



Kannaphallus leptosomus n. sp. (Monogenea: Heteraxinidae: Cemocotylineae) parasitizing *Scyris indica* (Carangiformes: Carangidae) from Malaysia

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Abstract A new monogenean species, *Kannaphallus leptosomus* n. sp., from the gills of the diamond trevally, *Scyris indica* Rüppell, caught off Terengganu, Peninsular Malaysia is described with molecular data. The new species differs from other species of the genus by the morphology of the largest clamp, the presence of a penis gun-associated needle, the unarmed genital atrium size, and the presence of two independent vaginal tubes. Previous records of *Kannaphallus* species were compiled, and four nominal

species including one species *incertae sedis* (*K. virilis* Unnithan, 1957; *K. lateriporis* Mamaev, 1988; *K. leptosomus* n. sp.; and *K. mochimae* Fuentes Zambrano, 1998 *incertae sedis*) and two undescribed species recorded as invalid names were listed. *Cemocotylloides carangis* Ramalingam, 1969 was considered a junior objective synonym of *K. univaginalis* Ramalingam, 1960; this species was treated as *Cemocotylloides univaginalis* n. comb. In addition, Unnithan's materials including type specimens of *K. virilis* could not be found in specimen repositories in India, and it appears that the specimens were probably not deposited in any institution or have been subsequently lost. Based on the phylogenetic analysis of 28S rDNA sequences, Heteraxinidae was broadly divided into two clades, and Heteraxininae and

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Cemocotylinae were shown as polyphyletic groups, respectively.

Introduction

The diamond trevally, *Scyris indica* Rüppell, a carangid fish belonging to the subfamily Caranginae, is widely distributed in the tropic and sub-tropic of the Indo-Pacific Ocean (Froese & Pauly, 2021). This species is one of the commercially important and cultured in Singapore (Chou & Lee, 1997) and one of the targets for sport fishing (Froese & Pauly, 2021).

The genus *Kannaphallus* Unnithan, 1957 (Monogenea: Heteraxinidae) was established as monotypic for *K. virilis* Unnithan, 1957 from the gills of *Atropus atropus* (Bloch & Schneider) (as *Caranx atropus*) (Perciformes: Carangidae) off Trivandrum, Kerala, South India (Unnithan, 1957). This genus is distinguishable from the other heteraxinid genera by the presence of asymmetric clamps, paired vaginas, and a sclerotized ejaculatory duct named the ‘penis gun’ that is associated with the cirrus (Price, 1962; Mamaev, 1988). Price (1962) classified *Kannaphallus* into the subfamily Heteraxininae under the family Heteraxinidae. However, Mamaev (1988) transferred the genus into the subfamily Cemocotylinae based on the common morphological features with species of *Cemocotyle* Sproston, 1946, *Cemocotylella* Price, 1962, and *Cemocotylelloides* Ramalingam, 1969.

There are four species included in *Kannaphallus*: *K. virilis*, *K. lateriporis* Mamaev, 1988 described from *Caranx sexfasciatus* Quoy & Gaimard in the Gulf of the Mannar, South India (Mamaev, 1988), *K. mochima* Fuentes Zambrano, 1998 from *Acanthurus coeruleus* Bloch & Schneider (Perciformes: Acanthuridae) in Mochima, Venezuela (Fuentes Zambrano, 1998), and *K. univaginalis* Ramalingam, 1960 from *Ca. sexfasciatus* in South India (Ramalingam, 1960). However, *K. univaginalis* was poorly described in the original description and considered as invalid by Price (1962). Nevertheless, Fuentes Zambrano (1998) treated it as a valid taxon without any further discussion.

During our parasitological survey of commercially important fishes in coastal waters of Malaysia, specimens of *Kannaphallus* species were collected from *Scyris indica* off Terengganu, Peninsular Malaysia. This is the first record of *Kannaphallus* species

occurrence in Malaysia. We herein describe those specimens as a new species of *Kannaphallus* with molecular analysis. In addition, the results of an investigation for type specimens of *K. virilis* in specimen repositories of India are reported.

Materials and methods

One specimen of *Scyris indica* caught by local fishermen off Terengganu on the east coast of the Peninsular Malaysia was purchased from a local fish market at Kuala Terengganu, Malaysia on 8 December 2019. The specimen was transported on ice to the Aquatic Science Laboratory of Universiti Sultan Zainal Abidin, Besut Campus and examined for parasites. Monogeneans were removed from the gills using forceps under a dissecting microscope and fixed in 70% ethanol in vials.

Haptor and anterior body were excised from one specimen, dehydrated through a graded ethanol series, cleared in xylene, and mounted in Canada balsam, and the remaining posterior body were stored in 99% ethanol for molecular analysis. The other monogenean specimens were soaked in distilled water for 3 min, flattened under a coverslip on glass slides. Those specimens were stained in Heidenhain’s iron hematoxylin, dehydrated through a graded ethanol series, cleared in xylene, and mounted in Canada balsam (see Kuramochi, 2003). Drawings were made using a drawing tube fitted on a Nikon Optiphot-2 compound microscope equipped with phase contrast (Nikon, Tokyo, Japan). Measurements were obtained from images taken by a CANON EOS Kiss X2 digital camera (Canon, Tokyo, Japan) fitted onto the compound microscope using ImageJ software (version 1.48i, <http://rsb.info.nih.gov/ij/>) and were represented by straight-line distances between extreme points, but the length of the ovo-vitelline duct was measured curve length. All measurements in the description and Table 2 are in micrometres and given as the range followed by the mean \pm standard deviation and number (n) of specimens examined in parentheses. This study was conducted under the Collaborative Research Agreement between Hiroshima University and Universiti Sultan Zainal Abidin, which was established on 10 February 2020, and all specimens examined were deposited in the South China Sea Repository and Reference Center, University

