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Research paper

Morphological and molecular data reveal a new genus and species from the family Transvenidae (Echinorhynchida: Palaeacanthocephala) from Bahía de Todos los Santos, Northeast Pacific, Mexico

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ABSTRACT

Echinorhynchids are a group of globally distributed acanthocephalan parasites mainly of freshwater, brackish and marine fishes and occasionally, reptiles and amphibians. During several parasitology surveys in the Gulf of Mexico and Northeast Pacific, Mexico, acanthocephalans were recovered from two marine fish species. The specimens from the Gulf of Mexico were identified as *Caballerorhynchus lamothei* (Cavisomidae), a typical parasite of the striped mojarra, whereas adult acanthocephalans from the Northeast Pacific, Mexico, from the Garibaldi fish exhibited morphological characteristics belonging to the family Transvenidae. Sequences from the small (SSU) and large (LSU) subunits of ribosomal DNA and cytochrome c oxidase subunit 1 (cox 1) of mitochondrial DNA were obtained for both species. The new sequences were aligned with other sequences available in the GenBank dataset from Echinorhynchida. Phylogenetic trees inferred with the combined (SSU + LSU), concatenated (SSU + LSU+ cox 1), and cox 1 datasets consistently placed the two species into two independent lineages. The species *C. lamothei* from Cavisomidae was placed in a clade together with members from Spinulacorpidae, Rhadinorhynchidae and Transvenidae, suggesting that Cavisomidae is paraphyletic. The unidentified specimens were nested inside a clade formed by members of Transvenidae. Morphologically, the new samples presented a combination of unique diagnostic traits, which was not observed in other members of the Transvenidae family. Therefore, the genus *Darwinorhynchus* was created to accommodate a new species named herein as *Darwinorhynchus bajacaliforniaensis* n. gen., n. sp. The current record from a transvenid acanthocephalan expands its distribution range to the northern Pacific in the Americas, Indian Ocean and Arabian Gulf.

1. Introduction

Acanthocephalans of the order Echinorhynchida Southwell and Macfie, 1925 are the most divergent and diverse group within the phylum Acanthocephala, with approximately 470 species classified into 82 genera, 12 subfamilies and 13 families; these parasites are associated mainly with freshwater, brackish and marine fishes and, sporadically, amphibians and reptiles distributed worldwide [1,2]. The classification at the family level is based mainly on morphological characters, such as the proboscis shape, number of proboscis hooks, trunk armature, location of the cerebral ganglion, and egg morphology. However, the number and shape of the cement glands in males remain the most important diagnostic traits [3,4]. Recently, phylogenetic analyses combining morphological and molecular characteristics revealed that some families of Echinorhynchida are paraphyletic or polyphyletic [5–8]. Current evidence suggests that most of the characters used to diagnose families are homoplasies rather than shared derived features [5]. Consequently, studies based on information from nuclear molecular markers have attempted to resolve the paraphyly or polyphyly of families, and several species and genera have been created or transferred, while even more new families have been proposed [7–11].

The parasite diversity of acanthocephalans from marine fishes on Mexican coasts has been documented by combining morphological and molecular characteristics, revealing an amazing diversity that has been documented through the recognition and description of new lineages and species [12–18]. However, the knowledge of the acanthocephalan

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fauna from marine fishes on Mexican coasts remains limited, especially given the high diversity of marine fishes that have not yet been explored from a helminthological perspective.

During several parasitological surveys of marine fishes along Mexican coasts, adult acanthocephalans were recovered from the intestines of two definitive host species, the striped mojarra (*Eugerres plumieri* L, Gerreidae) in the Gulf of Mexico and the Garibaldi fish (*Hypsypops rubicundus* Girard, Pomacentridae) in Northeast Pacific, Mexico. A careful morphological examination of our specimens, in combination with molecular analyses on the basis of sequences of the small (SSU) and large (LSU) subunits from the nuclear ribosomal genes plus cytochrome c oxidase (cox 1) sequences from the mitochondrial DNA, revealed the presence of two species. The specimens from the striped mojarra were identified as *Caballerorhynchus lamothei* Salgado-Maldonado, 1977, from the family Cavisomidae Meyer, 1932, whereas the specimens from the Garibaldi fish presented a unique combination of morphological traits belonging to a new genus and species from the family Transvenidae Pichelin and Cribb, 2001.

The main objectives of this study were *i*) to molecularly characterize the species *C. lamothei*, *ii*) to test the phylogenetic position within the order Echinorhynchida, and *iii*) to describe a new genus and species to accommodate our specimens from the Garibaldi within the family Transvenidae.

