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Rhadinorhynchus villalobosi sp. n. (Acanthocephala: Rhadinorhynchidae) from the gafftopsail pompano *Trachinotus rhodopus* (Carangiformes: Carangidae) from the Pacific coast in Mexico

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Abstract: A new species of Acanthocephala is described based on specimens found parasitising the intestine of the gafftopsail pompano *Trachinotus rhodopus* Gill in the State of Oaxaca, off the Pacific coast of Mexico. *Rhadinorhynchus villalobosi* sp. n. differs from the other 25 species of the genus known from the Pacific Ocean by a combination of morphological traits, such as the fewer number of rows of hooks along the proboscis, the distribution of spines of the trunk forming two fields, the position of genital pore, subterminal in both sexes, a shorter neck and cement glands, among others. The phylogenetic analyses based on sequences of the nuclear 18S and 28S rRNA genes, as well as the mitochondrial *cox1*, all agree that *R. villalobosi* sp. n. is part of the genus, and closely related to *Rhadinorhynchus trachinoti* Grano-Maldonado, Sereno-Uribe, Hernández-Payán, Pérez-Ponce de León et García-Varela, 2025, a recently described Mexican species, despite the marked morphological differences between the two and being distributed in different areas.

Keywords: Taxonomy, phylogeny, thorny-headed worms, Palaeacanthocephala

Rhadinorhynchus Lühe, 1911 includes around 47 species, most of them parasites of the intestine of marine fishes of the families Scombridae and Carangidae, distributed in various regions of the Pacific and Atlantic Oceans (Chaudhary et al. 2020). This genus is characterised by having a long and cylindrical trunk, slightly wider at the anterior region, with the presence of numerous small hypodermal nuclei, spines of the trunk in one or two fields separated by an aspinose area, or alternatively, fields united by spines on the sides. Spines of the anterior field form complete circles or rings around the trunk. Spines of the posterior field are larger in dorsal, ventral, or in both regions compared to the anterior field. Proboscis is elongated with 8–26 rows with 17–48 hooks each (Amin et al. 2019c).

Several authors have significantly contributed to the understanding of the diversity of the genus, primarily from the Pacific (for example Amin et al. 2019a–c, Kita et al. 2024). In the New World, there are only few published records in Mexico, Brazil, and Peru, referring new species described in the three countries (Braicovich et al. 2014, Amin and Heckmann 2017, Grano-Maldonado et al. 2025).

In Mexico, according to the records of the Colección Nacional de Helmintos (CNHE), Instituto de Biología (IB), Universidad Nacional Autónoma de Mexico (UNAM), a total of 76 species of Acanthocephala have been recorded, mostly in fish. Particularly, records of species of *Rhadinorhynchus* have been poorly documented, being *Rhadinorhynchus dujardini* Golvan, 1969 collected in *Ocyurus chrysurus* (Bloch) from Veracruz (Gulf of Mexico) (Montoya-Mendoza et al. 2014), *Rhadinorhynchus* cf. *pristis* (Rudolphi, 1802) of Santos-Bustos et al. (2020) from *Scomberomorus sierra* Jordan and Starks of Guerrero (Pacific Ocean), and *Rhadinorhynchus trachinoti* Grano-Maldonado, Sereno-Uribe, Hernández-Payán, Pérez-Ponce de León et García-Varela, 2025, in *Trachinotus rhodopus* Gill from Mazatlán, Sinaloa, the only taxa identified to species level to 2025. In addition, some records of *Rhadinorhynchus* sp. have been made in both slopes of Mexico, in fishes of the families Carangidae, Scombridae and Lutjanidae (Gallegos-Navarro et al. 2018, Santos-Bustos et al. 2018, Violante-González et al. 2024).

Previous phylogenetic studies regarding the class Paleacanthocephala were based on nuclear ribosomal and mitochondrial DNA sequences (Verweyen et al. 2011, Chaudhary et al. 2020), with a limited representation of species of *Rhadinorhynchus*. Interestingly, these studies have failed to recover *Rhadinorhynchus* as monophyletic, being poly- or

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Table 1. Primers used for amplification and sequencing of the tree molecular markers used in this study.

Marker	Primer name	Primer sequence (5´-3´)	Reference
cox1	507	AGTTCTAATCATAAR-GATATYGG	Nadler et al. (2006)
	HCO2198	TAAACTTCAGGGT-GACCAAAAAATCA	Folmer et al. (1994)
18S	18S F	GCAGCGCGGTAATTC-CAGCTC	García-Varela et al. (2020)
	18S R	GCAGGTTCACCTACG-GAAA	Garey et al. (1996)
28S	501	TCGGAAGGAACCAGC-TACTA	Smythe and Nadler (2006)
	504	CAAGTACCGTGAGG-GAAAGTTG	Smythe and Nadler (2006)

paraphyletic, depending on the molecular marker analysed or the phylogenetic method used. In the last years, there have been some advances in the phylogeny of the family, with the erection of the genus *Spinulacorpus* Huston et Smales, 2020 and the family Spinulacorpidae Huston et Smales, 2020 to accommodate *Rhadinorhynchus biformis* Smales, 2014 and resolve the paraphyly of the Rhadinorhynchidae (Huston and Smales 2020).

Recently, specimens of acanthocephalans parasitising the intestine of the gafftopsail pompano *T. rhodopus* (Carangidae) were collected in Puerto Ángel, Oaxaca, off the tropical Pacific coast of Mexico. Morphological analyses of the newly collected specimens indicate that it represents a new species, which is described and named herein.

MATERIALS AND METHODS

Specimen collection and morphological examination

A total of 110 specimens of the gafftopsail pompano *Trachinotus rhodopus* (total length 6.6–47 cm; mean 30 cm) were collected off Oaxaca coast in the Mexican Pacific and subjected to helminthological studies. Samplings were conducted throughout the year 2018 (see Martínez-Flores et al. 2023 for details). Acanthocephalans were relaxed in cold distilled water until the proboscis was totally everted. Subsequently, some specimens were fixed and preserved in 96% ethanol for molecular biology studies and some with 4% hot formaldehyde and preserved in 70% ethanol for studies of the morphological attributes. For morphological study, worms were punctured with a fine needle, stained with Mayer's paracarmine, differentiated in 2% acidulated alcohol, dehydrated in ascending ethanol concentration until reaching absolute ethanol, cleared in methyl salicylate, and permanently mounted on Canada balsam. Eight worms were processed for their study under scanning electron microscopy (SEM). Briefly, specimens were washed with Tween 20 (Aurion) and sonicated to remove organic residues; subsequently, they were dehydrated with absolute ethanol, dried to critical point with CO_2, coated with a gold-palladium mixture in an Emitech K550 metallizer. All worms were observed in a Hitachi S2460N microscope at the Laboratorio Nacional de la Biodiversidad (LANABIO), IB, UNAM.