Malaysia Terengganu, Terengganu, Malaysia (UMT-Platy). The host fish was identified morphologically based on Matsunuma et al. (2011); additionally, to confirm the host's identification, molecular analysis was carried out following Ohtsuka et al. (2020). The scientific names of fish used in this paper follow Kimura et al. (2022) for *Scyris*, *Platyccaranx* and *Turrrum* species, and Froese & Pauly (2021) for other fishes.

DNA was extracted from the body of a paratype using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). Partial fragments of the 28S rDNA sequence were amplified using the polymerase chain reaction (PCR) U178 (5'-GCA CCC GCT GAA YTT AAG-3': Lockyer et al. 2003) and LSU1200R (5'-GCA TAG TTC ACC ATC TTT CGG-3': Littlewood et al. 2000). Partial fragments of the mitochondrial cytochrome *c* oxidase subunit 1 gene (*cox1*) were amplified using the primer pair JB3 (5'-TTT TTT GGG CAT CCT GAG GTT TAT-3': Bowles et al. 1993) and COI-R trema (5'-CAA CAA ATC ATG ATG CAA AAG G-3': Miura et al. 2005). PCR was performed in a total volume of 15 µL, containing 7.5 µL KOD One PCR Master Mix (Toyobo, Osaka, Japan), 0.45 µL of each 10 µM primer, 0.7 µL of extracted DNA, and 5.9 µL of distilled water. The cycling for PCR consisted of an initial denaturation at 94°C for 2 min followed by 35 cycles of 98°C for 10 s, 56°C for 30 s, and 68°C for 30 s, with a final extension of 1 min at 68°C. The PCR products were purified using an ExoSAP-IT (USB Corporation, Cleveland, USA), and the sequencing was performed commercially (Macrogen Japan Corp., Kyoto, Japan). Sequence data and electropherograms were inspected and edited manually using MEGA7 (Kumar et al., 2016). The sequences obtained were submitted to the DNA Data Bank of Japan (DDBJ).

The obtained nucleotide sequence of *cox1* was subjected to a BLAST (<http://www.ncbi.nlm.nih.gov/>) search on 9 December 2021 for comparison with other sequences deposited in the International Nucleotide Sequence Databases (INSD). The phylogenetic relationships of Heteraxinidae species including the new species were estimated using maximum likelihood (ML) and Bayesian inference (BI) analyses. Sequences obtained in the present study for 28S rDNA was aligned with other heteraxinid sequences and two

sequences of Diclidophoridae retrieved from INSD (Table 1). The alignment was performed using MAFFT version 7 (Kato et al., 2019) using the “unalignlevel: 0.8” and “Leave gappy regions” options under the G-INS-i strategy. Ambiguous sites in the aligned datasets were removed with Gblocks ver. 0.91b (Castresana, 2000). The best-fit models were determined based on the Bayesian information criterion using IQ-TREE version 2.0.4. (Kalyaanamoorthy et al., 2017; Minh et al., 2020). The ML phylogeny was constructed under the TPM3+F+G4 model using IQ-TREE version 2.0.4 with 1,000 bootstrap replicates. BI phylogeny and Bayesian posterior probabilities were estimated using MrBayes 3.2.6 (Ronquist et al., 2012) under the GTR+G+I model. Two independent runs of four Markov chains were conducted for 1,000,000 generations and the tree was sampled every 100 generations. Parameter estimates and convergence were checked using Tracer v. 1.6.0 (Rambaut & Drummond, 2013); the first 25,000 samples from each run were discarded as burn-in and the remaining samples were analyzed.

Surveys of the type specimens of *K. virilis* Unnithan, 1957 were made by P. T. Aneesh (Department of Aquatic Biology & Fisheries, University of Kerala) at the following five institutions where Unnithan's specimens may have been deposited in India: the Indian Museum, Kolkata, the Department of Aquatic Biology & Fisheries, University of Kerala, Trivandrum, Cochin University of Science and Technology, the Western Ghat Field Research Centre of Zoological Survey of India, Kozhikode (ZSI/WGRC), and the Central Marine Fisheries Research Institute (CMFRI), Vizhinjam, Trivandrum during November 2021.

Mazocraeidea Bychowsky, 1957

Heteraxinidae Unnithan, 1957

Cemocotylinae Price, 1962

Kannaphallus Unnithan, 1957

Type species. *K. virilis* Unnithan, 1957.

Other species. *K. lateriporis* Mamaev, 1988; *K. leptosomus* n. sp.

Species incertae sedis. *K. mochimae* Fuentes Zambrano, 1998.

Table 1 List of 28S rDNA sequences of monogeneans used in this study with INSD (GenBank/ENA/DBJ) accession numbers.