2. Material and methods

2.1. Host collection and morphological study

During several field expeditions in 2021, 2022 and 2025, nine specimens of the striped mojarra (*E. plumieri*) were collected in the Sontecomapan lagoon, Veracruz, Gulf of Mexico (18° 33′ 20” N, 94° 59′21” W), and 34 Garibaldi (*H. rubicundus*) were collected in Todos Santos Bay, Baja California, Mexico (31° 48′ N, 116° 46′ W). Acanthocephalans were carefully removed from the intestines of their hosts and washed in a 0.85 % saline solution, placed in distilled water at 4 °C overnight, and subsequently fixed in 70 or 100 % ethanol. A few acanthocephalans were gently punctured in the body with a fine needle, stained with Mayer’s paracarmine, de-stained in 70 % acid ethanol, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted as permanent slides with Canada balsam. Specimens were deposited in the Colección Nacional de Helmintos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. Acanthocephalans were initially identified by conventional morphological criteria following the keys of Pichelin and Cribb [4], Amin et al. [18] and the original description of *C. lamothei* [19]. Measurements of the specimens are presented in micrometers unless otherwise stated and with the mean followed by the range in parentheses. For scanning electron microscopy (SEM), specimens were dehydrated through an ethanol series, critical point dried with CO_2, sputter coated with gold, and examined with a Hitachi Stereoscan Model SU1510 scanning electron microscope operating at 10 kV at the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM).

2.2. DNA sequencing and phylogenetic analyses

A total of four specimens, two of an undescribed genus and species and two of *C. lamothei,* were individually digested overnight at 56 °C in a solution containing 20 mM NaCl, 100 mM Na_2 EDTA (pH 8.0), 10 mM Tris–HCl (pH 7.6), 1 % sarkosyl, and 0.1 mg/ml proteinase K. Following digestion, genomic DNA was extracted from the supernatant using DNAzol reagent (Molecular Research Center, Cincinnati, OH, USA) according to the manufacturer’s instructions. Two regions of nuclear ribosomal DNA (rDNA) and one mitochondrial DNA region (mtDNA) were amplified using the polymerase chain reaction (PCR). A near complete fragment from the small subunit from 18S rDNA (~1800 bp; SSU) was amplified using two overlapping PCR fragments of 1000 bp: the SSU amplicon 1 using the forward primer 5′-AGA TTA AGC CAT GCA TGC GT-3′ and reverse primer 5’-AAC TTT TCG TTC TTG ATT AA TG-3′ and the SSU amplicon 2 using the forward primer 5’-GCA GCG CGG TAA TTC CAG CTC-3′ and reverse primer 5’-GCA GGT TCA CCT ACG GA AA-3′ [5]. A near complete fragment of the large subunit from 28S rDNA (~2900 bp; LSU) was amplified using three overlapping PCR fragments of 1200–1300 bp: the LSU amplicon 1 using the forward primer 5’-CAA GTA CCG TGA GGG AAA GTT GC-3′ and reverse primer 5’-CAG CTA TCC TGA GGG AA AC-3′, the LSU amplicon 2 using the forward primer 5’-ACC CGA AAG ATG GTG AAC TA TG-3′ and the reverse primer 5′- CTT CTC CAA CGT CAG TCT TC AA-3′, and, the LSU amplicon 3 using the forward primer 5′- CTA AGG AGT GTG TAA CAA CTC ACC-3′ and reverse primer 5’-CTT CGC AAT GAT AGG AAG AG CC-3′ [5]. Finally, the cytochrome c oxidase subunit 1 (cox 1) from the mitochondrial DNA was amplified using the forward primer 5’-AGTTCTAATCATAA(*R*)GATAT (Y)GG-3′ and reverse primer 5′ -TAAACTTCAGGGTGACCAAAAAATCA-3′ [20].

PCR amplifications were performed in a total volume of 25 μl containing 2 μl of each primer, 10 pmol/μl, 2.5 μl of 10× buffer, 1.5 μl of 2 mM $MgCl_2$, 2 μl of the genomic DNA and 1 U of Taq DNA polymerase (Platinum Taq, Invitrogen Corporation, California, United States). PCR cycling parameters for rDNA amplifications included denaturation at 94 °C for 3 min, followed by 35 cycles of 94 °C for 1 min, annealing at 50–58 °C (optimized for each fragment amplified) for 1 min, and extension at 72 °C for 1 min, followed by a post-amplification incubation at 72 °C for 7 min. Sequencing reactions were performed with the primers mentioned above using ABI Big Dye (Applied Biosystems, Boston, Massachusetts) terminator sequencing chemistry. Reaction products were separated and detected using an ABI 3730 capillary DNA sequencer. Contigs were assembled and base-calling differences resolved using Codoncode Aligner version 12.0.1 (Codoncode Corporation, Dedham, Massachusetts).