All the measurements in the text and tables are in micrometers, unless otherwise specified; the range value is followed by the mean in parenthesis and the sample size (n). Trunk length does not include proboscis, neck and evaginated bursa. Line drawings were made with a drawing tube attached to an optical microscope Zeiss Standard 25. Type specimens were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, UNAM, Mexico City, Mexico, in the Natural History Museum, London, UK (NHMUK 2025.1.3.12) and one specimen in the Institute of Parasitology, Academy of Sciences, České Budějovice, Czech Republic (IPCAS A-148).

Molecular analysis

Total DNA was extracted from five specimens of the new species using the Animal and Fungi DNA Preparation Kit (Jena Bioscience, Germany) and following the manufacturer instructions. Two nuclear markers, 18S and 28S nuclear ribosomal DNA (18S and 28S, respectively), as well as a fragment of the mitochondrial cytochrome c oxidase subunit I (*cox1*) were amplified for one specimen; for four additional specimens, the *cox1* sequences were amplified in order to evaluate the genetic distances within the new species. All the polymerase chain reactions (PCRs) reactions were conducted using the primers shown in Table 1. PCRs were realised as follows: for 18S, an initial denaturation at 94º C for 5 min, followed by 38 cycles of 94º C for 30 s, 48º C for 45 s, 72º C for 1.30 min and final extension at 72º C for 7 min. For 28S, an initial denaturation at 94º C for 5 min, followed by 35 cycles of 94º C for 1 min, 50º C for 30 s, 68º C for 45 s and final extension at 72º C for 7 min. For *cox1,* an initial denaturation at 94º C for 3 min, followed by 35 cycles of 94º C for 40 s, 40º C for 1 min, 72º C for 1 and final extension 72º C for 5 min.

Amplification reactions used 0.4 µl BigDye Terminator v.3.1 (Applied Biosystems, Waltham, MA, USA), with 2 µl 5x buffer, 4 µl ddH_2O, 1 µl of primer, and 3 µl of purified PCR product (10 µl total volume). The samples were purified using Sephadex G-50, adding 25 µl of 0.5 mM EDTA to each sample. Finally, an ABI-PRISM 3100 Applied Biosystems sequencer was used to read the sequences. Both procedures were carried out at LANABIO, IB, UNAM. Newly generated DNA sequences were reconciled and edited using Geneious Prime 2023 2.1 (https://www.geneious.com). For the phylogenetic analyses, species of Transvenidae (*Transvena annulospinosa* Pichelin et Cribb, 2001 and *Transvena pichelinae* Lisitsyna, Kudlai, Cribb et Smit, 2019) were selected as outgroup for phylogenetic analyses. Sequences of ten species of *Rhadinorhynchus* identified to species level available in GenBank were also included. The geographic distribution of these species mainly includes Australia, Vietnam and South Africa, with the Iberian Peninsula, Asia and the Americas marginally represented. In a separate analysis, the genetic distances of the *cox1* sequences were calculated in Mesquite (Maddison and Maddisson 2023) using the K2P (Kimura 1980) model of nucleotide substitution.

Sequence alignments and phylogenetic analyses

Newly generated DNA sequences were aligned together with published sequences for members of Rhadinorhynchidae obtained from GenBank (Table 2). Based on previous phylogenetic studies and preliminary analyses of our molecular data, we restricted our analysis only to one of the groups of the otherwise non-monophyletic *Rhadinorhynchus*. Importantly, such clade includes the type species of the genus, *Rhadinorhynchus pristis*. Formal analysis and nomenclatural changes in the genus are beyond the purposes of the present study. Alignment for each molecular dataset was performed using the MAFFT 7 online server (https://mafft.cbrc.jp/alignment/server/index.html).

Phylogenetic relationships of the concatenated dataset were investigated under two criteria: parsimony and maximum likelihood (ML). The first was executed in TNT (Goloboff et al. 2008) with a heuristic search with 100 replicates, addition of terminals at random, and Tree Bisection and Reconnection (TBR) algorithm; gaps were considered as missing data. Bootstrap values were obtained with 100 pseudoreplicates. Maximum likelihood was executed in IQ-Tree (Nguyen et al. 2015, Chernomor et al. 2016) with substitution models selected for each partition (K3Pu + F + I + G4, K2P + R2 and TPM2 + F + G4), one for each molecular marker. Support values were obtained through 100 bootstrap pseudoreplicates.

RESULTS

***Rhadinorhynchus villalobosi* sp. n.** Figs. 1–3

ZooBank number for species:
urn:lsid:zoobank.org:act:BF6038B7-A82C-441A-9438-46EFD3B292C8

General: Rhadinorhynchidae, with characters of *Rhadinorhynchus*. Sexual dimorphism present, females larger than males (Fig. 1A,B). Proboscis long and cylindrical, widens slightly anteriorly, armed with 10–14 interspersed rows of 16–28 hooks per row. Hooks dorsal and ventral slightly different in length between both sexes (Table 3). Anterior hooks short, enlarging towards middle region, decreasing towards posterior region. Posterior hooks small, increasing abruptly in size, acquiring straight shape in last row. Root of hooks simple and directed posteriorly (Fig. 1C,D). Females with more hooks and spines than males (Fig. 2A–D). Neck trapezoid, unarmed (Figs. 1A,B, 2C), with similar length and width. Trunk elongated, cylindrical, widens slightly towards anterior region; divided in two fields, separated by aspinose area (Figs. 2A–F). Anterior spines form 2–3 complete circles around trunk in females and males. Posterior spines mainly on ventral and lateral regions, less abundant on dorsal region, slightly longer and slimmer than anterior spines; spines reach posterior end of proboscis receptacle. Proboscis receptacle double walled, containing a cephalic ganglion almost equatorial. Lemnisci thinner and shorter than proboscis receptacle. Subterminal gonopore in both sexes (Fig. 3A,B). Body with small numerous hypodermic nuclei (Fig. 3C). Eggs fusiform (Fig. 3D).

