelania* spp., *Neoradina prasongi*, and *S. riquetii*, host a range of cercariae types, such as Parapleurolophocercous, Pleurolophocercous, Xiphidiocercariae, Megalurous, Echinostome, Amphistome, Rencolid, Cotylomicrocercous, Gymnocephalous, and Furcocercous cercariae (Dechruksa et al., 2007; Ukong et al., 2007; Chontanarith and Wongsawad, 2010; Krailas et al., 2011; Krailas et al., 2014; Namchote et al., 2015; Sritongtae et al., 2015; Anucherngchai et al., 2016;

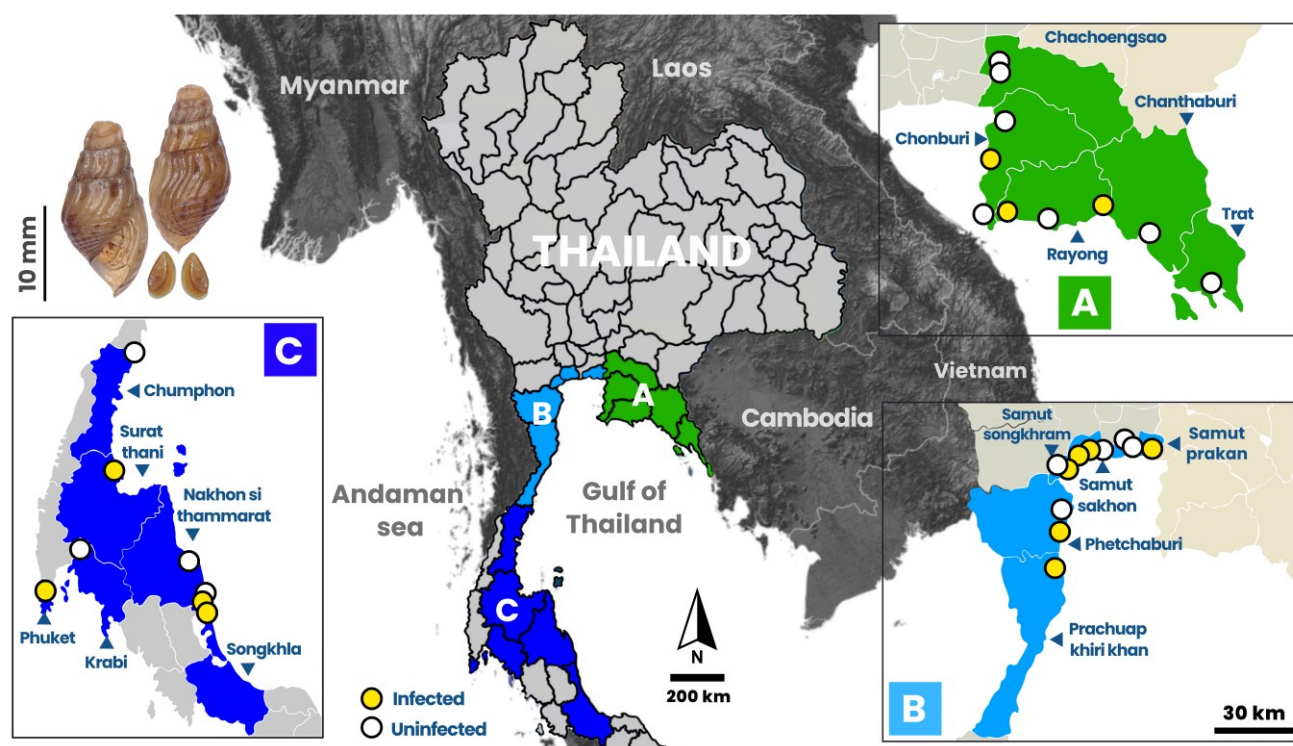


FIGURE 1. Shell morphology and distribution of *Sermyla riquetii* in 29 sampling sites, Eastern (A), Central (B) and Southern (C) parts of Thailand. The white dots indicate the locations where infected snails were not found, and the yellow dots represent the locations where infected snails were found.

Dechruksa et al., 2017; Veeravechsukij et al., 2018; Apiraksena et al., 2020).

The thiarid snail genus *Sermyla* inhabits freshwater and brackish environments in river mouths, mangrove forests, and coastal areas with tidal currents and comprises five recorded species: *S. riquetii* (Grateloup, 1840); *S. carbonata* (Reeve, 1859); *S. onca* (A. Adams and Angas, 1864); *S. kupaensis* Lentge-Maaß, Neiber, Gimnich and Glaubrecht, 2020; and *S. huberi* Thach, 2021. These species are found globally, including in Indonesia, Australia, the Philippines, Vietnam, and Thailand (Brandt, 1974; Glaubrecht et al., 2009; Maaß and Glaubrecht, 2012; Lentge-Maaß et al., 2021). In Thailand, *S. riquetii* has been documented as a host for the minute intestinal fluke *Haplorchis taichui* found along the east coast of the Gulf of Thailand (Sritongtae et al., 2015). However, traditional classification based solely on the morphological features of cercariae often presents challenges due to similarities in their key characteristics, highlighting the need for molecular methods to confirm species identification.

This study investigated *S. riquetii* populations in the Gulf of Thailand and the Andaman Sea coast, focusing on trematode infections and examining the larval stages of trematodes. Morphological and molecular approaches were employed to identify these larval

stages. The findings contributed to a survey of snail diversity and parasitic infections, providing valuable information for the effective control and prevention of parasitic diseases in humans and animals.

MATERIALS AND METHODS

Sampling Sites and Snail Collection

Sermyla riquetii specimens were collected from brackish waters, estuaries, and mangrove forests across 16 provinces along the coastal regions of the Gulf of Thailand and the Andaman Sea (Fig. 1). The geographic coordinates of each sampling site were recorded using a GPS device (Garmin eTrex 10, Taiwan) based on the WGS84 datum. Snails were collected from February 2023 to October 2023 by adopting the counts per unit time method (Olivier and Schneiderman, 1956). Five researchers collected the snails by hand and with scoops over a 10-minute interval per sampling site. The collected samples were stored in aeration tanks and transported to the Parasitology and Medical Malacology Research Unit (PaMaSU) at the Department of Biology, Faculty of Science, Silpakorn University, Nakhon Pathom, Thailand.

Examination of Trematode Infections and Morphological Identification of Trematodes

The snails were examined for trematode infections using the cercarial emergence and crushing methods described by Krailas et al. (2011, 2014). Cercarial emergence was employed to observe the release of cercariae, while the crushing method was used to detect other developmental stages, such as parthenita. Emergent cercariae were examined live or after vital staining with 0.5% neutral red, with morphological descriptions based on external features and internal structures. Identification of cercariae was based on keys provided by Komiya (1961), Schell (1970), Yamaguti (1971, 1975), and Ito (1980), as well as additional references from Krailas et al. (2011, 2014), Veeravechskij et al. (2018) and Apiraksena et al. (2020). For morphometric analysis, ten specimens of each cercaria species were fixed in 10% formalin were measured (in micrometres) under a microscope. The cercariae were then preserved in 95% ethanol for molecular analysis.

Molecular Analysis of Cercariae

The genomic DNA of cercariae was extracted using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). The nuclear internal transcribed spacer 2 (ITS2) regions were amplified via polymerase chain reaction (PCR) with the following primers: ITS2-F (5'-CTT GAACGC ACA TTG CGG CCA TGG G-3') and ITS2-R (5'-GCG GGT AAT CACGTC TGA GCC GAG G-3') (Sato et al., 2009). Reactions were set up with a volume of 20 µl containing 6 µl of genomic DNA (50–100 ng), 1 µl of each primer (10 µM), 2 µl of ddH₂O, and 10 µl of 2x PCR Master mix Solution i-pfu (iNtRON Biotechnology, Korea). The PCR thermal cycle involved initial denaturation at 94 °C for 4 min; 35 cycles of denaturation at 94 °C for 1 min, annealing at 60 °C for 30 s, and elongation at 72 °C for 2 min and a final elongation step at 72 °C for 7 min, after which the products were stored at –20 °C. The PCR products were then loaded on a 1% agarose gel for electrophoresis.

Subsequently, the PCR products were purified and sequenced by Macrogen (Seoul, South Korea). Forward and reverse sequences were assembled to generate consensus sequences using MEGA 11. Multiple sequence alignment was performed using MUSCLE under default settings. A phylogenetic tree was constructed using the Maximum Likelihood method based on the Kimura 2-parameter model with a gamma distribution (K2+G). Branch support was evaluated using 1,000 bootstrap replicates.

Ethical Standards

The authors affirmed that all research methods employed in this strictly adhere to the ethical standards established by national and institutional committees concerning the welfare and utilization of laboratory animals. Prior ethical approval was obtained from the Committee for Animal Scientific Research at Silpakorn University, Thailand under the reference number 12/2566.

RESULTS

Overview of Trematode Infections

A total of 6,137 *S. riquetii* snails were collected from 29 sites across 16 provinces in Thailand, namely, Trat, Chanthaburi, Rayong, Chon Buri, Chachoengsao, Samut Prakan, Samut Sakhon, Samut Songkhram, Phetchaburi, Prachuap Khiri Khan, Chumphon, Surat Thani, Nakhon Si Thammarat, Songkhla, Krabi, and Phuket. Trematode infections were detected in 35 snails from 12 sites in 10 provinces. Based on morphological characteristics, four cercarial species were identified and classified into three types: (i) pleurolophocercous cercariae (*Centrocestus formosanus* and *Stellantchasmus falcatus*), (ii) parapleurolophocercous cercariae (*Procerovum cheni*), and (iii) furcocercous cercariae (*Transversotrema laruei*). The overall prevalence was 0.57% (35/6,137). No cases of double or triple infections were observed. Pleurolophocercous cercariae were the most prevalent (0.33%), followed by parapleurolophocercous cercariae (0.21%) and furcocercous cercariae (0.033%) (Table 1).

Morphology of Cercariae

According to their morphological characteristics and previously reported morphological descriptions (Komiya, 1961; Schell, 1970; Yamaguti, 1971, 1975; Ito, 1980; Krailas et al., 2011, 2014; Veeravechskij et al., 2018; Apiraksena et al., 2020), the cercariae were assigned to three distinct morphological cercarial types known and found to date and attributable to at least two distinct trematode families.

TABLE 1. Locations and number of collected snails, infected snails, and cercariae obtained from the collected snails.