2.3. Alignments and phylogenetic analyses

Newly generated sequences were aligned with published sequences for other acanthocephalans retrieved from the GenBank dataset (Table 1). Alignments for the combined nuclear molecular marker (SSU + LSU), concatenated (SSU + LSU+ cox 1) and cox 1 were constructed using the software ClustalW [21]. A nucleotide substitution model was selected for the datasets using jModelTest version 2.1.7 [22]. Phylogenetic analyses were inferred through maximum likelihood (ML) with the program RAxML version 7.0.4 [23]. A GTRGAMMAI substitution model was used, and 10,000 bootstrap replicates were run to assess nodal support. In addition, a Bayesian analysis was carried out, using the program MrBayes 3.2.2 [24] with two Markov chain Monte Carlo (MCMC) runs for 10 million generations, sampling every 1000 generations, a heating parameter value of 0.2 and a burn-in of 25 %. The resulting phylogenetic trees were visualized and edited using FigTree v.1.4.4 [25].

3. Results

3.1. Morphological description

Taxonomy.
Class: Palaeacanthocephala Meyer, 1931.
Order: Echinorhynchida Southwell and Macfie, 1925.
Family: Transvenidae Pichelin and Cribb, 2001.
Genus: *Darwinorhynchus* n. gen.

Etymology: The genus has been named after Charles Darwin to honor his contributions to the field of evolutionary biology.

Diagnosis: Transvenidae. Trunk aspinose, cylindrical, gradually tapering toward both ends (Figs. 1 A, 2 A). Proboscis claviform with apical and basal hooks smaller than medial hooks, with a sensory pore at the proboscis base (Fig. 1 C, 2 A, B). Proboscis receptacle double-walled,

Table 1
Specimen information and GenBank accession numbers for species studied in the phylogenetic analyses. Sequences marked with bold were obtained in this study.