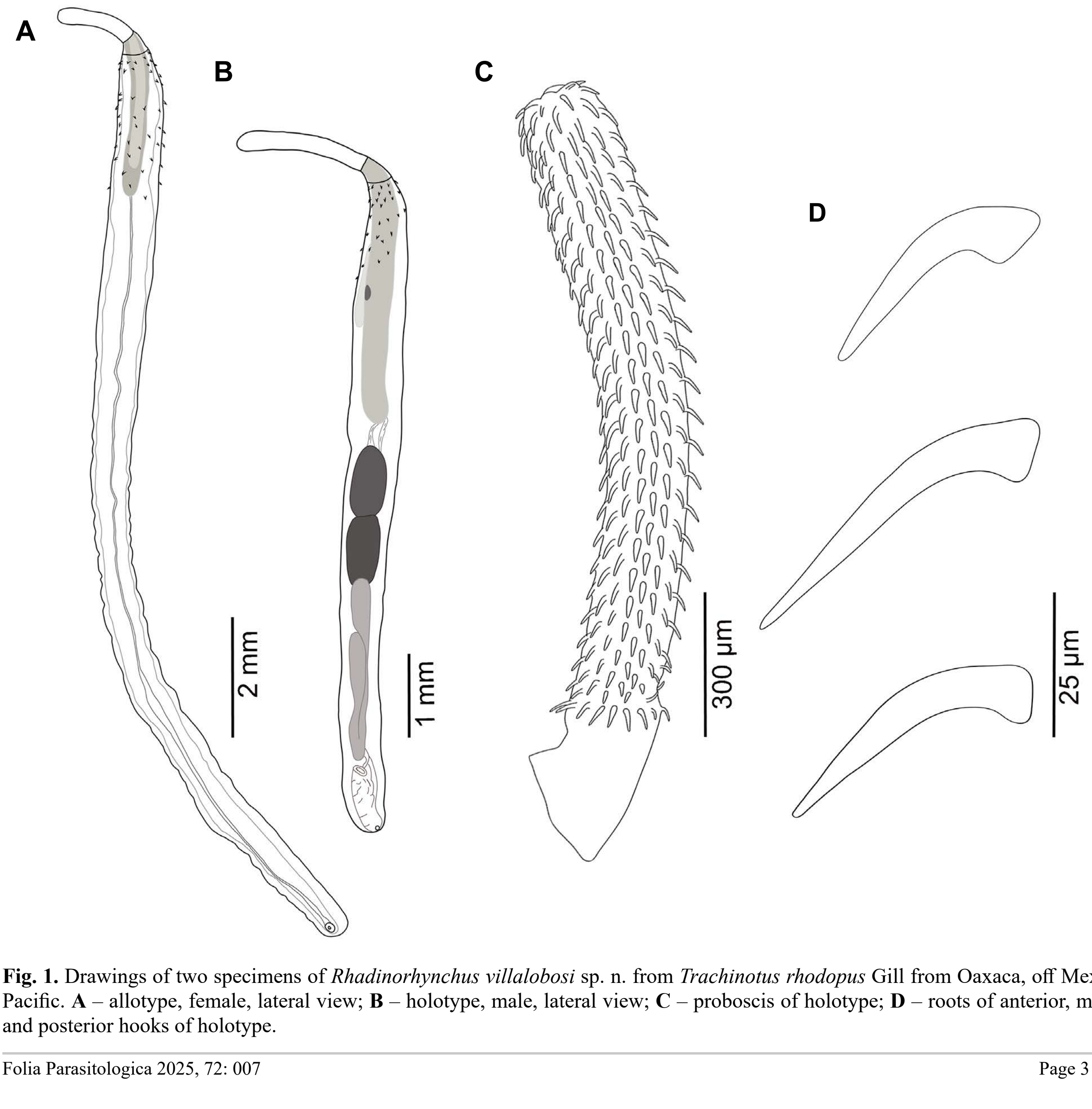

Fig. 1. Drawings of two specimens of *Rhadinorhynchus villalobosi* sp. n. from *Trachinotus rhodopus* Gill from Oaxaca, off Mexican Pacific. **A** – allotype, female, lateral view; **B** – holotype, male, lateral view; **C** – proboscis of holotype; **D** – roots of anterior, middle and posterior hooks of holotype.

Table 2. GeneBank sequence number of species of Acanthocephala used in the present study.

Species	Family	Host	18S	28S	*cox1*	Location	Reference
Transvena annulospinosa Pichelin et Cribb, 2001	Transvenidae	*Anampses neoguinaicus*	AY830153	AY829098	DQ089711	Unknow	García-Varela and Nadler (2005, 2006)
Transvena pichelinae Lisitsyna, Kudlai, Cribb et Smit, 2019	Transvenidae	*Thalassoma purpureum*	MN105737	MN105743	-	Sodwana Bay, South Africa	Lisitsyna et al. (2019)
Pararhadinorhynchus sodwanensis Lisitsyna, Kudlai, Cribb et Smit, 2019	Transvenidae	*Pomadasys furcatus*	MN105738	MN105744	-	Sodwana Bay, South Africa	Lisitsyna et al. (2019)
Pararhadinorhynchus sp.	Transvenidae	*Siganus fuscescens*	HM545903	HM545904	-	Unknow	Wang et al. (unpublished)
Rhadinorhynchus carangis Yamaguti, 1939	Rhadinorhynchidae	*Trachinotus coppingeri*	MN705830	MN705850	MN692684	Heron Island, Great Barrier Reef, Queensland, Australia	Huston et al. (2020)
Rhadinorhychus decapteri (Braicovich, Lanfranchi, Farber, Marvaldi, Luque and Timi, 2014)	Rhadinorhynchidae	*Decapterus punctatus*	KJ590123	KJ590124	KJ590125	Cabo Frio, Rio de Janeiro, Brazil	Braicovich et al. (2014)
Rhadinorhychus dorsoventrospinosus Amin, Heckmann et Nguyen Van Ha, 2011	Rhadinorhynchidae	*Decapterus kurroides*	MH384435* MH384475*	-	MN267179	Vietnam	Chaudhary et al. 2020
Rhadinorhynchus gerberi Lisitsyna, Kudlai, Cribb et Smit, 2019	Rhadinorhynchidae	*Trachinotus botla*	MN105739	MN105745	MN104897	Sodwana Bay, South Africa	Lisitsyna et al. (2019)
Rhadinorhynchus hiansi Soota et Bhattacharya, 1981	Rhadinorhynchidae	*Sarda orientalis*	MN203133	-	MN203136	Vietnam	Amin et al. (2020)
Rhadinorhynchus johnstoni Golvan, 1969	Rhadinorhynchidae	*Auxis thazard*	MN705827	MN705847	MN692680	Moreton Bay, Queenslet, Australia	Huston et al. (2020)
Rhadinorhynchus laterospinosus Amin, Heckmann et Nguyen Van Ha, 2011	Rhadinorhynchidae	*Auxis rochei*	MK457183	-	MK572744	Pacific Ocean (Vietnam)	Amin et al. (2019a)
Rhadinorhynchus mariserpentis (Steinauer, Garcia-Vedrenne, Weinstein et Kuris 2019)	Rhadinorhynchidae	*Regalecus russelii*	MK014866	MK014867	-	Kyushu Islet, Japan	Steinauer et al. (2019)
Rhadinorhynchus seriolae (Yamaguti, 1963)	Rhadinorhynchidae		LC777826	-	LC777825	Japan	Kita et al. (2024)
Rhadinorhynchus trachinoti	Rhadinorhynchidae	Sciaenidae	AY062433	AY829099	DQ089712	Unknown	García-Varela et al. (2002), García-Varela and Nadler (2005, 2006)
***Rhadinorhynchus villalobosi* sp. n.**	Rhadinorhynchidae	*Trachinotus rhodopus*	-	OQ676213	-	Puerto Ángel, Oaxaca, Mexico	Martínez-Flores et al. (2023)
***Rhadinorhynchus villalobosi* sp. n.**	Rhadinorhynchidae	*Trachinotus rhodopus*	-	OQ676214	-	Puerto Ángel, Oaxaca, Mexico	Martínez-Flores et al. (2023)
***Rhadinorhynchus villalobosi* sp. n.**	Rhadinorhynchidae	*Trachinotus rhodopus*	-	OQ676215	-	Puerto Ángel, Oaxaca, Mexico	Martínez-Flores et al. (2023)
***Rhadinorhynchus villalobosi* sp. n.**	Rhadinorhynchidae	*Trachinotus rhodopus*	PQ373610	PQ373609	PQ374008-PQ374012	Puerto Ángel, Oaxaca, Mexico	Present study
Rhadinorhynchus sp.	Rhadinorhynchidae	*Auxis thazard*	MN705828	MN705848	MN692681	Moreton Bay, Queenslet, Australia	Huston and Smales (2020)
Spinulacorpus biforme (Smales, 2014)	Rhadinorhynchidae	*Helotes sexlineatus*	MN705829	MN705849	MN692682	Moreton Bay, Queensland, Australia	Huston and Smales (2020)