Voucher Number	Location	Coordinates	Number of Collected Snails	Number of Infected Snails (Prevalence%)	Type: Cercariae Species
The Eastern Part					
Trat Province					
1. SUT0123003	Khlong Na Kluea, Mueang Trat District	12° 10' 31.45" N 102° 32' 31.10" E Alt. 4 m	13	0	0
Chanthaburi Province					
2. SUT0123009	Pak Nam Laem Sing 2, Laem Sing District	12° 27' 32.98" N 102° 08' 15.86" E Alt. 0.15 m	293	0	0
Rayong Province					
3. SUT0123017	Khlong Nong Phlong, Klaeng District	12° 42' 55.08" N 101° 46' 11.01" E Alt. 4 m	230	3 (1.3)	Parapleurolophocercous cercariae: <i>Procerovum cheni</i>
4. SUT0123023	Khlong Hin Khaw, Mueang Rayong District	12° 36' 38.01" N 101° 23' 11.12" E Alt. 6 m	133	0	0
5. SUT0123026	Phra Chedi Klang Nam (Samut Chedi), Mueang Rayong District	12° 39' 58.99" N 101° 14' 33.80" E Alt. 11 m	330	3 (0.91)	Pleurolophocercous cercariae: <i>Stellantchasmus falcatus</i>
Chon Buri Province					
6. SUT0123027	Khlong Lang Amphoe, Sattahip District	12° 39' 51.30" N 100° 54' 26.04" E Alt. 2 m	257	0	0
7. SUT0123028	Khlong Bang Lamung, Bang Lamung District	13° 02' 29.16" N 100° 55' 12.88" E Alt. 2 m	442	2 (0.45)	Pleurolophocercous cercariae: <i>Stellantchasmus falcatus</i>
8. SUT0123030	Khlong Kapi, Mueang Chon Buri District	13° 20' 46.05" N 100° 57' 20.85" E Alt. 2 m	39	0	0
Chachoengsao Province					
9. SUT0123031	Ban Hua Suan, Ban Pho District	13° 35' 27.99" N 101° 04' 44.12" E Alt. 2 m	86	0	0
10. SUT0123033	Khlong Suai, Ban Pho District	13° 36' 15.57" N 101° 04' 48.22" E Alt. 3 m	88	0	0
The Central Part					
Samut Prakan Province					
11. SUT0123036	Khlong Dan, Bang Bo District	13° 30' 57.88" N 100° 49' 20.45" E Alt. 3 m	124	4 (3.2)	Pleurolophocercous cercariae: <i>Stellantchasmus falcatus</i>
12. SUT0123038	Bang Pu Highway Police Public Service Center, Mueang Samut Prakan District	13° 31' 14.63" N 100° 39' 25.61" E Alt. 4 m	252	0	0
13. SUT0123039	Bang Pu Recreation Center, Mueang Samut Prakan District	13° 31' 13.35" N 100° 39' 14.58" E Alt. 3 m	42	0	0
Samut Sakhon Province					
14. SUT0123041	Khlong Khok Kham Khut Mai 1, Mueang Samut Sakhon District	13° 32' 17.51" N 100° 22' 32.69" E Alt. 2 m	190	0	0
15. SUT0123044	Kalong 1, Mueang Samut Sakhon District	13° 28' 28.13" N 100° 08' 33.77" E Alt. 2 m	349	1 (0.29)	Parapleurolophocercous cercariae: <i>Procerovum cheni</i>
16. SUT0123045	Kalong 2, Mueang Samut Sakhon District	13° 29' 01.39" N 100° 08' 25.25" E Alt. 2 m	35	0	0
Samut Songkhram Province					
17. SUT0123049	Don Hoi Lot 1, Mueang Samut Songkhram District	13° 22' 06.23" N 100° 00' 42.71" E Alt. 0.35 m	84	2 (2.4)	Pleurolophocercous cercariae: <i>Stellantchasmus falcatus</i>
18. SUT0123050	Don Hoi Lot 2, Mueang Samut Songkhram District	13° 22' 04.82" N 100° 00' 41.27" E Alt. 1 m	11	0	0
Phetchaburi Province					
19. SUT0123053	Saltwater barrier gate No.1 (km.19+500), Cha-am District	12° 51' 20.40" N 99° 59' 36.09" E Alt. 2 m	130	0	0
20. SUT0123057	Khlong Puek Tian, Tha Yang District	12° 57' 29.92" N 100° 01' 53.73" E Alt. 2 m	88	2 (2.3)	Pleurolophocercous cercariae: <i>Stellantchasmus falcatus</i>

TABLE 1. (Continue)

Voucher Number	Location	Coordinates	Number of Collected Snails	Number of Infected Snails (Prevalence%)	Type: Cercariae Species
Prachuap Khiri Khan Province 21. SUT0123061	Wat Tham Khao Tao, Hua Hin District	12° 27' 25.24" N 099° 58' 48.23" E Alt. 8 m	866	4 (0.46) 2 (0.23)	Pleurolophocercous cercariae: <i>Stellantchasmus falcatus</i> Furcocercous cercariae: <i>Transversotrema laruei</i>
The Southern Part					
Chumphon Province 22. SUT0123067	Ban Koh Teab Mangrove Forest Pathio District	10° 54' 02.73" N 099° 30' 08.88" E Alt. 5 m	2	0	0
Surat Thani Province 23. SUT0123070	Khlomg Phum Riang, Chaiya District	09° 23' 14.00" N 099° 15' 27.00" E Alt. 5 m	521	2 (0.38)	Parapleurolophocercous cercariae: <i>Procerovum cheni</i>
Nakhon Si Thammarat Province 24. SUT0123075	Ban Koh Nang Doi 1, Pak Phanang District	08° 23' 32.75" N 100° 06' 05.40" E Alt. 3 m	365	0	0
Songkhla Province 25. SUT0123080	Ban Pak Ra Wa, Ranot District	07° 53' 58.70" N 100° 20' 22.21" E Alt. 2 m	92	0	0
26. SUT0123081	Khlomg Rap Praek, Ranot District	07° 47' 04.58" N 100° 21' 13.95" E Alt. 3 m	350	5 (1.4) 3 (0.86)	Parapleurolophocercous cercariae: <i>Procerovum cheni</i> Pleurolophocercous cercariae: <i>Centrocestus formosanus</i>
27. SUT0123083	Khlomg Pak Trae 2, Ranot District	07° 45' 34.85" N 100° 22' 25.42" E Alt. 3 m	540	1 (0.19)	Parapleurolophocercous cercariae: <i>Procerovum cheni</i>
Krabi Province 28. SUT0123098	Khlomg Pak Lao, Ao Luek District	08° 28' 24.60" N 098° 40' 25.30" E Alt. 29.97 m	11	0	0
Phuket Province 29. SUT0123100	Bang La Mangrove Forest, Thalang District	07° 59' 31.03" N 098° 22' 58.58" E Alt. 9 m	174	1 (0.58)	Parapleurolophocercous cercariae: <i>Procerovum cheni</i>
Total			6,137	35 (0.57)	

Type 1. *Pleurolophocercous cercariae* Heterophyidae Leiper, 1909

1.1) *Centrocestus formosanus* (Nishigori, 1924) Price, 1932 (Fig. 2)

Cercariae exhibit a pear-shaped body with yellowish-brown pigment and spinulate tegument (Fig. 2A). Oral sucker located anteriorly, equipped with spines (Fig. 2B). A pair of eyespots lies above the penetration glands at the level of the pharynx (Fig. 2C). Short esophagus visible; ventral sucker situated between the intestinal bifurcation and excretory vesicle. Coarse brown granules dispersed throughout the body. Lateral cystogenous cells observable. Seven pairs of penetration glands anterolateral to ventral sucker. Elongated triangular genital primordium located between ventral sucker and thin-walled excretory vesicle (Fig. 2D). Tail is slender, longer than body, with indistinct dorsal and ventral finfolds and a terminal spine (Fig. 2E). Cercariae develop within redia (Fig. 2F).

Movement behavior.— Active by rolling and springing motion for 8–10 s., followed by resting phase of 45–50 s. Survival in water.— 3–4 h. post-emergence. Prevalence.— 3 *S. riquetii* infected. Locations: Khlomg Rap Praek. The prevalence was 0.049% (3/6,137) (Table 1).

Morphometric measurements of *C. formosanus* in this study (all measurements in micrometres, calculated from 10 cercariae)

Structure	Length (range)	Width (range)	Average (L × W)
Body	67–93	61–77	80 × 69
Tail	127–164	14–22	147 × 17
Eyespots	3–10	4–7	7 × 6
Pharynx	3–5	3–5	4 × 4
Oral sucker	26–34	19–37	30 × 24
Ventral sucker	15–26	10–12	21 × 11
Penetration gland	13–20	5–9	16 × 7
Excretory vesicle	21–34	7–10	27 × 8

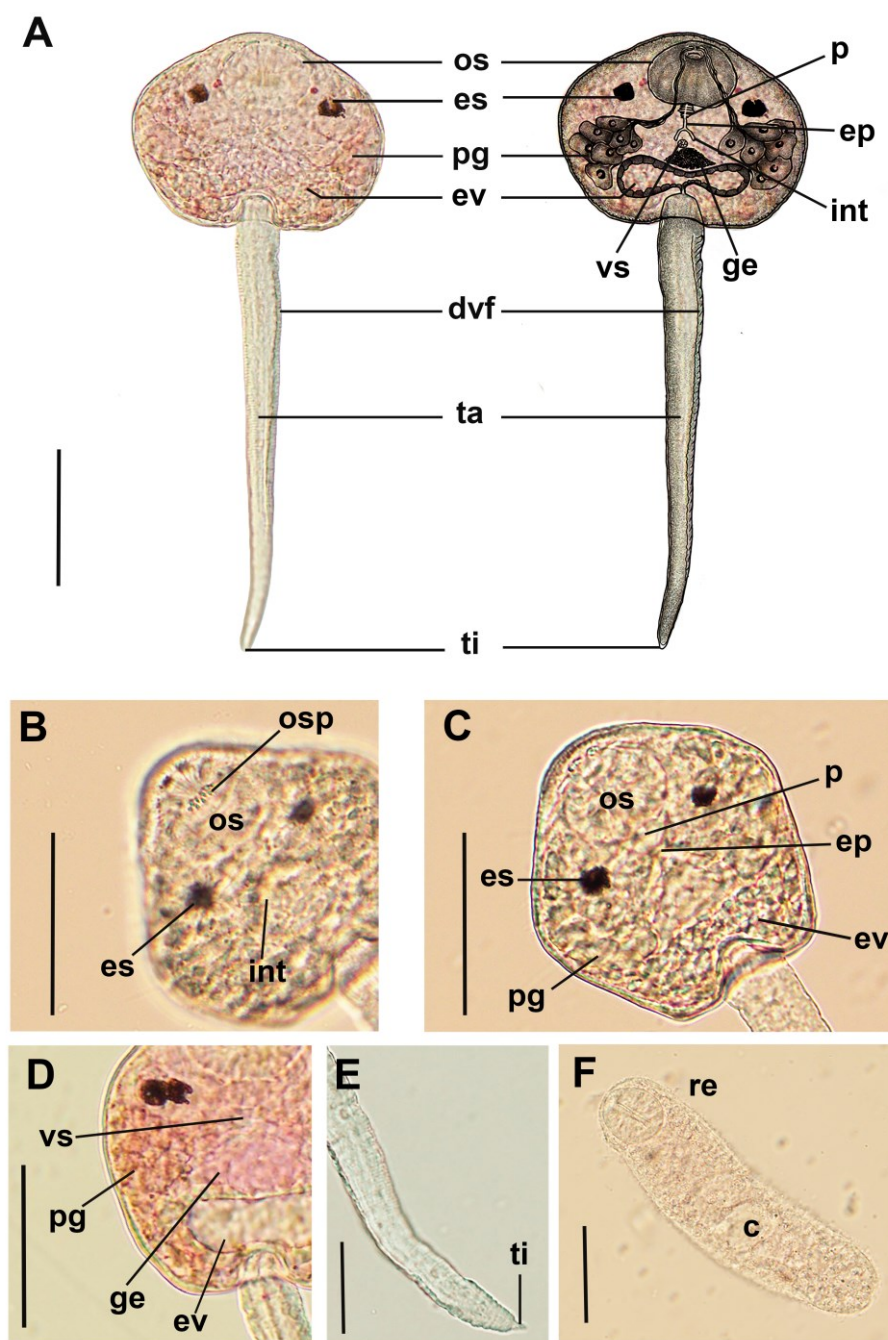


FIGURE 2. Images of *Centrocestus formosanus*. A. Specimen stained with 0.5% neutral red (DIC microscopy) and visualization of cercarial structures comparing with those of diagram; B–E. Body parts of cercariae and F. Redia stained with 0.5% neutral red (DIC microscopy). Abbreviations: c, cercaria; dvf, dorso-ventral finfold; ev, excretory vesicle; ep, esophagus; es, eyespot; ge, genital primordium; int, intestine; os, oral sucker; osp, oral spines; p, pharynx; pg, penetration gland; re, redia; ta, tail; ti, tip; vs, ventral sucker. Scale bars = 50 µm.