Monogenean species	Host	Locality		Accession number	Reference
		Country	Site		
Heteraxinidae					
Heteraxininae					
<i>Heteraxinoides atlanticus</i> Gayevskaya & Kovaleva, 1979 ^a	<i>Nemipterus japonicus</i> (Bloch) (Nemipteridae)	India	Arabian Sea, Mumbai	KU245366	Verma & Verma (2021)
<i>Probursata brasiliensis</i> Takemoto, Amato & Luque, 1993	<i>Oligoplites</i> sp. (Carangidae)	Brazil	–	AF382049	Olson & Littlewood (2002)
<i>Zeuxapta seriola</i> (Meserve, 1938)	<i>Seriola lalandi</i> Valenciennes (Carangidae)	Australia	Coral Sea, Heron Island	AF026103	Mollaret et al. (1997)
	<i>S. lalandi</i>	Australia	Great Australian Bight, Adelaide	EF653384	Aiken et al. (2007)
	<i>S. lalandi</i>	Chile	–	MT890121	Unpublished
	<i>S. lalandi</i>	Brazil	South Atlantic, Rio de Janeiro	MG981034	Camargo & Santos (2020)
Cemocotylinae					
<i>Cemocotyle carangis</i> (MacCallum, 1913)	<i>Caranx latus</i> (Agassiz) (Carangidae)	Brazil	South Atlantic, Rio de Janeiro	MG984598	Camargo & Santos (2020)
<i>Cemocotylelloides univaginalis</i> (Ramalingam, 1960) n. comb. ^b	<i>Caranx sexfasciatus</i> (Quoy & Gaimard)	India	Arabian Sea, Mumbai	KF804031	Tambireddy et al. (2016)
<i>Kannaphallus leptosomus</i> n. sp.	<i>Scyris indica</i> Rüppell (Carangidae)	Malaysia	South China Sea, Terengganu, Kuala Terengganu	LC664021	Present study
Lintaxininae					
<i>Bicotyle reticulata</i> (Goto, 1894) ^c	<i>Pampus punctatissimus</i> (Temminck & Schlegel) (Stromateidae)	Japan	Hiuchi-nada, Seto Inland Sea, Ehime	LC664020	Present study
Diclidophoridae					
<i>Diclidophora denticulate</i> (Olsson, 1876)	<i>Pollachius virens</i> (Linnaeus) (Gadidae)	UK	North Sea	AY157169	Lockyer et al. (2003)
<i>Choricotyle australiensis</i> Roubal, Armitage & Rohde, 1983	<i>Chrysophrys auratus</i> (Forster) (Sparidae)	New Zealand	South Pacific Ocean	MT782270	Hossen et al. (2020)

^a, ^bThese species names are registered as *Heteraxinoides* sp. and *Cemocotylelloides carangis*, respectively.

^cThe specimen of this species was collected, identified and analyzed by the first author as unpublished data.

***Kannaphallus leptosomus* n. sp.**

Type-host: *Scyris indica* Rüppell (Carangiformes: Carangidae: Caranginae).

Type-locality: Off Kuala Terengganu, Terengganu, Malaysia, east coast of the Peninsular Malaysia.

Type-materials: Holotype (UMTPlaty 0014) and 12 paratypes (UMTPlaty 0015–0026, 0029). All adult specimens.

Site of infection: Gill filament.

Representative DNA sequences: DDBJ accession numbers LC664021 (28S rDNA) and LC664022

(*cox1*). The sequences were obtained from a paratype (UMTPlaty 0029 [UMTGen 2479]).

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Kannaphallus leptosomus* n. sp. is urn:lsid:zoobank.org:act: 993E5C7E-AEAD-4531-931C-A099C570A468.

Etymology: The new scientific name is from Greek words (*leptós* = slender + *sôma* = body) and refers to the relatively slender body of the new species within the genus.

Description (Fig. 1)

Body (Fig. 1A) elongate, slightly expanding from the anterior end to the posterior end, total length 5441–8162 (6536 ± 761.3 , $n = 13$), maximum width 442–946 (612 ± 139.7 , $n = 13$) in front of the haptor, length: width ratio 1: 0.064–0.158 (0.095 ± 0.03 , $n = 13$). Haptor (Fig. 1A) asymmetrical with 34–42 (39 ± 3.0 , $n = 8$) clamps in total; long row 1325–1874 (1514 ± 166.3 , $n = 8$) in length with 24–32 (28 ± 2.8 , $n = 8$) clamps; short row 632–1061 (853 ± 133.3 , $n = 8$) in length with 10–12 (11 ± 0.9 , $n = 8$) clamps. Clamps (Fig. 1G) *Microcotyle*-type, largest clamp 76–92 × 82–97 ($85 \pm 4.4 \times 88 \pm 6.0$, $n = 11$), length: width ratio 1: 0.94–1.11 (1.04 ± 0.05 , $n = 11$), slightly asymmetrical, consisting of a pair of antero-lateral and postero-lateral sclerites, mid sclerite, accessory sclerite, and thin muscular base; antero-lateral and postero-lateral sclerites slender, taped toward both ends, left sclerites both slightly longer; mid sclerite with dorsal and ventral T-shaped terminations; slender trident-shaped accessory sclerite at dorsal termination of median sclerite. Anchor absent.