*Sequences not included in our analyses due to suspected contamination.

Males (based on nine mature specimens and three specimens used for SEM studies). Trunk 4.5–7.8 (6.8; n = 9) mm long by 0.25–0.72 (0.47; n = 9) mm wide. Anterior spines form 2–3 complete circles, 22–51 (36; n = 7) long by 6–15 (11; n = 7) wide. Posterior spines in 5–16 (9; n = 6) rows overpass length of lemnisci, slightly longer and wider than anterior spines, 19–55 (40; n = 7) vs 22–51 (36; n = 7), respectively. Proboscis 0.6–1.5 (1.19; n = 8) mm long by 0.10–0.25 (0.17; n = 9) mm wide. Proboscis receptacle 1.82–2.78 (2.32; n = 7) mm long by 0.12–0.23 (0.18; n = 7) mm wide. Dorsal hooks similar in length to ventral hooks, thinner. Posterior hooks smaller, penultimate rows remarkably reduced; hooks at base of proboscis elongated (Table 3; n = 9). Neck 107–257 (178; n = 9) long by 107–257 (180; n = 9) wide. Lemnisci thinner and short; proboscis receptacle, 1.43–1.97 (1.73; n = 4) mm long. Reproductive system in middle of the trunk, with continuous structures. Testes elongated, in tandem; anterior testes 0.42–1.02 (0.69; n = 9) mm long by 0.15–0.57 (0.28; n = 9) mm wide, slightly longer than posterior testes, 0.25–0.87 (0.59; n = 9) mm long by 0.17–0.53 (0.27; n = 9) mm wide. Four elongated cement glands, one pair long 90–162 (109; n = 7) and other short 68–103 (78; n = 7); cement glands parallel to sperm-duct, anterior to Saefftigen pouch, 195–204 (199; n = 2) long. Bursa muscular, 327–400 (367; n = 3) long by 473–591 (532; n = 2) wide, with numerous sensory papillae (Figs. 3 E, F). Subterminal gonopore (n = 7).

Females (based on five gravid specimens with mature eggs and two for SEM studies). Trunk 9.04–17.89 (13.84; n = 5) mm long by 0.23–0.81 (0.54; n = 5) mm wide. Anterior trunk spines form 2–3 complete circles, 31–44 (38; n = 5) long by 8–11 (10; n = 5) wide. Posterior trunk spines in 14–16 (15; n = 3) rows overpass length of proboscis receptacle; longer than anterior spines 33–66 (46; n = 3) vs 31–44 (38; n = 3). Proboscis 0.62–2.01 (1.35; n = 5) mm long by 0.1–0.25 (0.18; n = 5) mm wide. Dorsal hooks narrower than ventral hooks. Posterior hooks smaller, with penultimate rows notably reduced; hooks at base of proboscis elongated, almost straight (Table 3; n = 5). Neck 107–257 (210; n = 5)