Remarks.— Morphological and morphometric characteristics of the cercariae observed in this study correspond closely with descriptions provided by Nishigori (1924), Chen (1942), Martin (1958), and Veeravechskij et al. (2018) (Supplementary material 1). Diagnostic features include pear-shaped spinulate body, 7 pairs of penetration glands, terminal spine, tail finfolds, and triangular genital primordium anterior to the excretory vesicle.

1.2) *Stellantchasmus falcatus* Onji and Nishio, 1916 (Fig. 3)

Body oval-shaped with scattered yellowish-brown granules and fine spines (Fig. 3A). A few lateral bristles (little hair) project from the body surface (Fig. 3D). Oral sucker situated anteriorly, bearing mounting ring and oral spines in 3 horizontal rows (Fig. 3B). Pair of eyespots shows rectangular pigmented pattern (Fig. 3C). Seven pairs of penetration glands arranged

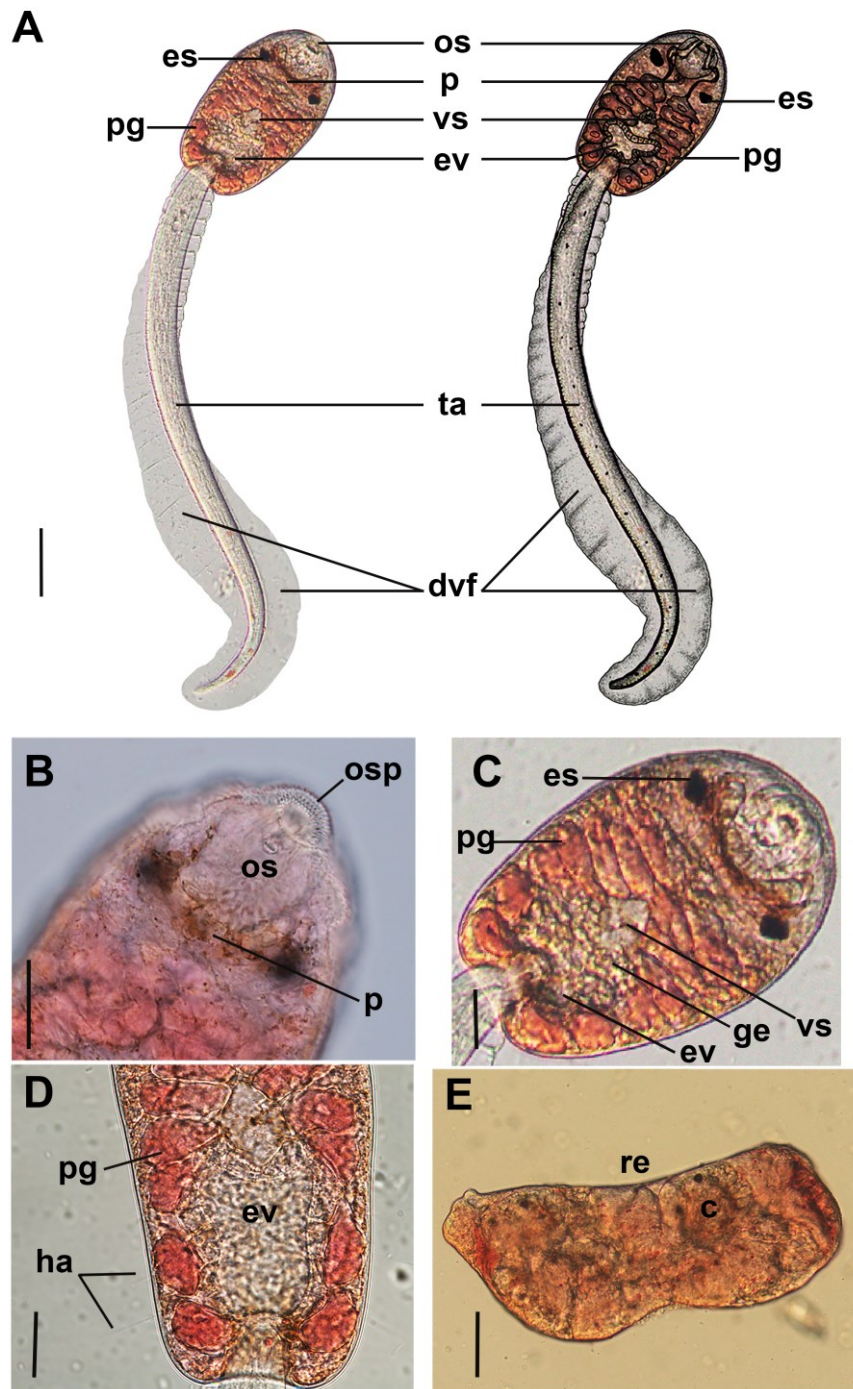


FIGURE 3. Images of *Stellantchasmus falcatus*. A. Specimen stained with 0.5% neutral red (DIC microscopy) and visualization of cercarial structures comparing with those of diagram; B–D. Body parts of cercariae and E. Redia stained with 0.5% neutral red (DIC microscopy). Abbreviations: c, cercaria; dvf, dorso-ventral finfold; ev, excretory vesicle; es, eyespots; ge, genital primordium; ha, hair; os, oral sucker; osp, oral spines; p, pharynx; pg, penetration gland; vs, ventral sucker; re, redia; ta, tail. Scale bars = 50 μ m.

laterally, from behind pharynx to posterior body; nuclei and granules evident in each lobe. Ventral sucker present mid-body as cluster of developing cells. Cystogenous cells distributed laterally. Genital primordium located between ventral sucker and excretory vesicle (Fig. 3C). Thick-walled excretory vesicle with bifurcated caudal tube into tail. Tail longer than body, origin concave; dorsal finfold begins near

base and extends over tip into ventral finfold (2/5 length). Cercariae develop within redia (Fig. 3E)

Movement behavior.— Float on water surface or mid-water, body below tail. Active for 3–4 s. in semicircular motion, resting for 5–10 min. At rest, body remains elevated while tail sinks.

Survival post-emergence.— 1–3 h.

Prevalence.— 17 *S. riquetii* infected.

Locations.— Phra Chedi Klang Nam (n=3), Khlong Bang Lamung (n=2), Don Hoi Lot 1 (n=2), Khlong Puek Tian (n=2), Khlong Dan (n=4), Wat Tham Khao Tao (n=4). The prevalence was 0.28% (17/6,137) (Table 1).

Morphometric measurements of *S. falcatus* in this study (all measurements in micrometres, calculated from 10 cercariae):

Structure	Length (range)	Width (range)	Average (L × W)
Body	107–148	72–93	128 × 80
Tail	443–471	20–32	455 × 23
Eyespots	9–12	6–9	10 × 8
Pharynx	8–11	6–9	9 × 8
Oral sucker	30–38	28–39	35 × 33
Ventral sucker	16–35	19–26	30 × 22
Penetration gland	15–37	10–21	25 × 14
Excretory vesicle	33–42	18–36	38 × 23
Dorso-ventral finfold	300–377	27–34	340 × 31

Remarks.— Morphological traits correspond with Martin (1958) and Noda (1959) (Supplementary material 2). Key features include 3-row oral spines, rectangular pigment eyespots, 14 penetration glands with nuclei, and long tail with finfolds.

Type 2. *Parapleurolophocercous cercariae* Heterophyidae Leiper, 1909

Procerovum cheni Hsü, 1951 (Fig. 4)

Body oval, yellowish, covered with fine spines (Fig. 4A). Oral sucker anterior, mouth surrounded by transverse spines (Fig. 4B). Pair of pigmented eyespots near anterior; pharynx situated posterior to eyespots (Fig. 4C). Seven pairs of penetration glands extending from pharynx to posterior body. Cystogenous cells lateral, mid-body, from behind eyespots to posterior end. Excretory vesicle thick-walled, saccular (Fig. 4C). Tail longer than body, with lateral finfold at one-third tail trunk; dorso-ventral finfold at distal portion (Fig. 4D). Cercariae develop within redia (Fig. 4E).

Movement behavior.— Active in water column, body lower than tail. Moves in semicircular bounce for 3–4 s.; rests 5–10 min. At rest, body elevates while tail sinks.

Survival post-emergence.— 2–4 h.

Prevalence.— 13 *S. riquetii* infected. Locations: Khlong Nong Phlong (n=3), Kalong 1 (n=1), Khlong Phum Rieng (n=2), Khlong Rap Praek (n=5), Khlong Pak Trae 2 (n=1), Bang La Mangrove Forest (n=1). The prevalence was 0.21% (13/6,137) (Table 1).

Morphometric measurements of *P. cheni* in this study (all measurements in micrometres, calculated from 10 cercariae):

Structure	Length (range)	Width (range)	Average (L × W)
Body	104–120	90–108	111 × 98
Tail	366–416	23–28	402 × 26
Eyespots	9–14	6–11	11 × 8
Pharynx	8–10	7–9	9 × 8
Oral sucker	32–38	30–38	36 × 34
Penetration gland	17–26	8–17	20 × 12
Excretory vesicle	49–65	20–28	59 × 23
Lateral finfolds	137–153	17–25	148 × 21
Dorso-ventral finfold	225–277	24–29	257 × 26

Remarks.— Morphological features agree with description by Hsü (1951) and Apiraksena et al. (2020) (Supplementary material 3). Distinguishing characteristics include yellowish body, anterior oral spines, pigmented eyespots, 7 pairs of penetration glands, and distinctive lateral and dorso-ventral tail finfolds.

Type 3. *Furcocercous cercariae* Transversotrematidae Witenberg, 1944

Transversotrema laruei Velasquez, 1958 (Fig. 5)

Body bowl-like, light brown, covered with scale-like spines and granules (Fig. 5A). Mouth opening and pharynx anterior, near globular ventral sucker. Narrow esophagus; intestinal caeca forming a ring. Eyespots round. Genital pore and seminal vesicle anterior. Testes paired, lobed, within intestinal loop. Ovary anterolateral to left testis. Small excretory vesicle near posterior end (Fig. 5A, B). Tail longer than body, ending in spatulate furcae (Fig. 5D). Bilateral appendages with adhesive pads at tail base (Fig. 5C). Cercariae develop within redia (Fig. 5E).

Movement behavior.— Active screwing motion 8–10 s.; rests 2–3 min. At rest, furcae float; body folds.

Survival in water.— 2–3 h. post-emergence.

Prevalence.— 2 *S. riquetii* infected. Locations: Wat Tham Khao Tao. The prevalence was 0.033% (2/6,137) (Table 1).