Mouth (Fig. 1A, D) subterminal, wide; its margin irregular, wavy, and anterior margin associated with grand cells. Eye-spots absent. A pair of prohaptor suckers (Fig. 1D) oval, muscular, lying in each lateral wall of buccal cavity, 50–69 × 49–95 ($61 \pm 5.7 \times 73 \pm 10.4$, $n = 13$). Pharynx (Fig. 1D) oval to elliptical, 50–76 × 39–53 ($59 \pm 6.2 \times 45 \pm 3.9$, $n = 14$). Esophagus (Fig. 1A, D) with small lateral diverticula. Intestinal bifurcation dorsal to genital atrium. Intestinal ceca with lateral and median diverticula, extending into haptor; not confluent posteriorly.

Testes (Fig. 1A) numerous, 100–151 (120 ± 16.8 , $n = 11$) in number, spherical to oval, 69–94 (81 ± 6.8 , $n = 12$) long, 40–60 (51 ± 6.5 , $n = 12$) wide; testicular zone intercecal, posterior to germarium, entering anterior side of haptor, 1864–2823 × 201–420 ($2221 \pm 303.1 \times 274 \pm 71.9$, $n = 11$). Vasa efferentia (Fig. 1E) with thin wall, traveling up while merging each other, then becoming vas deferens at the top of the testicular zone. Vas deferens (Fig. 1A, C, E) running anteriorly, heavily coiled on anterior of germarium, surrounded by accessory grands, meandering slightly along the midline and traveling anteriorly, expanded seminal vesicle. Seminal vesicle (Fig. 1C) elongate, muscular, 158–268 × 45–62 ($225 \pm 27.1 \times 56 \pm 5.4$, $n = 13$), containing prostatic cells, lying postero-lateral to part of ejaculatory bulb; its duct meandering, ascending to anterior part of ejaculatory bulb, looping downwards and entering base of ejaculatory bulb. Ejaculatory bulb (Fig. 1C) muscular, ovate, 46–62 × 46–74 ($56 \pm 5.4 \times 60 \pm 7.9$, $n = 13$), connecting base of sclerotized ejaculatory duct, ‘penis gun’, as named by Unnithan (1957). Penis gun (Fig. 1B, C) straight, tapering towards anterior end; extreme tip slightly expanded and slightly bifurcated from which needle associated with base of cirrus arises; 199–228 (212 ± 8.0 , $n = 14$) long including the needle part, 169–182 (176 ± 4.1 , $n = 14$) long excluding the needle part, 20–26 (24 ± 1.8 , $n = 14$) wide at base, needle part 35–54 (48 ± 6.0 , $n = 14$) long. Cirrus muscular, round bowl-shaped, unarmed, 12–27 (19 ± 4.4 , $n = 14$) in diameter, opening posterior to uterine opening in genital atrium. Genital atrium (Fig. 1C) muscular, ovate to pyriform, unarmed, 104–189 × 75–134 ($151 \pm 22.7 \times 101 \pm 16.7$, $n = 14$), length: width ratio 1: 0.50–0.75 (0.67 ± 0.08 , $n = 14$), opening mid-ventrally at level of the intestinal bifurcation.

Germarium (Fig. 1E) elongate in the shape of a question mark, intercecal, middle third of the body, width at midline 32–62 (44 ± 9.6 , $n = 9$). Oviduct (Fig. 1E) slightly muscular, arising to the right of the anterior terminal of germarium, running downwards, turning left while branching to genitointestinal canal, then entering the vitelline duct to form the oovitelline duct on the midline near the proximal part of germarium, 131–191 (151 ± 20.9 , $n = 7$) long. Oovitelline (Fig. 1E) duct running sinistrally, turning upwards and forming oötype surrounded Mehlis’ grand and continuing to uterus, 92–118 (107 ± 10.8 ,