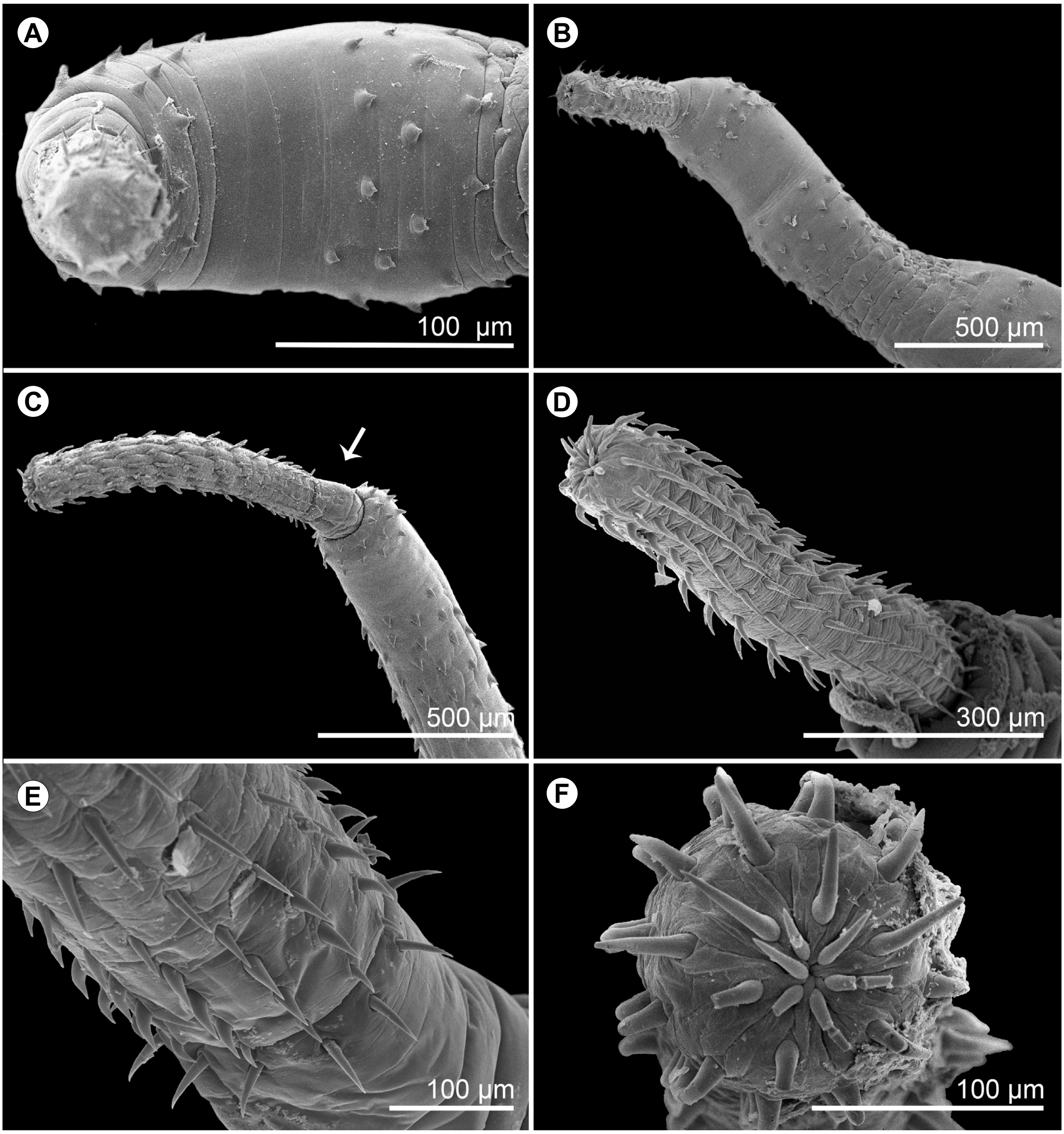

Fig. 2. SEM micrographs of specimens of *Rhadinorhynchus villalobosi* sp. n. from *Trachinotus rhodopus* Gill from Oaxaca, Mexico. **A** – ventral view of trunk spines divided into two fields separated by an aspinous area; **B** – anterior spines of the trunk form complete rings, while posterior spines are mainly distributed in ventral and lateral areas, with few in number in the dorsal region; **C** – differentiated neck (arrow); **D** – distribution of proboscis hooks in alternate rows; **E** – posterior hooks of proboscis reduced; basal hooks elongated, straight; **F** – anterior proboscis hooks.

long by 128–257 (214; n = 5) wide. Proboscis receptacle 2.03–3.7 (2.8; n = 2) mm long by 0.17–0.25 (0.21; n = 2) mm. Lemnisci slender and shorter than proboscis receptacle, 2.03–2.55 (2.29; n = 2) mm long. Reproductive system long 7.07–14.52 (10.1; n = 5) mm, occupying 80% of trunk. Uterine bell 1542 (n = 1); selector apparatus not observed; uterus 3257 (n = 1) and vagina 235 (n = 1). Subterminal gonopore (n = 4). Mature eggs, containing a fully developed acanthor, fusiform, with polar extensions, 46–68 (59; n = 7) long by 11–15 (13; n = 7) wide.

Taxonomic summary

Type host: Gafftopsail pompano, *Trachinotus rhodopus* Gill (Carangiformes: Carangidae).

Type locality: Puerto Ángel, Oaxaca, Mexico (15.6597, 96.4916).

Site of infection: Posterior intestine.

Type specimens: Holotype, male, whole mount (CNHE 12866); allotype, female (CNHE 12867), 12 paratypes, whole mounts of 8 males and 4 females (CNHE 13007); NHMUK (2025.1.3.12) and IPCAS (A-148).

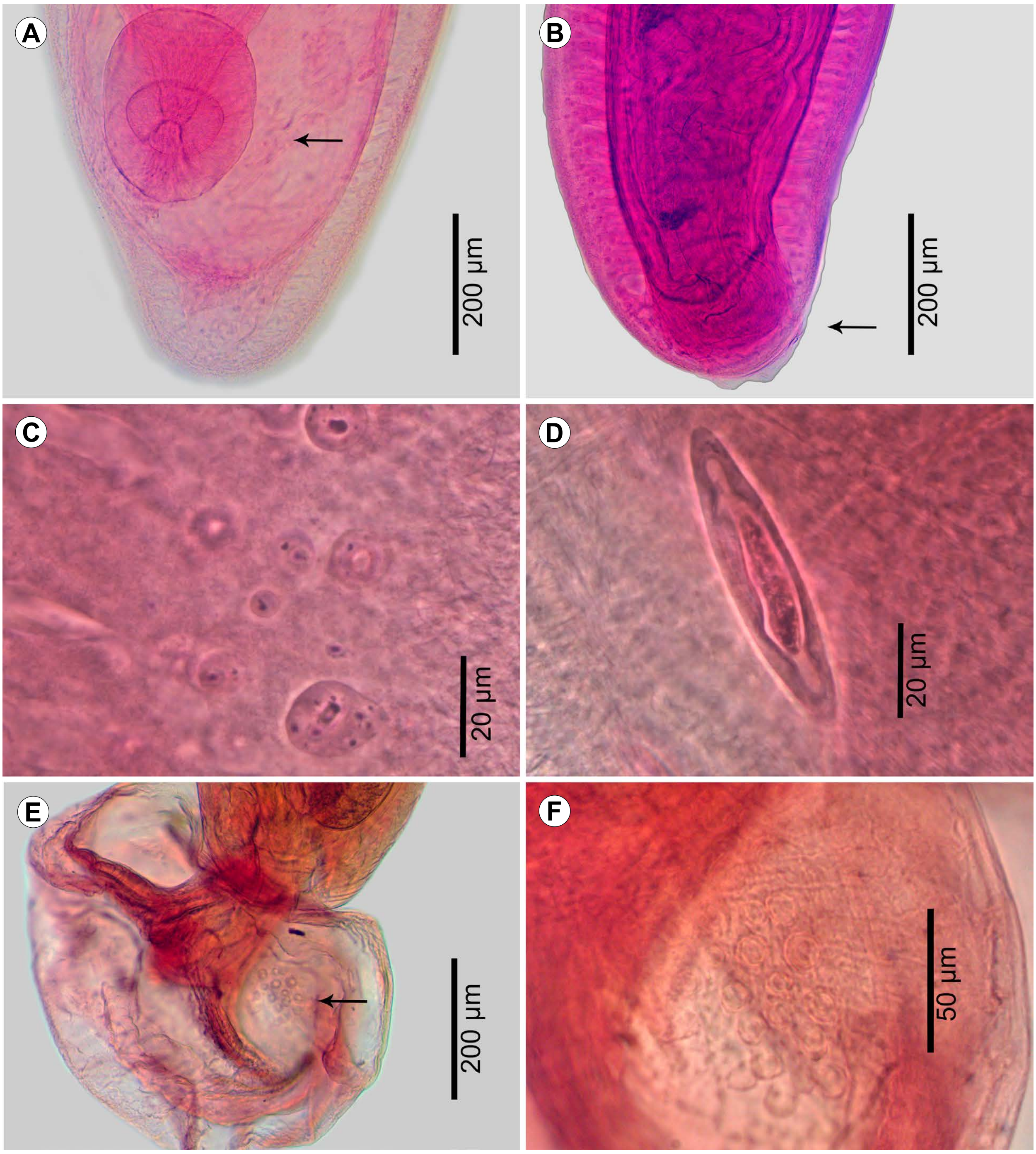

Fig. 3. Microphotographs of specimens of *Rhadinorhynchus villalobosi* sp. n. from *Trachinotus rhodopus* Gill from Oaxaca, off Mexican Pacific. **A** – subterminal gonopore of female (arrow); **B** – subterminal gonopore of male indicated with arrow; **C** – hypodermic nuclei; **D** – fusiform egg; **E** – extended bursa with sensory papillae (arrow); **F** – sensory papillae on bursa.