Morphometric measurements of *T. laruei* in this study (all measurements in micrometres, calculated from 10 cercariae):

Structure	Length (range)	Width (range)	Average (L × W)
Body	243–453	362–658	395 × 586
Genital pore	17–29	20–36	22 × 27
Eyespots	10–25	10–20	19 × 16
Mouth	39–70	30–55	61 × 44
Ventral sucker	74–149	70–148	121 × 117
Ovary	41–95	23–64	76 × 37
Testes	55–118	33–80	96 × 63
Excretory vesicle	61–94	20–44	75 × 31
Tail stem	309–653	64–116	555 × 90
Tail furca	110–227	47–97	192 × 76
Appendages	91–162	37–79	138 × 64

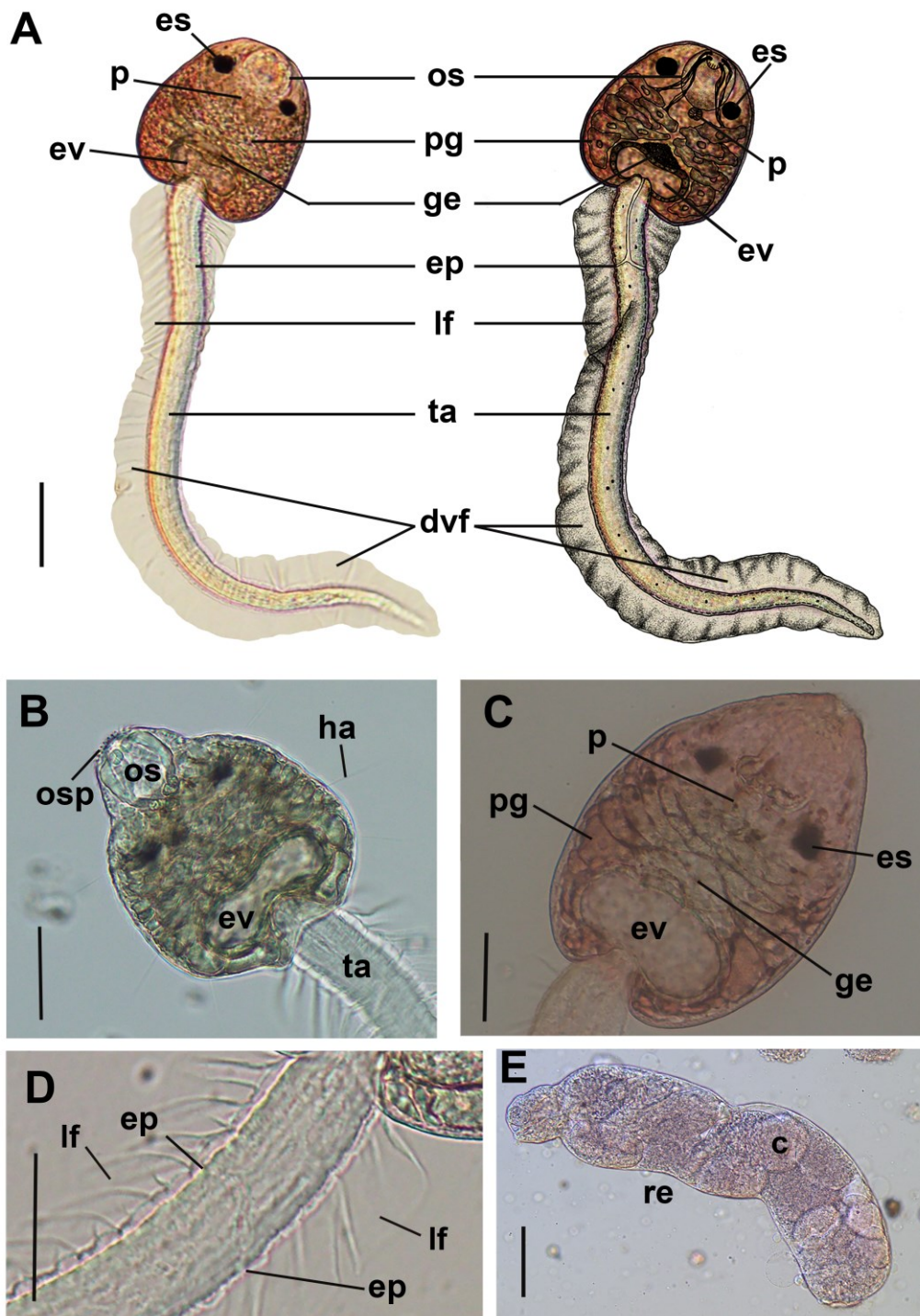


FIGURE 4. Images of *Procerovum cheni*. A. Specimen stained with 0.5% neutral red (DIC microscopy) and visualization of cercarial structures comparing with those of diagram; B–D. Body parts of cercariae and E. Redia stained with 0.5% neutral red (DIC microscopy). Abbreviations: c, cercaria; dvf, dorso-ventral finfold; ev, excretory vesicle; ep, excretory pore; es, eyespot; ge, genital primordium; ha, hair; lf, lateral finfold; os, oral sucker; osp, oral spines; p, pharynx; pg, penetration gland; re, redia; ta, tail. Scale bars = 50 µm.

Remarks.— Morphology consistent with Velasquez (1958), Ukong et al. (2007), Krailas et al. (2014), and Veeravechskij et al. (2018) (Supplementary material 4). Diagnostic features include ring-shaped intestinal

caeca, spatulate furcae, scale-like tegumental spines, and paired terminal tail appendages with adhesive pads.

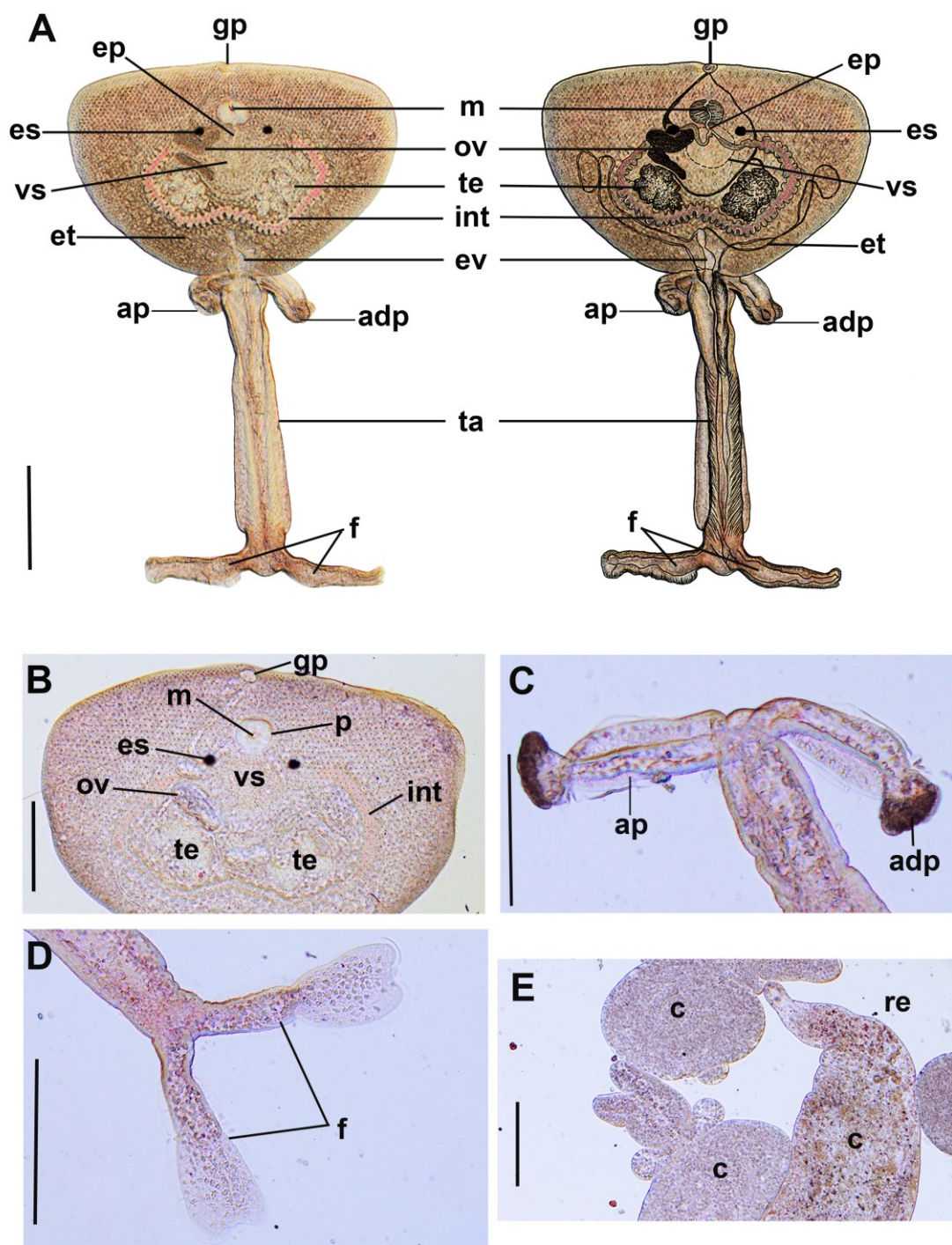


FIGURE 5. Images of *Transversotrema laruei*. A. Specimen stained with 0.5% neutral red (DIC microscopy) and visualization of cercarial structures comparing with those of diagram; B–D. Body parts of cercariae and E. Redia stained with 0.5% neutral red (DIC microscopy). Abbreviations: adp, adhesive pad; ap, appendages; c, cercaria; es, eyespot; ev, excretory vesicle; ep, esophagus; et, excretory tubule; f, furca; gp, genital pore; int, intestine; m, mouth; ov, ovary; p, pharynx; re, redia; ta, tail; te, testes; vs, ventral sucker. Scale bars = 200 μ m.

Molecular Analysis

Phylogenetic analysis based on ITS2 sequences was performed to confirm species identification of four trematode taxa morphologically classified in this study.

Three heterophyid trematodes; *Centrocestus formosanus*, *Stellantchasmus falcatus*, and *Procerovum cheni* were analyzed alongside related sequences obtained from GenBank. *Echinostoma mekongi* (MT409010.1)

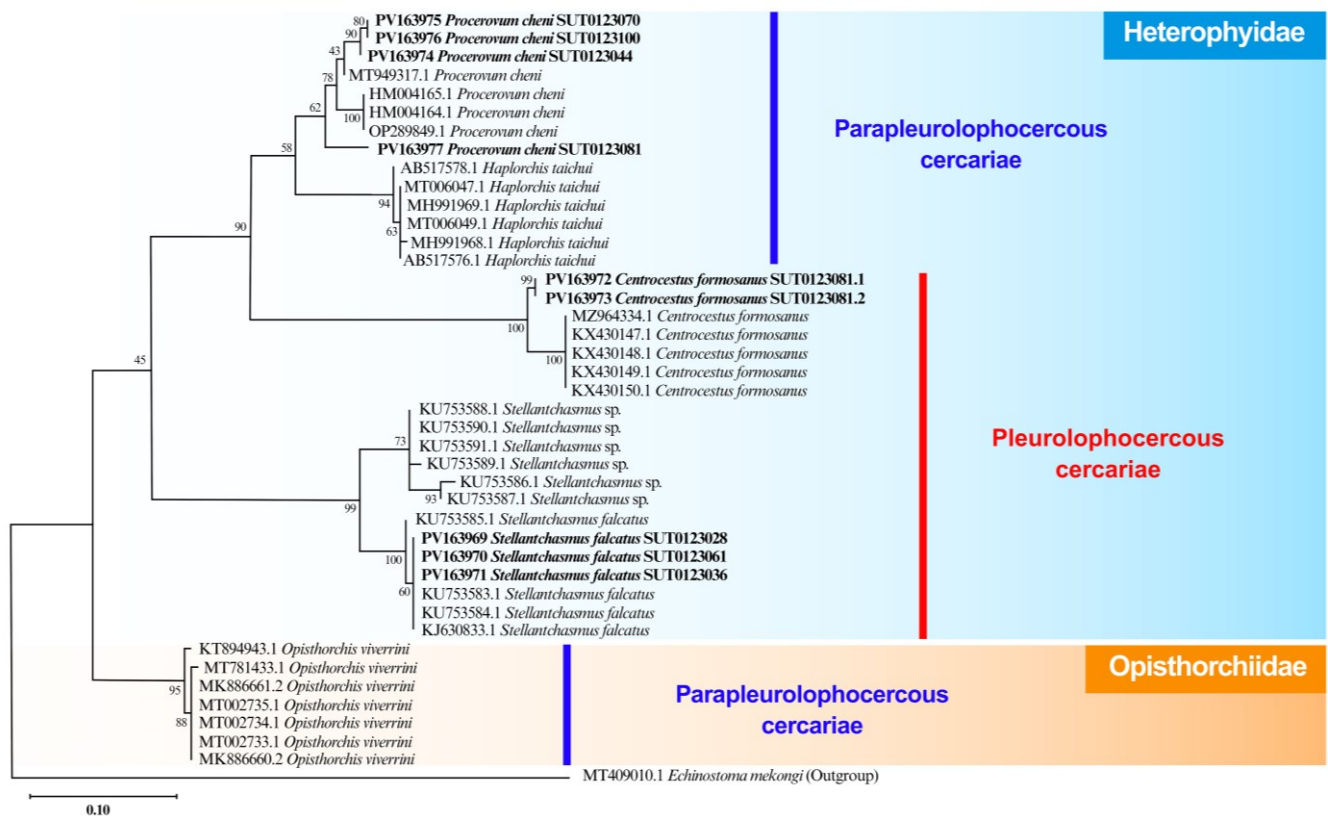


FIGURE 6. A phylogenetic tree of trematodes was constructed using ITS2 sequences based on maximum-likelihood analysis (1,000 bootstrap replications) and other published DNA sequences obtained from GenBank. The nodes are annotated with bootstrap support values ≥ 50 . Taxon names and vouchers or GenBank accession numbers are provided at the tips of the tree (Table 2).

was used as the outgroup for maximum-likelihood (ML) tree construction. Additional species included in the analysis were *Haplorchis taichui* (AB517576.1, AB517578.1, MH991968.1, MH991969.1, MT006047.1, MT006049.1) and *Opisthorchis viverrini* (MK886660.2, MK886661.2, MT002733.1, MT002734.1, MT002735.1, MT781433.1, KT894943.1), selected due to their morphological similarity and comparable life cycles. Amplification of ITS2 sequences for *Transversotrema laruei* (Furcocercous cercariae, Family: Transversotreematidae) was unsuccessful; however, species identification was confirmed through morphological characteristics.