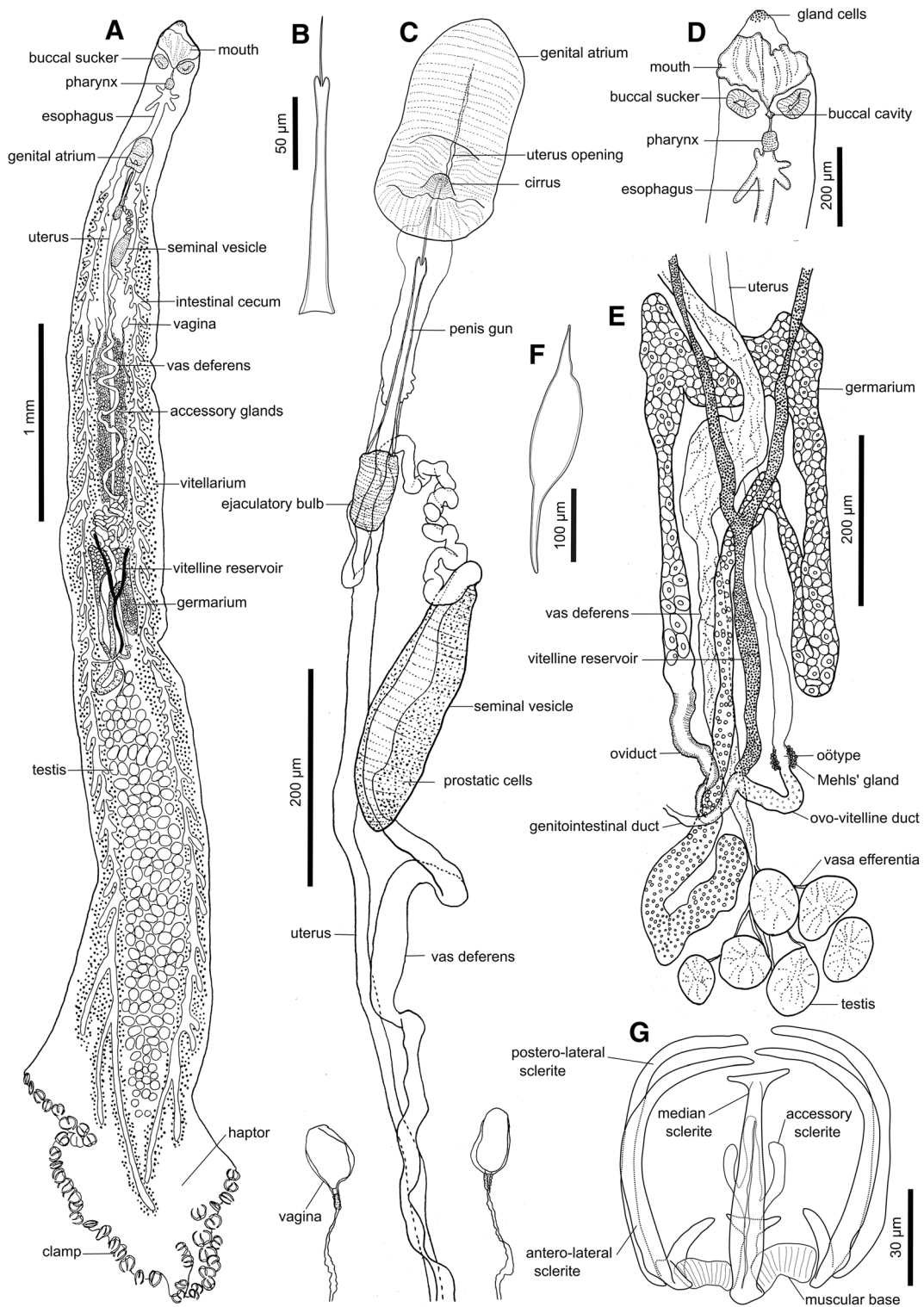


Fig. 1 *Kannaphallus leptosomus* n. sp. parasitizing *Scyris indica* Rüppell off Terengganu, east coast of the Malay Peninsula. A–E, G: holotype, ventral view (UMTPlaty 0014); F: paratype (UMTPlaty 0017). A, whole body; B, penis gun; C, anterior part of reproductive system; D, anterior end; E, posterior part of reproductive system; F, egg in uterus; G, closed clamp.

n = 7) long. Uterus (Fig. 1C, E) running midline anteriorly on dorsal side; opening vertical slit-shaped, anterior to cirrus in genital atrium. Two vaginae (Fig. 1A, C), individually opening on both sides of dorsal surface at interceca, level of anterior one-fifth between posterior margin of seminal vesicle and anterior margin of germarium; opening cup shape, weakly sclerotized, $49\text{--}74 \times 23\text{--}37$ ($62 \pm 7.0 \times 32 \pm 4.5$, n = 13); each vaginal duct possessing small muscular sphincter near their openings, flowing into the longitudinal vitelline ducts. Sperm receptacle absent. Vitelline reservoir (Fig. 1A, E) Y-shaped, slender, median, ventral to germarium; vitellarium coextensive with intestinal ceca, extending into haptor. Genitointestinal canal (Fig. 1E) dextral, connecting to the right of intestinal cecum. Egg (Fig. 1F) spindle-shaped, $279\text{--}369 \times 54\text{--}65$ (314×59 , n = 3) with short filament.

Remarks

The new species is assigned to *Kannaphallus* due to the presence of the genus characteristics defined by Unnithan (1957), Price (1962), and Yamaguti (1963), such as the presence of asymmetric clamps, paired vaginae, and a penis gun associated with the cirrus. Morphological measurements and features of *Kannaphallus* species, including invalid ones, are presented in Table 2. *Kannaphallus leptosomus* n. sp. is readily separated from *K. mochimae incertae sedis* by the possession of an armed cirrus and lack of a penis gun of the latter (Fuentes Zambrano, 1998). The new species is distinguished from *K. virilis* by the following features: the presence of a needle associated with the tip of the penis gun (Unnithan, 1957; Lebedev et al., 1970) and a larger clamp ($76\text{--}92 \times 82\text{--}97$ μm vs. $32\text{--}52 \times 40\text{--}60$ μm : Unnithan, 1957). The clamp of the new species is also larger than that of *K. lateriporis* (vs. 65×62 μm : Mamaev, 1988). Furthermore, the new species differs from *K. lateriporis* by a longer penis gun associated with the needle and larger genital atrium ($199\text{--}228$ μm vs. $74\text{--}82$ μm : Mamaev, 1988 and $104\text{--}189 \times 78\text{--}134$ μm vs. $40\text{--}41 \times 37\text{--}40$ μm : Mamaev, 1988, respectively). The vertical duct of the vagina connecting each vaginal duct reported by Mamaev (1988) in *K. lateriporis* is absent from *K. leptosomus* n. sp. The new species is also distinguished from the two *Kannaphallus* species reported

by Pillai (1968) (see the Discussion) by the sizes of the clamp, penis gun, and egg (see Table 2).