Infection parameters: Prevalence 48% (n = 110); abundance = 3.68 (n = 110); mean intensity = 7.64 (n = 110); intensity range = 1–81 acanthocephalans per fish.

Representative DNA sequence: The newly generated sequences were deposited in GenBank under the following accession number: 18 rDNA: PQ373610; 28S rDNA: PQ373609; *coxI*: PQ374008-374012.

Etymology: The name of the new species honors Alejandro Villalobos Figueroa (1918–1982), a prominent Mexican biologist and carcinologist who was born in Pochutla, Oaxaca, near the type locality of the new species described herein.

Remarks. The hooks of the proboscis of *Rhadinorhynchus villalobosi* sp. n. are arranged in rows that match the range established for *Rhadinorhynchus* species (8–26 rows and 17–48 hooks per row). In addition, the traits of our specimens also fit with the diagnoses presented by Amin et al. (2019c): Proboscis long, claviform; hooks slightly dorsoventrally differentiated, projecting at right angle to proboscis basally; trunk long, cylindrical, slightly dilated anteriorly; trunk spines anterior, in two fields separate

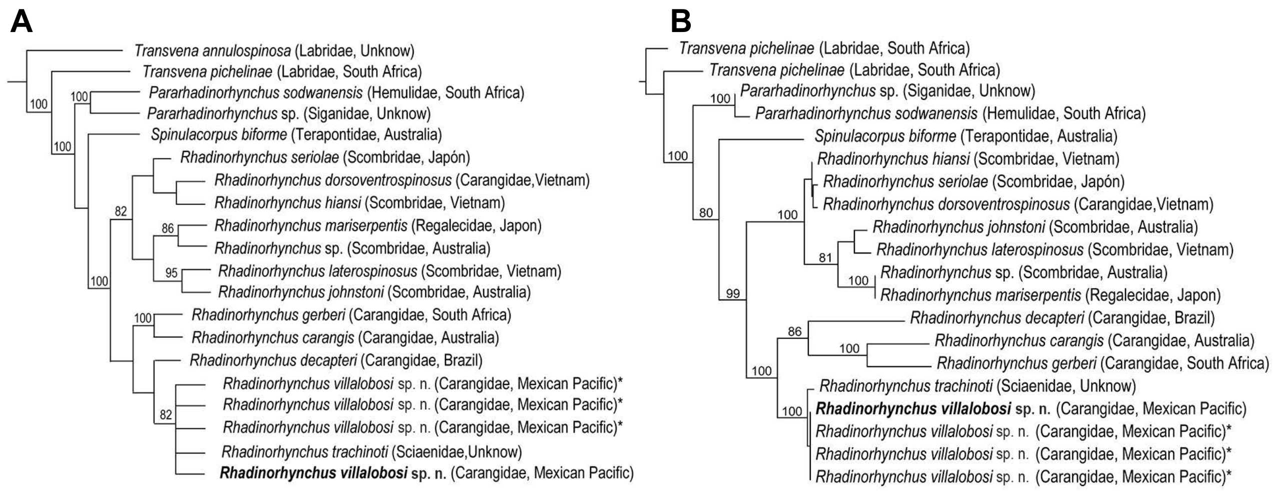

Fig. 4. A – Phylogenetic trees resulting from parsimony; **B** – Maximum Likelihood analysis of species of *Rhadinorhynchus* Lühe, 1911 based on 18S, 28S and *cox1* sequences. Numbers above nodes indicate bootstrap values. In bold, samples of *Rhadinorhynchus villalobosi* sp. n., parasite of *Trachinotus rhodopus* Gill from Mexican Pacific. * indicates previously published sequences.

by aspinose area; four cement glands, long, tubular; bursa with sensory papillae, among others.

According to WoRMS (2025), 47 species of the genus *Rhadinorhynchus* have been described worldwide. Particularly, for the Pacific Ocean 25 valid species are known, the majority reported for Australian, Japan and Vietnam (Amin et al. 2019a,b). *Rhadinorhynchus villalobosi* sp. n. with 10–14 hooks by row can be differentiated from five species by having a smaller number of rows of hooks in the proboscis: *Rhadinorhynchus johnstoni* Golvan, 1969 (15–17); *R. ditrematis* Yamaguti, 1939 (15–16); *R. zhukovi* Golvan, 1969 (16); *R. laterospinosus* Amin, Heckmann et Nguyen Van Ha, 2011 (18), and *R. ornatus* Van Cleave, 1918 (22–24) (Amin et al. 2009, 2011).

Another group of species, *R. australis* Amin, Rubstova et Van Ha, 2019, *R. biformis*, *R. pichelinae* Smales, 2014, *R. circumspinus* Amin, Rubtsova et Nguyen, 2019, *R. pomatomi* Smales, 2014, *R. polydactyli* Smales, 2014, *R. decapteri* (Braicovich, Lanfranchi, Farber, Marvaldi, Luque et Timi, 2014), and *R. carangis* Yamaguti, 1939 differs from the new species in the arrangement of the trunk spine armature (single filed *vs* two field of trunk spines, respectively) (Smales 2014, Amin et al. 2011, 2019c). *Rhadinorhynchus bicircumspinis* Hooper, 1983, *R. trachuri* Harada 1935, *R. seriolae* (Yamaguti, 1963), and *R. oligospinosus* Amin et Heckmann, 2017 can be separated of the new species because they have the genital pore terminal in males (see Golvan 1969, Hooper 1983, Amin and Heckman 2017, Amin 2020), while in the Mexican species is subterminal in both sexes.

Due to the egg size, *R. dorsoventrospinosus* Amin, Heckmann et Nguyen Van Ha, 2011 (100 µm) and *R. multispinosus* Amin, Rubtsova et Nguyen, 2019 (92–112 µm) can be separated from new species (Amin et al. 2011, 2019c), which eggs have 46–68 µm in length. *Rhadinorhynchus villalobosi* sp. n. differs from *R. pacificus* Amin, Rubtsova et Nguyen, 2019 by having 12 rows of spines in the posterior field of trunk (Amin et al. 2019c), while the new species have 16 and a shorter neck (107–257 µm *vs* 312–364 µm, respectively). Females of *Rhadinorhynchus pristis* are longer than those of *R. villalobosi* sp. n. (70 mm vs 10–20 mm) and its eggs are almost 2 or 3 times larger than those of the Mexican species (see Amin et al. 2011).