The resulting ML phylogenetic tree revealed clear clustering of the ITS2 sequences into two major clades (Fig. 6): - Clade I: Included species from the family Heterophyidae. Four *P. cheni* sequences isolated in this study (PV163974, PV163975, PV163976, PV163977; 309–362 bp) clustered with four GenBank reference sequences (*P. cheni*: MT949317.1, OP289849.1, HM004164.1, HM004165.1) with high bootstrap support. Two *C. formosanus* sequences (PV163972, PV163973; 350–353 bp) grouped with five GenBank

reference sequences (KX430147.1, KX430148.1, KX430149.1, KX430150.1, MZ964334.1). All *P. cheni* and *C. formosanus* sequences formed monophyletic subclades with strong support and clustered with *H. taichui* sequences. - Clade II: Included representatives from both Heterophyidae and Opisthorchiidae. Three *S. falcatus* sequences from this study (PV163969, PV163970, PV163971; 355–359 bp) grouped with four GenBank *S. falcatus* sequences (KU753585.1, KU753583.1, KU753584.1, KJ630833.1). Additional *Stellantchasmus* spp. sequences (KU753588.1, KU753590.1, KU753591.1, KU753586.1, KU753587.1) also clustered within this clade. Sequences of *O. viverrini* formed a distinct subclade within the same major grouping, indicating evolutionary relatedness among members of the two families. The phylogenetic tree (Fig. 6) and associated metadata confirm the molecular identity of cercarial stages collected in this study and support the morphological identification of these trematode species (Table 2, Supplementary material 5 and 6).

TABLE 2. List of internal transcribed spacer 2 (ITS2) sequences used for phylogenetic analysis.

Species of Trematodes	Location/Country	Voucher Code	Genbank Accession Number	Stage of Trematode	References
<i>Centrocestus formosanus</i>	Khlong Rap Praek, Ranot District, Songkhla Province, Thailand	SUT 0123081.1	PV163972	Cercariae	This study
	Khlong Rap Praek, Ranot District, Songkhla Province, Thailand	SUT 0123081.2	PV163973	Cercariae	This study
	Mae Tang, San Sai, and Meuang District, Chiang Mai Province, Thailand	-	KX430147.1	Adult	Wongsawad et al. (2017b)
		-	KX430148.1		
		-	KX430149.1		
		-	KX430150.1		
	Yen Bai Province and Thanh Hoa Province, Vietnam	-	MZ964334.1	Cercariae	Nguyen et al. (2024)
<i>Stellantchasmus falcatus</i>	Khlong Bang Lamung, Bang Lamung District, Chon Buri Province, Thailand	SUT 0123028	PV163969	Cercariae	This study
	Khlong Dan, Bang Bo District, Samut Prakan Province, Thailand	SUT 0123036	PV163971		
	Wat Tham Khao Tao, Hua Hin District, Prachuap Khiri Khan Province, Thailand	SUT 0123061	PV163970		
	Thailand	-	KJ630833.1	Metacercariae	Chontanarith and Wongsawad (2014, Unpublished)
	Thailand	-	KU753583.1	Adult	Wongsawad et al. (2017a)
		-	KU753584.1		
		-	KU753585.1		
<i>Stellantchasmus</i> sp.	Thailand	-	KU753586.1	Adult	Wongsawad et al. (2017a)
		-	KU753587.1		
		-	KU753588.1		
		-	KU753589.1		
		-	KU753590.1		
		-	KU753591.1		
<i>Procerovum cheni</i>	Kalong 1, Mueang Samut Sakhon District, Samut Sakhon Province, Thailand	SUT 0123044	PV163974	Cercariae	This study
	Khlong Phum Rieng, Chaiya District, Surat Thani Province, Thailand	SUT 0123070	PV163975		
	Khlong Rap Praek, Ranot District, Songkhla Province, Thailand	SUT 0123081	PV163977		
	Bang La Mangrove Forest, Thalang District, Phuket Province, Thailand	SUT 0123100	PV163976		
	Thailand	-	HM004164.1	Adult	Thaenkham et al. (2010)
		-	HM004165.1		
	Khlong Nong Jik, Mueang District, Krabi Province, Thailand	SUT 172004	MT949317.1	Cercariae	Apiraksena et al. (2020)
	-	-	OP289849.1	-	Jumawan et al. (2022)
<i>Haplorchis taichui</i>	Thailand	-	AB517576.1	Adult	Thaenkham et al. (2010)
		-	AB517578.1		
	Wa River (Nan drainage, Chao, Phraya River system), Bo Kluea District, Nan Province, Thailand	SUT 0515090	MH991968.1	Cercariae	Veeravechskij et al. (2018)
	km 50+350 Loei River (Loei drainage, Mekong River system), Phu Luang District, Loei Province, Thailand	SUT 0516125	MH991969.1		
<i>Opisthorchis viverrini</i>	Northern Thailand	-	MT006047.1	Eggs	Buathong et al. (2020)
		-	MT006049.1		
	Eastern Thailand	-	MK886660.2	Eggs	Boondit et al. (2020)
		-	MK886661.2		
		-	MT002733.1		
	Northern Thailand	-	MT002734.1	Eggs	Buathong et al. (2020)
		-	MT002735.1		
		-	KT894943.1		
<i>Echinostoma mekongi</i>	Binh Dinh Province, Central Vietnam	-	MT781433.1	Cercariae	Dao et al. (2016, Unpublished)
	Bangkok Metropolitan Region, Thailand	-	MT409010.1	Adult	Rachprakhon and Purivirojkul (2021)
<i>Echinostoma mekongi</i>	Mekong River, Cambodia	-	MT409010.1	Adult	Cho et al. (2020)

DISCUSSIONS

Sermyla Adams and Adams, 1854 (Thiaridae) is a benthic gastropod inhabiting the brackish waters, river mouths, mangrove forests, and coastal areas influenced by tidal currents. Its distribution spans Southeast Asia and extends to Australia (Glaubrecht et al., 2009; Lentge-Maaß et al., 2021). However, the capability of this snail genus to serve as an intermediate host for trematodes has not been comprehensively examined. Thiarid gastropods have frequently been reported as the first intermediate hosts of trematodes, which affect the respiratory, intestinal, and hepatic systems in domestic animals and humans. However, evidence of such a role for *Sermyla* is lacking.

In Thailand, other thiarid snails such as *Melanoides tuberculata*, *M. jugicostis*, *Tarebia granifera*, and *Mieniplotia scabra* (= *Thiara scabra*) have been reported as intermediate hosts for a diverse array of trematodes. The 10 cercarial types encompassing 22 species are as follows: (i) parapleurolophocercous cercariae (*Haplorchis pumilio*, *H. taichui*, and *Stictodora tridactyla*); (ii) pleurolophocercous cercariae (*Centrocestus formosanus*); (iii) xiphidiocercariae (*Acanthatrium hitaense*, *Loxogenoides bicolor*, *Loxogenes liberum*, *Haematoloechus similis*, *Maritreminoides caridinae*, and *M. obstipus*); (iv) megalurous cercariae (*Cloacitrema philippinum* and *Philophthalmus gralli*); (v) furcocercous cercariae (*Cardicola alseae*, *Alaria mustelae*, *Transversotrema laruei*, *Apatemon gracilis*, and *Mesostephanus appendiculatus*); (vi) echinostome cercariae (*Echinochasmus pelecani*); (vii) amphistome cercariae (*Gastrothylax crumenifer*); (viii) renicolid cercariae (*Cercaria caribbea* LXVIII); (ix) cotylo-microcercous cercariae (*Podocotyle* (*Podocotyle*) *leporis*); and (x) gymnocephalous cercariae (Dechruksa et al., 2007, 2017; Ukong et al., 2007; Krailas et al., 2011, 2014; Veeravechsukij et al., 2018).

This study confirms the role of *Sermyla riquetii*, the sole species reported in Thailand (Brandt, 1974; Namchote et al., 2015; Lentge-Maaß et al., 2021), as an intermediate host for trematodes with an overall prevalence of 0.57% (35/6,137 snails). Three cercarial types and four trematode species were identified as follows: (i) pleurolophocercous cercariae (*Centrocestus formosanus* and *Stellantchasmus falcatus*), (ii) parapleurolophocercous cercariae (*Procerovum cheni*), and (iii) furcocercous cercariae (*Transversotrema laruei*). These findings align with previous studies of thiarid snails including *M. tuberculata*, *M. jugicostis*, *T. granifera*, and *M. scabra* as intermediate hosts for trematodes (Krailas et al., 2011, 2014; Veeravechsukij et al., 2018). However, this work is the first comprehensive

report of *S. riquetii* hosting these specific trematodes in Thailand.

Pleurolophocercous cercariae were the most prevalent, with *C. formosanus* identified at Khlong Rap Praek in Songkhla Province (prevalence, 0.86%). This finding represents the first report of *C. formosanus* utilizing *S. riquetii* as an intermediate host in Thailand. This parasite's zoonotic potential is significant because it causes gastrointestinal symptoms in humans and animals.

Centrocestus, a genus first described by Looss in 1899, includes *C. formosanus* (Nishigori, 1924) Price, 1932, a digenean trematode of the family Heterophyidae. This parasite requires three distinct types of hosts to complete its life cycle. Originally, *C. formosanus* was first isolated in 1924 from the intestine of a dog experimentally infected with metacercariae obtained from freshwater fish in Taiwan (Nishigori, 1924). Studies on its life cycle were conducted in China and Brazil (Chen, 1942, 1948; Yu and Mott, 1994; Fernandez et al., 2003; Pinto and Melo, 2010), identifying *M. tuberculata* as its first intermediate host. At present, this parasite is globally distributed, with reports spanning Asia (Taiwan, China, Japan, the Philippines, Vietnam, Thailand, Lao PDR, and India), Europe (Turkey), and the Americas (United States, Mexico, and Brazil) (Chai et al., 2009; Öktener et al., 2010; Phan et al., 2010; Johnson et al., 2012). Various freshwater fish species, including *Puntius brevis*, *P. gonionotus*, *P. meiacanthus*, *Hampala dispar*, *Cyclocheilichthys armatus*, *Anabas testudineus*, and *Henicorhynchus siamensis*, serve as its second intermediate hosts (Srisawangwong et al., 1997; Han et al., 2008; Eom et al., 2015). Natural definitive hosts include dogs, foxes, chickens, and ducks (Chai et al., 2009; Anh et al., 2010). Reports of *C. formosanus* infection in humans are rare. In Thailand, two species, *C. formosanus* and *C. caninus*, were found to infect humans from the provinces of Chiang Mai and Chiang Rai (Waikagul et al., 1997; Radomyos et al., 1998). Human infections have also been documented in Taiwan (Nishigori, 1924), China (Yu and Mott, 1994; Li et al., 2010), and Vietnam (De and Le 2011). *Centrocestus formosanus* infections have been previously reported in *M. tuberculata* (Krailas et al., 2014), *M. jugicostis* (Dechruksa et al., 2017), and *T. granifera* (Veeravechsukij et al., 2018).