Kannaphallus univaginalis described by Ramalingam (1960) was considered an invalid taxon by Price (1962), but Fuentes Zambrano (1998) treated it as a valid taxon. Ramalingam (1960) named the monogenean as “*Kannaphallus univaginalis* n. sp.” with a short and limited description with figures and the development of functional asymmetry. Although the description is certainly inadequate, this paper fully meets the criteria for establishing a new scientific name (ICZN, 1999), and as a result, *Kannaphallus univaginalis* is remained as a valid name to this date. Nevertheless, Ramalingam (1969) used the same specimens of Ramalingam (1960) to describe *Cemocotylelloides carangis* Ramalingam, 1969 and admitted that he had already reported it as *K. univaginalis* (Ramalingam, 1969: p. 231). Therefore, *Cemocotylelloides carangis* is considered as a junior objective synonym. The species is henceforth treated as *Cemocotylelloides univaginalis* n. comb. which is readily separated from *Kannaphallus* species due to the presence of only one vagina (Ramalingam, 1969).

The partial cytochrome *c* oxidase subunit I gene sequence (538 bp) from the host was deposited in GenBank (accession number: OM868132). The sequence showed 99.43% similarity to sequences of the same species in GenBank (KU179066) and in the BOLD identification engine (Ratnasingham & Hebert, 2007). *Scyris* is composed of 2 species: *S. indica* and *S. alexandrina* (Geoffroy Saint-Hilaire) (Kimura et al., 2022), and the similarity of *cox1* sequences of each species registered in INSD is less than 90%, thus this confirms the identification of the host species.

Note of the type specimen of *Kannaphallus virilis* Unnithan, 1957

Unnithan (1957) erected the genus *Kannaphallus* Unnithan, 1957 for placing the new species *Kannaphallus virilis* Unnithan, 1957, based on three specimens collected from the gill of the marine fish *Caranx atropus* (now *Atropus atropus*), collected at Trivandrum in Kerala, India from 10 November 1955. Unfortunately, Unnithan (1957) did not mention the deposition of the type materials. The survey of specimens housed at the Indian Museum, Kolkata, the Department of Aquatic Biology & Fisheries, University of Kerala, Trivandrum, and Cochin

Table 2 Morphological characteristics, measurements, and counts of *Kannaphallus* species.

Species	<i>K. leptosomus</i> n. sp.	<i>K. virilis</i>	<i>K. virilis</i>	<i>K. lateriporis</i>	<i>K. mochimae</i> (<i>incertae</i> <i>sedis</i>)	<i>Kannaphallus</i> sp. 1 as <i>K.</i> <i>bivagina</i> (invalid)*	<i>Kannaphallus</i> sp. 2 as <i>K.</i> <i>carangis</i> (invalid)*
Source of data	Present study	Unnithan (1957)	Lebedev et al. (1970)	Mamaev (1988)	Fuentes Zambrano (1998)	Pillai (1968)	Pillai (1968)
Specimens examined	14	3	No data	3	No data	65	6
Locality	Terengganu, Kuala Terengganu, Malaysia	Trivandrum, India	Gulf of Tonkin, Vietnam	Gulf of the Mannar, India	Mochima, Venezuela	Trivandrum, India	Neendakara near Quilon, India
Host	<i>Scyris indica</i>	<i>Atropus atropus</i>	<i>Scyris indica</i> ; <i>Platyecarax malabaricus</i>	<i>Caranx sexfasciatus</i>	<i>Acanthurus coeruleus</i>	<i>Turram gymnostethus</i>	<i>Caranx</i> sp.
Host family	Carangidae	Carangidae	Carangidae	Carangidae	Acanthuridae	Carangidae	Carangidae
Body	5441–8162 × 442–946	3500–3600 × 825–840	10260–11530 × 700	3980–4370 × 1000–1060	1511–1990 × 556–733	7722–10298 × 425–612	2680–4680 × 400–890
Prohaptor sucker	50–69 × 49–95	45–60 × 60–75	—	50	40–51 × 32–46	82–102 × 48–68	40–64 × 36–62
Pharynx	50–76 × 39–53	45	—	60	40–41 × 26–32	42–44 × 32–36	40–62 × 36–62
Haptor	625–1185 × 346–1562	1050–1100	—	—	—	—	—
Length of long row	1325–1874	—	—	1460–1580	1156–1378	642–1050	840–1400
No. of clamps of long row	24–32	28–31	16–29	29–38	47–51	24–30	24–35
Length of shorter row	632–1061	—	—	400–500	489–578	—	390–560
No. of clamps of shorter row	10–12	12–15	11–14	7–12	22–25	8–10	12–14
Clamp	76–92 × 82–97	32–52 × 40–60	—	65 × 62	58–70 × 40–58	32–44 × 36–54	50–52 × 80–88
Form of accessory sclerite	trident	conical	trident	trident	absent	trident	trident
No. of testes	100–151	> 100	> 150	110–130	15–20	—	170
Testis	69–94 × 40–60	45–60	—	—	40–41 × 52–62	—	—
Testicular zone	1864–2823 × 201–420	1100 × 255	—	—	—	2210–2420 × 138	1120–1850 × 160–280
Seminal vesicle	158–268 × 45–62	150 × 60	—	—	—	—	125 × 55
Ejaculatory bulb	46–74 × 24–32	40 × 20	—	—	absent	—	—