Rhadinorhynchus selkirki Van Cleave, 1921 differs from *R. villalobosi* sp. n. by having longer dorsal and ventral hooks (53–89 and 83–94 µm *vs* 19–77 and 17–77 µm, respectively) (Van Cleave 1921). Two other species distributed in the Pacific waters, *R. cololabis* Laurs et McCauley, 1964, and *R. chongmingmensis* Huang, Zheng, Deng, Fan et Ni, 1988, differs from the species herein described by posses lemisci equal in length than proboscis receptacle (Laurs and McCauley 1964), and lemisci as long as trunk (Hang et al. 1988), meanwhile in *R. villalobosi* sp. n., lemnisci are shorter than proboscis receptacle.

Recently, a new species, *Rhadinorhynchus trachinoti*, was described from the northern Pacific coast of Mexico Grano-Maldonado et al. (2025). Both species differ in the position of the genital pores in both sexes [terminal in *R. trachinoti* and subterminal in our specimens]; the number of spines on the trunk, since *R. trachinoti* present 3 to 4 complete circles of anterior spines on the trunk of females and males and only 2 to 3 in *R. villalobosi*. Finally, the difference in the size of the cement glands is remarkable; in *R. trachinoti* the long pair measures 1125 and the short pair 984, while in *R. villalobosi* these structures measure 109 and 78, respectively.

Phylogenetic analyses and *cox1* genetic distances

DNA sequences of the 18S, 28S and *cox1* were generated from one specimen of *R. villalobosi* sp. n. from *Trachinotus rhodopus* from Puerto Ángel, Oaxaca. These newly generated sequences were included in the final dataset that includes 20 terminals and 2,389 aligned nucleotides (18S = 1,199 bp, 28S = 659 bp and *cox1* = 531). The *cox1* dataset included 17 terminals and 531 bp, including five samples of the new species; the dataset included one taxon with one sequence of *Transvena annulospinosa*. Parsi-

Table 3. Distribution, length and width of proboscis hooks of males and females of *Rhadinorhynchus villalobosi* sp. n. from Mexican Pacific.

Hooks	Male				Female			
	No. from the anterior region							
	Dorsal hooks		Ventral hooks		Dorsal hooks		Ventral hooks	
	Length	Wide	Length	Wide	Length	Wide	Length	Wide
1	26–55 (45)	8–13 (10)	37–57 (50)	8–15 (11)	42–66 (51)	8–13 (11)	44–55 (48)	11–15 (12)
2	48–64 (56)	11–15 (13)	33–66 (55)	11–19 (14)	55–77 (63)	11–15 (13)	57–73 (66)	15–19 (16)
3	48–66 (56)	11–15 (13)	37–64 (54)	11–19 (14)	55–77 (63)	13–19 (16)	51–71 (62)	15–19 (16)
4	44–68 (55)	11–15 (12)	53–64 (58)	13–19 (15)	51–75 (63)	13–19 (15)	51–71 (62)	15–19 (16)
5	48–66 (55)	11–15 (12)	51–64 (58)	13–19 (15)	53–73 (63)	13–19 (15)	51–68 (61)	15–19 (16)
6	48–62 (54)	11–15 (12)	51–64 (58)	13–19 (15)	55–73 (63)	11–19 (14)	51–66 (60)	13–19 (16)
7	51–62 (55)	11–15 (12)	51–66 (59)	13–17 (15)	55–77 (63)	11–17 (14)	51–66 (59)	13–19 (16)
8	46–62 (55)	8–15 (11)	51–66 (57)	13–17 (15)	55–75 (63)	11–17 (14)	53–71 (61)	13–19 (16)
9	48–64 (56)	8–15 (12)	51–66 (59)	13–17 (15)	53–73 (62)	11–17 (14)	51–73 (60)	13–19 (16)
10	48–62 (55)	8–15 (11)	55–66 (61)	13–17 (15)	53–73 (62)	11–17 (14)	53–73 (61)	11–19 (15)
11	48–62 (54)	8–15 (10)	55–66 (60)	13–17 (14)	53–73 (61)	8–17 (13)	51–73 (60)	13–19 (15)
12	35–57 (51)	8–13 (10)	48–66 (59)	13–17 (14)	46–73 (59)	8–17 (13)	51–73 (60)	13–19 (15)
13	28–57 (50)	8–13 (10)	35–66 (58)	11–17 (14)	39–66 (55)	8–17 (12)	28–73 (55)	11–19 (14)
14	28–57 (49)	8–13 (10)	28–68 (56)	11–17 (13)	42–73 (59)	8–17 (13)	37–73 (56)	11–19 (14)
15	26–57 (49)	8–13 (10)	28–68 (56)	11–17 (13)	26–73 (54)	8–17 (13)	33–71 (56)	11–17 (14)
16	22–57 (45)	8–13 (10)	24–68 (55)	11–17 (13)	22–73 (56)	11–17 (13)	33–77 (60)	11–19 (14)
17	35–57 (47)	8–13 (10)	48–64 (55)	11–17 (13)	19–73 (51)	6–17 (12)	19–75 (52)	6–17 (13)
18	33–57 (45)	8–13 (10)	44–64 (54)	8–17 (12)	35–68 (52)	6–17 (11)	31–75 (53)	11–17 (13)
19	33–51 (42)	6–11 (9)	39–57 (51)	8–15 (11)	35–66 (54)	11–15 (13)	31–75 (58)	11–17 (14)
20	33–48 (39)	6–11 (8)	33–57 (46)	8–13 (10)	31–62 (51)	11–15 (13)	31–73 (57)	11–17 (14)
21	33–51 (40)	6–11 (9)	28–53 (45)	8–13 (10)	35–62 (52)	11–13 (11)	24–68 (51)	11–17 (14)
22	28–66 (47)	8–11 (10)	24–68 (53)	8–15 (11)	35–55 (48)	11–13 (11)	22–68 (49)	6–13 (11)
23	28–39 (34)	8–11 (10)	24–48 (35)	8–11 (9)	51–53 (52)	11–13 (11)	22–66 (48)	6–13 (11)
24	39–53 (46)	8	44–53 (48)	11–13 (11)	37–75 (52)	8–13 (11)	33–77 (59)	11–15 (13)
25	-	-	-	-	39	11	57	13
26	-	-	-	-	39	8	57	13
27	-	-	-	-	39	8	48	13
28	-	-	-	-	62	11	73	11

mony analysis resulted in a single most parsimonious tree with 1,553 steps (Fig. 4A), and ML resulted in a tree with a score of -ln = -9769.160 (Fig. 4B).