Stellantchasmus, a genus within the Heterophyidae, produces cercariae of the Pleurolophocercous type. In this study, *S. falcatus* was detected in *S. riquetii* across multiple provinces (six provinces), with notable prevalence in Phra Chedi Klang Nam, Rayong Province (0.91%); Khlong Bang Lamung, Chon Buri Province (0.45%); Khlong Dan, Samut Prakan Province (3.2%); Don Hoi Lot 1, Samut Songkhram

Province (2.4%); Khlong Puek Tian, Phetchaburi Province (2.3%); and Wat Tham Khao Tao, Prachuap Khiri Khan Province (0.46%). *Stellantchasmus falcatus* was first reported in 1916 (Onji and Nishio, 1916). This parasite has infected humans in Japan, the Philippines, Korea, the United States, and Thailand. In Thailand, several cases have been reported in the northern and northeastern regions (Kliks and Tantachamrun, 1974; Tantachamrun and Kliks, 1978; Radomyos et al., 1998; Sripalwit et al., 2015). Its life cycle involves *T. granifera* and other thiarid snails as first intermediate hosts and fish such as *Dermogenys pusillus* and *Liza subviridis* as second intermediate hosts (Wongsawad et al., 2000; Pubua and Wongsawad, 2007; Chuboon and Wongsawad, 2009; Sripalwit et al., 2015). This minute trematode significantly maintains its transmission cycles, with human infections linked to severe pathology. Infections with this parasite can result in its eggs migrating to vital organs, such as the brain or heart, through the blood vessels and causing moderate to severe colicky pain and, in extreme cases, death (Africa et al., 1940; Kliks and Tantachamrun, 1974). *Stellantchasmus falcatus* in *S. riquetii* was previously reported by the Parasitology and Medical Malacology Research Unit, Department of Biology, Faculty of Science, Silpakorn University (PaMaSU) in 2017. Infections were found in two locations in Chon Buri Province: Khlong Bang Lamung and Khlong Tesaban Saensuk, with prevalence of 0.94% and 2.08%, respectively (Phanpeng et al., 2017).

The detection of *P. cheni* in *S. riquetii* from five provinces marks the first report of this parasite in Thailand. *Procerovum* has a limited geographical range, with species recorded in China, Japan, the Philippines, and Australia. Infections with this parasite are predominantly associated with birds and less frequently with mammals, including humans. This genus comprises small flukes belonging to the subfamily Haplorchiinae (Africa and Garcia, 1935; Africa, 1938; Chen, 1949; Hsü, 1950a, 1950b; Velasquez, 1973a, 1973b; Smales and Cribb, 1997). The following three species of *Procerovum* have been described: *P. calderoni* (Africa and Garcia, 1935; Price, 1940), *P. varium* (Onji and Nishio, 1916), and *P. cheni* (Hsü, 1951). *Procerovum calderoni* was first reported in dogs, cats, and two humans in the Philippines, with *Thiara riquetii* (= *S. riquetii*) identified as its first intermediate host. Meanwhile, *P. varium* in adult stages was obtained from experimental dogs infected with metacercariae isolated from mullet fish in Japan (Onji and Nishio, 1916; Price, 1940; Velasquez, 1973b). *Procerovum* adult worms can be distinguished from *Haplorchis* by the ventrogenital

complex structure, particularly the presence of an expulsores and a gonotyl with numerous spines. These characteristics have led to the reclassification of some species formerly placed in *Haplorchis* to *Procerovum* (Umadevi and Madhavi, 2000; Thaenkham et al., 2010). In this study, *P. cheni* infection was detected in *S. riquetii* specimens from five provinces: Khlong Nong Phlong, Rayong Province (1.3%); Kalong 1, Samut Sakhon Province (0.29%); Khlong Phum Riang, Surat Thani Province (0.38%); Khlong Rap Praek (1.4%) and Khlong Pak Trae 2 (0.19%), Songkhla Province; and Bang La Mangrove Forest, Phuket Province (0.58%). Earlier studies identified *Thiara tuberculata* (= *M. tuberculata*), *Sermyla riquetii*, *Stenomelania denisoniensis*, and *S. cf. punctata* as the first intermediate hosts for *Procerovum* spp. (Velasquez, 1973b; Surin, 1993; Umadevi and Madhavi, 2000; Apiraksena et al., 2020). *Stenomelania denisoniensis* was found to host *Procerovum* cercariae in Tinaroo Dam, North Queensland, Australia (Surin, 1993). *Procerovum varium* metacercariae were detected in freshwater fish from a stream in Visakhapatnam, India (Umadevi and Madhavi, 2000). In Thailand, *P. cheni* was previously reported in *S. cf. punctata* from Krabi Province (Apiraksena et al., 2020). *Procerovum* infections can cause extraintestinal diseases, including ocular parasitism in humans. *Procerovum* induced ocular infection was first documented in the Philippines. In South India, *P. varium* was implicated in an ocular granuloma in a single patient. It was also molecularly identified as the cause of ocular granulomatous inflammation in 13 out of 42 affected children (Arya et al., 2016). The prevalence of *Procerovum* infections appears concentrated in seaside regions.

The Furcocercous cercariae identified in this study were *T. laruei*, a trematode belonging to the family Transversotrematidae. This family includes four genera and approximately 30 known species, all of which are ectoparasitic trematodes. These species are primarily hosted by marine fishes in the Indo-West Pacific region and freshwater fishes from adjacent land masses (Cutmore et al., 2024). Owing to their unique infection site, i.e., beneath the scales of their fish hosts, these parasites are rarely detected during routine fish dissections. In this study, *T. laruei* infected two *S. riquetii* specimens from a single location, namely, Wat Tham Khao Tao in Prachuap Khiri Khan Province, with a prevalence of 0.23%. This finding aligns with earlier reports that distinguished cercariae from *Thiara riquetii* (= *S. riquetii*) and metacercariae in the muscles and intestines of sea bass in the Philippines (Velasquez, 1961). In Thailand, *T. laruei* has previously been reported as widespread, infecting

snails such as *M. tuberculata* and *T. granifera* across all regions (Krailas et al., 2014; Veeravechskij et al., 2018). Although no significant losses in aquaculture due to this parasite have been documented, infections with *T. laruei* can negatively affect fish health. Symptoms caused by *T. laruei* and other ectoparasites include visible lesions or ulcers on the skin and fins and inflammation around attachment sites. Secondary bacterial or fungal infections may also develop at the parasite's entry points, exacerbating its impact (Shinn et al., 2015; Towers, 2015). Effective management of these parasites involves improving biosecurity measures, controlling intermediate hosts (e.g., snails), and minimizing stress and crowding in fish farming operations. Further research into integrated pest management strategies and host-parasite interactions is essential to mitigate these impacts and ensure the sustainability of aquaculture.

The phylogenetic tree constructed from the ITS2 sequences of the trematode populations confirmed the identities of *C. formosanus*, *S. falcatus*, and *P. cheni*, thereby supporting our morphological findings. However, molecular techniques could not distinguish between Parapleurolophocercous and Pleurolophocercous cercariae, which is consistent with the findings of Waikagul and Thaenkham (2014). Moreover, the phylogenetic tree indicates that some genera within the Heterophyidae are closely related to the Opisthorchiidae. This relationship, confirmed by Thaenkham et al. (2012) using all available GenBank data, including 18S ribosomal DNA and internal transcribed spacer 2 (ITS2) sequences, suggests that the two families are inseparable. A fundamental reassessment of these families and their constituent genera is warranted, integrating both morphological and molecular data.

This study represents the first confirmed report in Thailand of *Centrocestus formosanus*, *Procerovum cheni*, and *Transversotrema laruei* infecting the thiarid snail *Sermyla riquetii*. While previous studies have documented these trematode species in other thiarid hosts such as *Melanoides tuberculata* and *Tarebia granifera*, their presence in *S. riquetii* had not been previously verified. This finding significantly expands the known host range of these medically important trematodes and suggests that *S. riquetii*, a widely distributed snail in estuarine and mangrove ecosystems, may play a more critical role in zoonotic parasite transmission than previously recognized. These newly documented host-parasite associations also underscore the ecological complexity of brackish water habitats and highlight the need for broader surveillance of under-studied snail taxa. The inclusion of *T. laruei*, an ectoparasitic trematode typically under-

detected in routine parasitological surveys, further demonstrates the value of integrating morphological and molecular approaches for comprehensive biodiversity assessment. Collectively, these results provide an important contribution to trematode ecology in Southeast Asia and reinforce the public health relevance of *S. riquetii* in coastal parasite transmission networks.

ACKNOWLEDGMENTS

This research was supported by the Department of Biology, Faculty of Science, and Silpakorn University, Thailand. The financial support came from the Faculty of Science grant no. SRIF-JRG-2564-10, SRIF-JRG-2567-06, and Thailand Science Research and Innovation (TSRI) National Science, Research and Innovation Fund (NSRF) (Fiscal Year 2024 and 2025). We thank our students in Parasitology and Medical Malacology Research Unit, Department of Biology, Faculty of Science, Silpakorn University (PaMaSU) for their dedicated field and laboratory work and acknowledge also the graduate research assistant scholarships SCSU-STA-2565-03, SCSU-STA-2565-05, and SCSU-STA-2565-06. We are indebted to the reviewers and the editor for their instructive comments and suggestions to the manuscript.

LITERATURE CITED

- Adams, A. and Angas, G.F. 1864. Descriptions of new species of freshwater shells collected by Mr.F.G. Waterhouse, during J. Mc Donall Stuart's overland journey from Adelaide to the north-west coast of Australia. *Proceedings of the Zoological Society of London*, 8: 414–418.
- Adams, H. and Adams, A. 1854. The genera of recent Mollusca; arranged according to their organization. In three volumes, Van Voorst, Vol. I, Part X, London.
- Africa, C.M. 1938. Description of three trematodes of the genus *Haplorchis* (Heterophyidae) with notes on two other Philippine members of this genus. *Philippine Journal of Science*, 66: 299–307.
- Africa, C.M. and Garcia, E. 1935. Two more new heterophyid trematodes from the Philippines. *Philippine Journal of Science*, 57: 443–450.
- Africa, C.M., De Leon, W., and Garcia, E.Y. 1940. Visceral complications in intestinal heterophyidiasis of man. *Acta Medica Philippina*, 1: 1–32.
- Anh, N.T., Madsen, H., Dalsgaard, A., Phuong, N.T., Thanh, D.T. and Murrell, K.D. 2010. Poultry as reservoir hosts for fishborne zoonotic trematodes in Vietnamese fish farms. *Veterinary Parasitology*, 169: 391–394.
- Anucherngchai, S., Tejangkura, T. and Chontanarath, T. 2016. Epidemiological situation and molecular identification of cercarial stage in freshwater snails in Chao-Phraya basin, Central Thailand. *Asian Pacific Journal of Tropical Biomedicine*, 6: 539–545.