Table 2 continued

Species	<i>K. leptosomus</i> n. sp.	<i>K. virilis</i>	<i>K. virilis</i>	<i>K. lateriporis</i>	<i>K. mochimae</i> (<i>incertae</i> <i>sedis</i>)	<i>Kannaphallus</i> sp. 1 as <i>K.</i> <i>bivagina</i> (invalid)*	<i>Kannaphallus</i> sp. 2 as <i>K.</i> <i>carangis</i> (invalid)*
Penis gun	199–228 × 20–26	150 × 15	267	74–82	absent	118–128	160–180
Penis gun excluding needle part	169–182 × 20–26	—	—	—	—	—	—
Cirrus	12–27	20	—	—	34	—	—
No. of genital spine	absent	absent	—	absent	28	absent	absent
Genital atrium	104–189 × 75–134	135–150 × 90–105	133 × 103	40–41 × 37–40	62–64	101–144 × 78–116	—
Vaginal pore	49–74 × 23–37	32	—	—	16	—	—
Egg	279–359 × 54–65	—	—	150–160 × 50–60	—	158–172 × 58–72	130 × 55

*Pillai (1968) did not satisfy the publication criteria defined by the International Commission on Zoological Nomenclature (ICZN, 1999, 2012: Articles 8.1.2 and 8.1.3). Thus, those two scientific names were judged to be invalid and were regarded *Kannaphallus* sp. 1 and sp. 2 in this paper

University of Science & Technology failed to reveal any of Unnithan's (1957) specimens including the types for *K. virilis*. The survey of repositories of the Western Ghat Field Research Centre of Zoological Survey of India, Kozhikode (ZSI/WGRC) (established in April 1980) and the Central Marine Fisheries Research Institute (CMFRI), Vizhinjam (well established after 1960) also failed to reveal the materials. Further, if the author indeed deposited the types in any repositories, he would have been required to mention the registration number. However, since there were no museum records of Unnithan's (1957) materials in any of the repositories surveyed, it appears that those specimens were probably never deposited in any institution or have been subsequently lost.

Molecular data analysis

Comparing the *cox1* sequence of *K. leptosomus* **n. sp.** from other monogeneans available on INSD by BLASTn search, the closest hits were *Microcotyle sebastis* Goto, 1894 (DQ412044: Park et al., 2007,

MT876115–MT876119: Song et al., 2021, MW730642: direct submission, 76.42–78.14% identity with 85–99% coverage), *Microcotyle caudata* Goto, 1894 (MT180126: Nam et al., 2020, LC472527–LC472531: Ono et al., 2020, MW730633–MW730634: direct submissions, 76.52–78.40% identity with 77–99% coverage), *Microcotyle kasago* Ono, Matsumoto, Nitta & Kamio, 2020 (LC472525–LC472526: Ono et al., 2020, 77.16–77.25% identity with 83% coverage) and *Zeuxapta seriola* (Meserve, 1938) (KP119183–KP119357: Sepúlveda & González, 2015, 77.01–77.39% identity with 82% coverage).

The trimmed multiple sequence alignment of 28S rDNA fragments consisted of 544 base pairs. Sequences of two diclidophorids were used as the outgroups following Tambireddy et al. (2016). The topologies of the trees constructed by ML and BI analysis were almost identical (Fig. 2). *Kannaphallus leptosomus* **n. sp.** was placed as a sister group with another Cemocotyline species, *Cemocotylloides carangis*. This clade showed affinity with two species of Heteraxononae, *Zeuxapta seriola* and

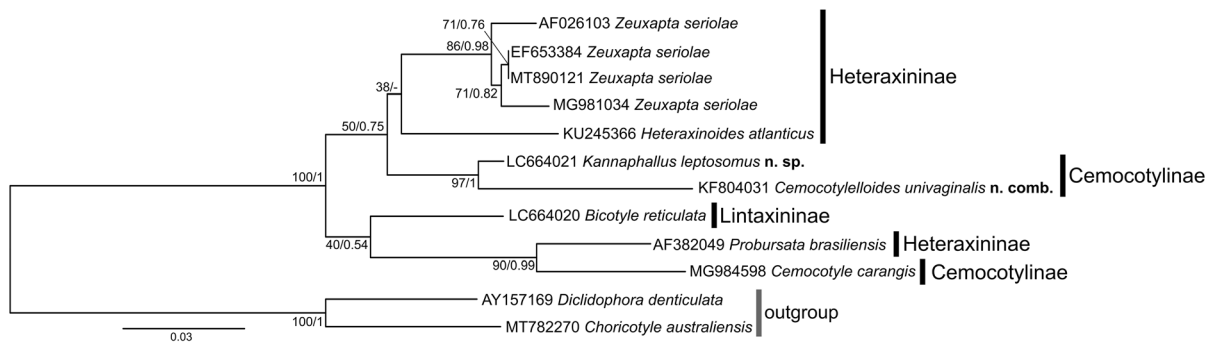


Fig. 2 Maximum Likelihood (ML) tree for the Heteraxinidae based on partial 28S rDNA data (544 bp) using two species of Diclidophoridae as the outgroup. The corresponding INSD accession numbers are shown. The tree includes results for ML and Bayesian inference with BS/PP branch support.