Both analyses resulted in the similar topologies, with species of the family Rhadinorhynchidae sister to *Spinulacorpus biforme* (Smales, 2014), a member of the family Spinulacorpidae, and then sister to species of Transvenidae (2 species of *Pararhadinorhynchus* Johnston et Edmonds, 1947 and 2 of *Transvena* Pichelin et Cribb, 2001. Both phylogenetic methods found *Rhadinorhynchus* as a monophyletic group with good node support. ML tree shows poor node support in some of the relationships within *Rhadinorhynchus*, these parts of the tree are collapsed in the parsimony tree. Parsimony tree recovers *R. decapteri* sister to the new species, whereas the ML tree recovers *R. decapteri* forming a clade with *R. carangis* and *R. gerberi* Lisitsyna, Kudlai, Cribb et Smit, 2019, and then sister to *R. villalobosi* sp. n.

The genetic distance of *cox1* between five specimens of *R. villalobosi* is 0.3%, compared to that of *R. trachinoti* recorded in a scienid by García-Varela and Nadler (2005) and Grano-Maldonado et al. (2025), while comparing it with *R. decapteri*, a closely related species, this value is 3%.

DISCUSSION

The parsimony and ML tree topologies recovered here are, in general, consistent with previous studies involving species of Echinorhynchida (García-Varela and Nadler 2005, Lisitsyna et al. 2019, Huston et al. 2020), especially in terms of the monophyly of *Rhadinorhynchus*. Regarding the species of *Rhadinorhynchus*, two groups were recovered with good support values in our analyses (see Fig. 4). The first group includes *Rhadinorhynchus hiansi* Soota et Bhattacharya, 1981, *R. dorsoventrospinosus*, *R. laterospinosus*, *R. johnstoni*, *R. mariserpentis* (Steinauer, García-Vedrenne, Weinstein et Kuris, 2019), *R. seriolae* and an unidentified species of *Rhadinorhynchus* from Australia (Huston and Smales 2020). This group was recovered under both methods. Interestingly, this clade includes species from Asia-Pacific and Australia, most of them parasites of Scombridae. The second clade groups species parasites of carangids, including *Rhadinorhynchus villalobosi* sp. n. and four species from different points of the Pacific: *R. carangis*, *R. decapteri*, *R. trachinoti* and *R. gerberi*.

The DNA sequences generated in the present study of *R. villalobosi* sp. n., were found closely related with a sample that has been used in previous phylogenetic studies (*Rhadinorhynchus* sp.), which in accordance with Grano-Maldonado et al. (2025) belongs to *R. trachinoti* collected in Chamela Bay, parasitising an unidentified fish of the family Sciaenidae (see fig. 5 in Grano-Maldonado et al. 2025). Previously, García-Varela et al. (2002) obtained the 18S sequence from presumably the same DNA sample, establishing the host as member of the family Sciaenidae, without indicating the sampling locality. In posterior publications, sequences of the 28S and *cox1* were also generated, but neither host species nor locality information were provided (García-Varela and Nadler 2005, 2006).

Braicovich et al. (2014) and Steinauer et al. (2019) included the same sequences of *Rhadinorhynchus* sp. in their phylogenetic analysis and consider, without justification, that this sample was collected in Mexico, without more details of the sampling locality or host. Molecular data may indicate that *R. trachinoti* and *R. villalobosi* are conspecific, however, we decided to maintain the latter as a separate species based on the morphological differences described before (i.e. position of the genital pores, the number of spines on the trunk and the size of the cement gland); in addition, both species are distributed in different regions (North and Tropical Pacific, respectively) separated by approximately 1500 km. Further studies should focus on the critical evaluation of morphologic and molecular variability of both species considering that any of the sources of information should predominate over the others. Furthermore, the fact that *R. trachinoti* is able to parasitise species of both, Scombridae and Sciaenidae needs to be clarified. Based on the text, Grano-Maldonado et al. 2025 implied that *R. trachinoti* is specific to *Trachinotus rhodopus* (Carangidae) whereas in their *cox1* phylogenetic tree, and based on previous publications, it can be derived that this species can also parsitise species of Sciaenidae, a fish family that is not included in the host list for the genus (see Grano-Maldonado et al. 2025).

Based on our results and in terms of the host preferences of the species of *Rhadinorhynchus*, it seems that this group of acanthocephalans has a closed phylogenetic association with fish species of the families Scombridae and Carangidae (see Fig. 4), and the finding of *R. mariserpentis* parasitising species of Regalecidae, could be result of a host switching event or an accidental infection. The presence of *Rhadinorhynchus* cf. *pristis* in Mexico reported by Santos-Bustos et al. (2020) is questionable because the type species was described in the North Atlantic Ocean (Amin et al. 2011). However, it is difficult to discard this record in the absence of morphological information.

Rhadinorhynchus villalobosi sp. n. was one of the two species with the highest prevalence and abundance throughout the year of sampling made by Martínez-Flores et al. (2023). This species was dominant in the infracommunities of *T. rhodopus* in two of the five samplings carried out. The possible explanation for this fact is the predominance of crustacean ingestion in the diet of this carangid, which in some cases has represented up to 76% of the host's food content (Danemann 1993). For example, in some *Rhadinorhynchus* species, crustaceans such as the euphausiid and mysiid and to lesser extent ostracods have been reported as intermediate hosts (Gregori et al. 2013, Grano-Maldonado et al. 2025).

To date, 47 species of *Rhadinorhynchus* are recognised, but DNA sequences are available for only 11 species, including *R. villalobosi* sp. n., and several sequences from undetermined species. This makes it difficult to clarify the evolutionary relationships of the group. In some studies on Echinorhynchida (Braicovich et al. 2014, Steinauer et al. 2019, Chaudhary et al. 2020), it has been suggested that there are sequences associated with misidentified specimens, such as those corresponding to *R. pristis* from Indonesia and *Rhadinorhynchus lintoni* Cable et Linderoth, 1963 from Hawaii by Verweyen et al. (2011), which is the reason why they were not included in the phylogenetic analysis of this work.

Likewise, the authors of this work have noted a possible contamination in the sequence of the 18S gene of *R. dorsoventrospinosus* carried out by Chaudhary et al. (2020), since when performing BLAST search, it is highly similar to some species of arthropods; therefore, some available sequences of the group should be taken with caution.

In conclusion, morphological analyses support *Rhadinorhynchus villalobosi* sp. n. as a valid species within *Rhadinorhynchus*; coincidences between DNA sequences should be clarified to confirm its independence from *R. trachinoti* using other genes or sequencing specimens with diagnostic characteristics of each species, particularly the position of the genital pore; likewise, some biogeographic, environmental and behavioral aspects should be analysed.

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