- Apiraksena, K., Namchote, S., Komsuwan, J., Dechraksa, W., Tharapoom, K., Veeravechskij, N., Glaubrecht, M. and Krailas, D. 2020. Survey of *Stenomelania* Fisher, 1885 (Cerithioidea, Thiariidae): The potential of trematode infections in a newly-recorded snail genus at the coast of Andaman Sea, South Thailand. *Zoosystematics and Evolution*, 96: 807–819.
- Arya, L.K., Rathinam, S.R., Lalitha, P., Kim, U.R., Ghatani, S. and Tandon, V. 2016. Trematode fluke *Procerovum varium* as cause of ocular inflammation in children, South India. *Emerging Infectious Diseases*, 22: 192–200.
- Bawm, S., Khaing, N.H.E., Win, S.Y., Thein, S.S., Khaing, Y., Thaw, Y.N., Soe, N.C., Chel, H.M., Hayashi, N., Htun, L.L., Katakura, K., Nonaka, N. and Nakao, R. 2022. Morphological and molecular identification of trematode cercariae related with humans and animal health in freshwater snails from a lake and a dam in Myanmar. *Parasitology Research*, 121: 653–665.
- Boondit, J., Suwannahitorn, P., Siripattanapong, S., Leelayoova, S., Mungthin, M., Tan-Ariya, P., Piyaraj, P., Naaglor, T. and Ruang-Areerate, T. 2020. An epidemiological survey of *Opisthorchis viverrini* infection in a lightly infected community, eastern Thailand. *American Journal of Tropical Medicine and Hygiene*, 102: 838–843.
- Brandt, R.A.M. 1974. The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde*, 105: 1–423.
- Buathong, S., Phaiphilai, K., Ruang-Areerate, T., Sitthichot, N., Thita, T., Mungthin, M. and Suwannahitorn, P. 2020. Genetic differentiation of *Opisthorchis*-like eggs in northern Thailand using stool specimens under national strategic plan to control liver fluke infection and cholangiocarcinoma. *American Journal of Tropical Medicine and Hygiene*, 103: 1118–1124.
- Chai, J.Y. 2013a. Praziquantel treatment in trematode and cestode infections: an update. *Infection and Chemotherapy*, 45: 32–43.
- Chai, J.Y. 2013b. Paragonimiasis. In: Aminoff, M.J., Boller, F. and Swaab, D.F. (Eds). *Handbook of Clinical Neurology*, Elsevier, Amsterdam, p. 283–296. 114: 283–296.
- Chai, J.Y. and Jung, B.K. 2022. General overview of the current status of human foodborne trematodiasis. *Parasitology*, 149: 1262–1285.
- Chai, J.Y., Murrell, K.D. and Lymbery, A. J. 2005. Fish-borne parasitic zoonoses: status and issues. *International Journal for Parasitology*, 35: 1233–1254.
- Chai, J.Y., Shin, E.H., Lee, S.H., and Rim, H.J. 2009. Foodborne intestinal flukes in Southeast Asia. *The Korean Journal of Parasitology*, 47: 69–102.
- Chen, H.T. 1942. The metacercaria and adult of *Centrocestus formosanus* (Nishigori, 1924), with notes on the natural infection of rats and cats with *C. armatus* (Tanabe, 1922). *Journal of Parasitology*, 28: 285–298.
- Chen, H.T. 1948. Some early larval stages of *Centrocestus formosanus* (Nishigori, 1924). *Lingnan Science Journal*, 22: 93–105.
- Chen, H.T. 1949. Systematic consideration of some heterophyid trematodes in the subfamilies Haplorchinae and Stellantchasmae. *Annals of Tropical Medicine and Parasitology*, 43: 304–312.
- Cho, J., Jung, B.K., Chang, T., Sohn, W.M., Sinuon, M. and Chai, J.Y. 2020. *Echinostoma mekongi* n. sp. (Digenea: Echinostomatidae) from riparian people along the Mekong River in Cambodia. *The Korean Journal of Parasitology*, 58: 431–443.
- Chontanarith, T. and Wongsawad, C. 2010. Prevalence of *Haplorchis taichui* in field-collected snails: a molecular approach. *The Korean Journal of Parasitology*, 48: 343–346.
- Chontanarith, T. and Wongsawad, C. 2014. Prevalence of metacercarial infection in fish, experimental development and phylogenetic analysis of *Stellantchasmus falcatus* (Trematoda: Heterophyidae) in Thailand. [Unpublished manuscript].
- Chuboon, S. and Wongsawad, C. 2009. Molecular identification of larval trematode in intermediate hosts from Chiang Mai, Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 40: 1216–1220.
- Clausen, J. H., Madsen, H., Murrell, K.D., Phan Thi, V., Nguyen Manh, H., Viet, K.N. and Dalsgaard, A. 2012. Relationship between snail population density and infection status of snails and fish with zoonotic trematodes in Vietnamese carp nurseries. *PLoS Neglected Tropical Diseases*, 6: e1945.
- Cutmore, S.C., Bennett, M.B. and Cribb, T.H. 2024. Morphological and molecular identification of metacercariae infecting teleost fishes of Moreton Bay, Australia. *Systematic Parasitology*, 101: 57.
- Dao, T.T.H., Nguyen, T.T.G., Gabriel, S. and Dorny, P. 2016. Duck opisthorchiasis in the human Opisthorchiasis endemic Binh Dinh Province, Central Vietnam. [Unpublished manuscript].
- De, N.V. and Le, T.H. 2011. Human infections of fish-borne trematodes in Vietnam: prevalence and molecular specific identification at an endemic commune in Nam Dinh province. *Experimental Parasitology*, 129: 355–361.
- Dechraksa, W., Glaubrecht, M. and Krailas, D. 2017. Natural trematode infections of freshwater snail *Melanoides jugicostis* Hanley & Theobald, 1876 (Family Thiariidae), the first intermediate host of animal and human parasites in Thailand. *Silpakorn University Science and Technology Journal*, 11: 9–16.
- Dechraksa, W., Krailas, D., Ukong, S., Inkapatanakul, W. and Dangprasert, T. 2007. Trematode infections of freshwater snails family Thiariidae in Khek River. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 38: 1016–1028.
- Eom, K.S., Park, H.S., Lee, D., Sohn, W.M., Yong, T.S., Chai, J.Y., Min, D.Y., Rim, H.J., Insisiengmay, B. and Phommasack, B. 2015. Infection status of zoonotic trematode metacercariae in fishes from Vientiane Municipality and Champasak Province in Lao PDR. *The Korean Journal of Parasitology*, 53: 447–453.
- Fernandez, M.A., Thiengo, S.C. and Simone, L.R.L. 2003. Distribution of the introduced freshwater snail *Melanoides tuberculatus* (Gastropoda: Thiariidae) in Brazil. *The Nautilus*, 117: 78–82.
- Glaubrecht, M., Brinkmann, N. and Pöppe, J. 2009. Diversity and disparity 'down under': Systematics, biogeography and reproductive modes of the 'marsupial' freshwater Thiariidae (Caenogastropoda, Cerithioidea) in Australia. *Zoosystematics and Evolution*, 85: 199–275.
- Grateloup, J.P.S. de. 1840. Description de plusieurs coquilles nouvelles ou peu connues de mollusques exotiques vivants. *Actes de la Société Linnéenne de Bordeaux*, 11: 394–455.
- Han, E.T., Shin, E.H., Phommakorn, S., Sengvilaykham, B., Kim, J.L., Rim, H.J. and Chai, J.Y. 2008. *Centrocestus formosanus* (Digenea: Heterophyidae) encysted in the freshwater fish, *Puntius brevis*, from Lao PDR. *The Korean Journal of Parasitology*, 46: 49–53.
- Hsü, P.K. 1950a. A new trematode of the genus *Procerovum* from ducks and chickens in Canton (Trematoda: Heterophyidae). *Peking Natural History Bulletin*, 19: 39–43.
- Hsü, P.K. 1950b. Some heterophyid metacercariae belonging to the genera *Haplorchis* and *Procerovum* (Heterophyidae). *Lingnan Science Journal*, 23: 1–20.
- Hsü, P.K. 1951. A comparative study of the early larval stages of some heterophyid trematodes belonging to the genera *Haplorchis* and *Procerovum* (Trematoda: Heterophyidae). *Lingnan Science Journal*, 23: 235–256.
- Ito, J. 1980. Studies on Cercariae in Japan. Shizuoka University, Shizuoka, pp. 516–538.