Heteraxinoides atlanticus. On the other clade, *Bicotyle reticulata* (Lintaxininae) diverged first, then *Probursatra brasiliensis* (Heteraxininae) and *Cemocotyle carangis* (Cemocotylineae) formed a clade.

Discussion

The present collection from *S. indica* represents the first record of *Kannaphallus* in Malaysia. In total, 10 monogenean species from Caranginae were recorded in Southeast Asia (Lim, 1998). However, the list of Southeast Asian monogeneans completed by Lim (1998) overlooked *K. virilis* reported from Vietnam by Lebedev (1970) and Lebedev et al. (1970).

Lebedev (1970) and Lebedev et al. (1970) reported *K. virilis* from *S. indica* (as *Alectis indicus*) and *Platycaranx malabaricus* (Bloch & Schneider) (as *Caranx malabaricus*) in the Gulf of Tonkin, North Vietnam, and Lebedev et al. (1970) provided a short description but no figure. There were two major differences between this redescription and the original description by Unnithan (1957), but Lebedev et al. (1970) did not mention them: the accessory sclerite shape (conical: Unnithan, 1957 vs. trident: Lebedev et al., 1970) of the clamp and the penis gun length (150 μm : Unnithan, 1957 vs. 267 μm : Lebedev et al., 1970). The former difference may result from an observational mistake by Unnithan (1957) because the accessory sclerite is a small and thin structure, whereas those of other congeners have trident-shaped structure (Table 2). On the other hand, the difference in penis gun length (117 μm) is too long to be considered intraspecific variation because the variation in the

length is less than 30 μm in other species (see Table 2). Furthermore, the specimens reported by Lebedev et al. (1970) were substantially longer than those of other species, including the new species, *K. leptosomus* n. sp. (Table 2). Therefore, the record of Lebedev et al. (1970) may not be *K. virilis* and it cannot be confirmed if the specimens reported by Lebedev et al. (1970) included *K. leptosomus* n. sp. A reexamination of their specimens or *Kannaphallus* species that parasitize the reported hosts in the region is required.

Kannaphallus mochimae is the only *Kannaphallus* species that parasitizes an acanthurid host (Fuentes Zambrano, 1998). However, the original description of this species lacks the morphological features possessed by *Kannaphallus* species: the longitudinal vaginal ducts, asymmetrical clamp, accessory sclerite, unarmed genital atrium, penis gun, and conspicuous seminal vesicle. Furthermore, other *Kannaphallus* species have been recorded from carangids in the western Indo-Pacific, whereas only *K. mochimae* has been obtained from the Atlantic Ocean (Unnithan, 1957; Pillai, 1968; Young, 1970; Lebedev, 1970; Lebedev et al., 1970; Mamaev, 1988; Fuentes Zambrano, 1998; present study). Therefore, we consider *K. mochimae* regarded as *incertae sedis* in the genus. *Kannaphallus mochimae* is morphologically similar to *Probursata* species (Heteraxinidae: Heteraxininae) reported from the Western Atlantic, and *Probursata* species also possesses two vaginae (Bravo-Hollis, 1984; Takemoto et al., 1993). However, *K. mochimae* lacks two features of *Probursata*: the accessory sclerite of the clamp and the muscular auricular expansions of the genital atrium (Bravo-Hollis, 1984; Takemoto et al., 1993; Fuentes Zambrano, 1998).

Unfortunately, Fuentes Zambrano (1998) did not provide information on the deposit of type specimens and its whereabouts are unknown. We believe that re-examination of some characteristics (e.g., the morphology of the clamp and genital atrium) can determine the generic position of this species based on newly collected specimens.

Pillai (1968) described two *Kannaphallus* species in his doctoral dissertation, which has so far been overlooked by subsequent researchers: *K. bivagina* Pillai, 1968 from *Turrum gymnostethus* (Cuvier) (as *Carangoides gymnostethoides* Bleeker) and *K. carangis* Pillai, 1968 from *Caranx* sp. in Trivandrum and Neendakara, Kerala, South India, respectively. However, this did not satisfy the publication criteria defined by the International Commission on Zoological Nomenclature (ICZN, 1999, 2012: Articles 8.1.2 and 8.1.3). Thus, all scientific names described in this paper and its authorship were judged to be invalid, and those two species were regarded *Kannaphallus* sp. 1 and sp. 2 in this paper. According to the descriptions of Pillai (1968), these two species can be distinguished from other *Kannaphallus* species by the following features: the vaginal opening position, clamp size, and the unarmed genital atrium (see Table 2). Therefore, they may be independent taxa. Re-examinations of these specimens and a formal publication of descriptions are expected.

In the 28S rDNA-based phylogenetic analysis presented in this study (Fig. 2), Heteraxinidae was broadly divided into two clades, and Heteraxininae and Cemocotylinae were shown as polyphyletic groups, respectively. This family consists of 5 sub-families, 16 genera, and c. 60 species (Mamaev, 1990; Gibson, 2021), and the molecular information of limited species is insufficient to change the classification based on the present phylogenetic analysis. Broad taxon sampling of Heteraxinidae is required for a detailed understanding of the phylogenetic relationships and reconstruction of the family.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national, and international guidelines for the care and use of animals were followed.

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