- Johnson, P.T., Rohr, J.R., Hoverman, J.T., Kellermanns, E., Bowerman, J. and Lunde, K.B. 2012. Living fast and dying of infection: host life history drives interspecific variation in infection and disease risk. *Ecology Letters*, 15: 235–242.
- Jumawan, J.C., Alinsug, M.V., Deocar, C.C. and Estano, L.A. 2022. GenBank: OPO71665.1. Agriculture Research Section, DOST Philippine Nuclear Research Institute, Manila, Philippines. [Direct Submission].
- Kliks, M. and Tantachamrun, T. 1974. Heterophyid (trematoda) parasites of cats in North Thailand, with notes on a human case found at necropsy. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 5: 547–555.
- Komiyama, Y. 1961. The Excretory System of Digenetic Trematodes, Meguro Parasitological Museum, Tokyo, 109 p.
- Krailas, D., Namchote, S., Koonchornboon, T., Dechruksa, W. and Boonmekam, D. 2014. Trematodes obtained from the thiarid freshwater snail *Melanoides tuberculata* (Müller, 1774) as vector of human infections in Thailand. *Zoosystematics and Evolution*, 90: 57–86.
- Krailas, D., Namchote, S. and Rattanathai, P. 2011. Human intestinal flukes *Haplorchis taichui* and *Haplorchis pumilio* in their intermediate hosts, freshwater snails of the families Thiaridae and Pachychilidae, in Southern Thailand. *Zoosystematics and Evolution*, 87: 349–360.
- Leiper, R.T. 1909. London School of Tropical Medicine. Report of helminthologist for six months ending 30th April, 1908. In: Report of the Advisory Committee for the Tropical Diseases Research Fund for the Year 1908, 35–39.
- Lentge-Maaß, N., Neiber, M.T., Gimnich, F. and Glaubrecht, M. 2021. Evolutionary systematics of the viviparous gastropod *Sermyla* (Gastropoda: Cerithioidea: Thiaridae), with the description of a new species (Note: Nomenclatural availability of *S. kupaensis* established in 2020). *Zoological Journal of the Linnean Society*, 192: 736–762.
- Li, T., He, S., Zhao, H., Zhao, G. and Zhu, X.Q. 2010. Major trends in human parasitic diseases in China. *Trends in Parasitology*, 26: 264–270.
- Looss, A. 1899. Weitere beiträge zur kenntnis der trematoden-fauna Aegyptens, zugleich versuch einer natürlichen gliederung des genus *Distomum* Retzius. *Zoologische Jahrbücher*, 12: 521–784.
- Lu, X.T., Gu, Q.Y., Limpanont, Y., Song, L.G., Wu, Z.D., Okanurak, K. and Lv, Z.Y. 2018. Snail-borne parasitic diseases: an update on global epidemiological distribution, transmission interruption and control methods. *Infectious Diseases of Poverty*, 7: 1–6.
- Maaß, N. and Glaubrecht, M. 2012. Comparing the reproductive biology of three “marsupial”, eu-viviparous gastropods (Cerithioidea, Thiaridae) from drainages of Australia’s monsoonal north. *Zoosystematics and Evolution*, 88: 293–315.
- Martin, W.E. 1958. The life histories of some Hawaiian heterophyid trematodes. *Journal of Parasitology*, 44: 305–318.
- Martin, I.G.L. and Cabrera, E.C. 2018. Morphological characterization of emerging cercariae among lymnaeid snails from Barangay Cawongan, Padre Garcia, Batangas, Philippines. *Journal of Parasitology Research*, 2018: 5241217.
- Namchote, S., Sritongtae, S., Butnin, S., Wongwain, P. and Krailas, D. 2015. Larval stage of trematodes obtained from brackish water snails in the central and east coast of the gulf of Thailand. *Scientific Research and Essays*, 10: 386–401.
- Noda, K. 1959. The Larval Development of *Stellantchasmus falcatus* (Trematoda: Heterophyidae) in the First Intermediate Host. *Journal of Parasitology*, 45: 635–642.
- Nguyen, P.T.X., Dorny, P., Van Hoang, H., Losson, B., Mignon, B. and Bui, D.T. 2024. Environmental influence on abundance and infection patterns of snail intermediate hosts of liver and intestinal flukes in North and Central Vietnam. *Parasitology Research*, 123: 134.
- Nishigori, M. 1924. The life cycles of two new species of Heterophyidae, *Monorchotrema Taihokui* and *M. taichui* found in Formosa. Preliminary note. *Taiwa Igakkai Zasshi*, 237: 567–570.
- Ökten, A., Yurdakul, N., Alaş, A. and Solak, K. 2010. Fish-borne parasitic zoonoses in Turkish waters. *Gazi University Journal of Science*, 23: 255–260.
- Olivier, L. and Schneiderman, M. 1956. A method for estimating the density of aquatic snail populations. *Experimental Parasitology*, 5: 109–117.
- Onji, Y. and Nishio, T. 1916. On the trematodes whose intermediate host is brackish water fishes. *Chiba Igaku Semmon Gakko Zasshi*, 81: 229–249. (in Japanese)
- Phan, V.T., Ersbøll, A.K., Bui, T.Q., Nguyen, H.T., Murrell, D. and Dalsgaard, A. 2010. Fish-borne zoonotic trematodes in cultured and wild-caught freshwater fish from the Red River Delta, Vietnam. *Vector-Borne and Zoonotic Diseases*, 10: 861–866.
- Phanpeng, L., Dechruksa, W., Krailas, D., Boonmekam, D. and Namchote, S. 2017. Cercarial infections, *Stellantchasmus falcatus* (Trematode: Heterophyidae) of snails *Sermyla riqueti* in Chonburi and Rayong Provinces, Thailand. In: Proceedings of the 10th Silpakorn University Conference on Academic Research and Creative Arts: Integration of Art and Science, 64–71. (In Thai)
- Pinto, H. A. and Melo, A.L. 2010. *Melanoides tuberculata* as intermediate host of *Philophthalmus gralli* in Brazil. *Revista do Instituto de Medicina Tropical de Sao Paulo*, 52: 323–327.
- Prasopdee, S., Tesana, S., Cantacessi, C., Laha, T., Mulvenna, J., Grams, R., Loukas, A. and Sotillo, J. 2015. Proteomic profile of *Bithynia siamensis goniomphalos* snails upon infection with the carcinogenic liver fluke *Opisthorchis viverrini*. *Journal of Proteomics*, 113: 281–291.
- Price, E.W. 1932. On the genera *Centrocestus* Looss and *Stannosoma* Tanabe. *Journal of Parasitology*, 18: 309.
- Price, E.W. 1940. A review of the heterophyoid trematodes, with special reference to those parasitic in man. Third International Congress for Microbiology, New York, 446–447.
- Prueksapanich, P., Piyachaturawat, P., Aumpansub, P., Ridditid, W., Chaiteerakij, R. and Rerknimitr, R. 2018. Liver fluke-associated biliary tract cancer. *Gut and Liver*, 12: 236–245.
- Pubua, J. and Wongsawad, C. 2007. Redescription of the trematode metacercariae from the mullet (*Liza subviridis*) and half-beak (*Dermogenus pusillus*). *The Southeast Asian Journal of Tropical Medicine and Public Health*, 38: 106–109.
- Rachprakhon, P. and Purivirojkul, W. 2021. Very low prevalence of *Opisthorchis viverrini* cercariae in *Bithynia siamensis siamensis* snails from the canal network system in the Bangkok Metropolitan Region, Thailand. *Parasite*, 28: 2.
- Radomyos, B., Wongsaroj, T., Wilairatana, P., Radomyos, P., Praevanich, R., Meesomboon, V. and Jongsuksuntikul, P. 1998. Opisthorchiasis and intestinal fluke infections in northern Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 29: 123–127.
- Reeve, L. A. 1859. Monograph of the genus *Melania*. In: Reeve, L.A. (ed), *Conchologica Iconica: or, Illustrations of the Shells of Molluscos Animals*. Vol. XII, London.
- Salim, M., Masroor, M.S. and Parween, S. 2021. An overview on trematodes developing disease complications causing cancer in human. *World Journal of Advanced Research and Reviews*, 12: 362–374.
- Sato, M., Thaenkharn, U., Dekumyoy, P. and Waikagul, J. 2009. Discrimination of *O. viverrini*, *C. sinensis*, *H. pumilio* and *H. taichui* using nuclear DNA-based PCR targeting ribosomal DNA ITS regions. *Acta Tropica*, 109: 81–83.

- Schell, S. C. 1970. How to Know the Trematode. W.C. Brown Co, USA, 355 p.
- Shinn, A., Pratoomyot, J., Bron, J., Paladini, G., Brooker, E. and Brooker, A. 2015. Economic impacts of aquatic parasites on global finfish production. *Global Aquaculture Advocate*, 18: 58–61.
- Smales, L.R. and Cribb, T.H. 1997. Helminth parasite communities of the water-rat, *Hydromys chrysogaster*, from Queensland. *Wildlife Research*, 24: 445–457.
- Sripalwit, P., Wongsawad, C., Chontanarith, T., Anuntalabhochai, S., Wongsawad, P. and Chai, J.Y. 2015. Developmental and phylogenetic characteristics of *Stellantchasmus falcatus* (Trematoda: Heterophyidae) from Thailand. *The Korean Journal of Parasitology*, 53: 201–207.
- Srisawangwong, T., Pinlaor, S., Kanla, P. and Sithithaworn, P. 1997. *Centrocestus formosanus*: surface morphology of metacercaria, adult and egg. *Journal of Helminthology*, 71: 345–350.
- Sritongtae, S., Namchote, S., Krailas, D., Boonmekam, D. and Koonchornboon, T. 2015. Cercarial infections of brackish water snails on the east coast of southern Thailand. *Proceedings of the Joint International Tropical Medicine Meeting*, 3: 1–15.
- Surin, J. 1993. A description of a pleurolophocercous cercaria of *Procerovum* sp. from the *Haplorchis* group of heterophyid trematodes. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 24: 692–696.
- Suwanatrai, A., Saichua, P. and Haswell-Elkins, M. 2018. Epidemiology of *Opisthorchis viverrini* Infection. *Advances in Parasitology*, 101: 41–67.
- Tantachamrun, T. and Kliks, M. 1978. Heterophyid infection in human ileum: report of three cases. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 9: 228–231.
- Thach, N. N. 2021. New Shells of South Asia and Taiwan, China, Tanzania: Seashells, Freshwater, Land Snails: with 116 New Species & Subspecies and Rejected Synonyms, Accepted Species. 48Hr books Company, Akron, Ohio, USA, 202 p.
- Thaenkham, U., Blair, D., Nawa, Y. and Waikagul, J. 2012. Families Opisthorchiidae and Heterophyidae: are they distinct?. *Parasitology International*, 61: 90–93.
- Thaenkham, U., Dekumyoy, P., Komalamisra, C., Sato, M. and Waikagul, J. 2010. Systematics of the subfamily Haplorchiinae (Trematoda: Heterophyidae), based on nuclear ribosomal DNA genes and ITS2 region. *Parasitology International*, 59: 460–465.
- Tookhy, N.A., Mahiza, M.I.N., Mansor, R., Yasmin, A.R., Ahmad, N.I., Hamzah, N.H. and Idris, L.H. 2022. Rumen Fluke in Cattle and Buffaloes in Asia: A Review. *Pertanika Journal of Tropical Agricultural Science*, 45: 781–803.
- Towers, L. 2015. Economic impact of aquatic parasites on global finfish aquaculture production. *The Fish Site*. <https://thefishsite.com/articles/economic-impact-of-aquatic-parasites-on-global-fish-aquaculture-production>. Accessed 16 May 2024
- Ukong, S., Krailas, D., Dangprasert, T. and Channgarm, P. 2007. Studies on the morphology of cercariae obtained from freshwater snails at Erawan Waterfall, Erawan National Park, Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 38: 302–312.
- Umadevi, K. and Madhavi, R. 2000. Observations on the morphology and life cycle of *Procerovum varium* (Onji & Nishio, 1916) (Trematoda: Heterophyidae). *Systematic Parasitology*, 46: 215–225.
- Veeravechskij, N., Namchote, S., Neiber, M.T., Glaubrecht, M. and Krailas, D. 2018. Exploring the evolutionary potential of parasites: Larval stages of pathogen digenic trematodes in their thiarid snail host *Tarebia granifera* in Thailand. *Zoosystematics and Evolution*, 94: 425–460.
- Velasquez, C.C. 1958. *Transversotrema laruei*, a new trematode of Philippine fish (Digenea: Transversotrematidae). *Journal of Parasitology*, 44: 449–451.
- Velasquez, C.C. 1961. Further studies on *Transversotrema laruei* Velasquez with observations on the life cycle (Digenea: Transversotrematidae). *Journal of Parasitology*, 47: 65–70.
- Velasquez, C.C. 1973a. Observations on some Heterophyidae (Trematoda: Digenea) encysted in Philippine fishes. *Journal of Parasitology*, 59: 77–84.
- Velasquez, C.C. 1973b. Life cycle of *Procerovum calderoni* (Africa and Garcia, 1935), Price, 1940 (Trematoda: Digenea: Heterophyidae). *Journal of Parasitology*, 59: 813–816.
- Waikagul, J. and Thaenkham, U. 2014. Approaches to Research on the Systematics of Fish-Borne Trematodes. Academic Press, London, 154 p.
- Waikagul, J., Wongsaroj, T., Radomyos, P., Meesomboon, V., Praewanich, R. and Jongsuksantikul, P. 1997. Human infection of *Centrocestus caninus* in Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 28: 831–835.
- Witenberg, G. 1944. *Transversotrema haasi* a new fish trematode. *Journal of Parasitology*, 30: 179–180.
- Wongsawad, C., Nantararat, N. and Wongsawad, P. 2017a. Phylogenetic analysis reveals cryptic species diversity within minute intestinal fluke, *Stellantchasmus falcatus* Onji & Nishio, 1916 (Trematoda, Heterophyidae). *Asian Pacific Journal of Tropical Medicine*, 10: 165–170.
- Wongsawad, C., Rojanapaibul, A., Mhad-arehin, N., Pachanawan, A., Marayong, T., Suwattanacoupt, S., Rojtinnakorn, J., Wongsawad, P., Kumchoo, K. and Nichapu, A. 2000. Metacercaria from freshwater fishes of Mae Sa stream, Chiang Mai, Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health*, 31: 54–57.
- Wongsawad, C., Wongsawad, P., Sukontason, K., Maneepitaksanti, W. and Nantararat, N. 2017b. Molecular phylogenetics of *Centrocestus formosanus* (Digenea: Heterophyidae) originated from freshwater fish from Chiang Mai Province, Thailand. *The Korean Journal of Parasitology*, 55: 31–37.
- Yamaguti, S. 1971. Synopsis of Digenetic Trematodes of Vertebrates. Vol. I. Keigaku Publishing Co., Tokyo, Japan, 1074 p.
- Yamaguti, S. 1975. A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates. Keigaku Publishing Co., Kyoto, Japan, 590 p.
- Yu, S.H. and Mott, K. E. 1994. Epidemiology and morbidity of food-borne intestinal trematode infections. *Tropical Disease Bulletin*, 91: 125–152.