Taxon name	Family	Host	SSU	LSU	cox 1	Reference
Acanthocephalus anguillae	Paracanthocephalidae	*Proteus anguinus*	MN394414	MN394419		Amin et al. [39].
Acanthocephalus anguillae	Paracanthocephalidae	*Anguilla anguilla*	MN394412	MN394417		Amin et al. [39].
Acanthocephalus anguillae	Paracanthocephalidae		AF469413			Herlyn et al. [40].
Acanthocephalus anguillae	Paracanthocephalidae	*Asellus aquaticus*	AY830151	AY829106	DQ089718	García-Varela and Nadler [5,41].
Acanthocephalus dirus	Paracanthocephalidae	*Semotilus atromaculatus*	MW172276	MW172283		García-Varela and Andrade-Gómez [10].
Acanthocephalus lucii	Paracanthocephalidae	*Perca fluviatilis*	AY830152	AY829101		García-Varela and Nadler [5].
Acanthocephalus lucii	Paracanthocephalidae	*Perca fluviatilis*	MW172277	MW172284		García-Varela and Andrade-Gómez [10].
Acanthocephalus clavula	Paracanthocephalidae	*Anguilla anguilla*	MW172278	MW172285		García-Varela and Andrade-Gómez [10].
Acanthocephalus nanus	Paracanthocephalidae	*Cynops pyrrhogaster*	LC129889			Nakao [42].
Acanthocephalus rhinensis	Paracanthocephalidae	*Anguilla anguilla*	MW172279	MW172286		García-Varela and Andrade-Gómez [10].
Acanthocephaloides propinquus	Arhythmacanthidae	*Gobius bucchichi*	AY830149	AY829100	DQ089713	García-Varela and Nadler [5,41].
Caballerorhynchus lamothei	Cavisomidae	*Eugerres plumieri*	**PX139054**	**PX139057**	**PX132614–615**	**This study**
Calakmulrhynchus amini	Arhythmacanthidae	*Mayaheros urophthalmus*	EU732662	EU732661		García-Varela and Andrade-Gómez [10].
Centrorhynchus sp.	Centrorhynchidae	*Falco peregrinus*	AY830155	AY829104	DQ089716	García-Varela and Nadler [5,41].
Corynosoma enhydri	Polymorphidae	*Enhydra lutris*	AF001837	AY829107	DQ089719	García-Varela and Nadler [5,41].
Darwinorhynchus bajacaliforniaensis	Transvenidae	*Hypsypops rubicundus*	**PX139052–053**	**PX139055–056**	**PX132612–613**	**This study**
Dentitruncus truttae	Illiosentidae	*Salmo trutta*	JX460863		DQ089710; OQ569928	Irena et al. [43]; Vardic Smrzlic et al. [44].
Echinorhynchus cotti	Echinorhynchidae	*Cottus reinii*		MW172287		García-Varela and Andrade-Gómez [10].
Echinorhynchus cotti	Echinorhynchidae	*Cottus reinii*	MW172280	MW172288		García-Varela and Andrade-Gómez [10].
Echinorhynchus borealis	Echinorhynchidae	*Perca fluviatilis*	MW172281	MW172289		García-Varela and Andrade-Gómez [10].
Echinorhynchus bothniensis	Echinorhynchidae	*Platichthys flesus*		KM656143		Wayland et al. [45].
Echinorhynchus brayi	Echinorhynchidae	*Pachycara crassiceps*		KM656151		Wayland et al. [45].
Echinorhynchus gadi	Echinorhynchidae		AY218123		AY218095	Giribet et al. [46].
Echinorhynchus gadi	Echinorhynchidae	*Macrourus berglax*	JX014222			Verweyen et al. [47].
Echinorhynchus gadi	Echinorhynchidae	*Gadus morrhua*	U88335			Aleshin et al. [48].
Echinorhynchus truttae	Echinorhynchidae	*Thymallus thymallus*	AY830156	AY829097	DQ089710	García-Varela and Nadler [5,41].
Echinorhynchus truttae	Echinorhynchidae	*Salmo trutta*		KM656147		Wayland et al. [45].
Filisoma argusum	Cavisomidae	*Scatophagus argus*			MK305841	Pinky et al. (Unpublished).
Filisoma caudata	Cavisomidae	*Kyphosus incisor*			MHOO4410–411; MH021180	Costa Fernandes et al. [49].
Filisoma bucerium	Cavisomidae	*Kyphosus elegans*	AF064814	AY829110	DQ089722	García-Varela et al. [50]. García-Varela and Nadler [5,41].
Filisoma filiforme	Cavisomidae	*Kyphosus bigibbus*	MN705826	MN705846	MN692678–679	Huston et al. [7].
Filisoma rizalinum	Cavisomidae	*Scatophagus argus*	JX014229			Verweyen et al. [47].
Gorgorhynchoides bullocki	Rhadinorhynchidae	*Eugerres plumiere*	AY830154	AY829103	DQ089715	García-Varela and Nadler [5,41].
Heterosentis sp.	Arhythmacanthidae	*Acanthopagrus australia*	MN705825	MN705845	MN692676	Huston et al. [7].
Tegorhynchus sp.	Leptorhynchoididae		AY830158	AY829092	DQ089705	García-Varela and Nadler [5,41].
Koronacantha mexicana	Leptorhynchoididae	*Pomadasys leuciscus*	AY830157	AY829095	DQ089708	García-Varela and Nadler [5,41].
Koronacantha pectinaria	Leptorhynchoididae	*Microlepidotus brevipinnis*	AF092433	AY829094	DQ089707	García-Varela et al. [50]. García-Varela and Nadler [5,41].
Leptorhynchoides thecatus	Leptorhynchoididae	*Lepomis cyanallus*	AF001840	AY829093	DQ089706	Near et al. [51]; García-Varela and Nadler [5,41].
Longicollum pagrisomum	Pomphorynchidae	*Oplegnathus fasciatus*	KY490052			Liang et al. [52].
Pararhadinorhynchus sp.	Transvenidae	*Siganus fuscescens*	HM545903	HM545904		Wang et al. (Unpublished).
Paratrajectura longcementglandatus	Transvenidae	Percid fish	MK770616		MK770615	Sharifdini et al. [53].
Pararhadinorhynchus magnus	Transvenidae	*Scatophagus argus*	MN395027			Chaudhary et al. [54].

(*continued on next page*)

Table 1 (*continued*)

Taxon name	Family	Host	SSU	LSU	cox 1	Reference
Pararhadinorhynchus sodwanensis	Transvenidae	*Pomadasys furcatus*	MN105738	MN105744		Lisitsyna et al. [30].
Pomphorhynchus bulbocolli	Pomphorynchidae	*Lepomis macrochirus*	AF001841	AY829096	DQ089709	Near et al. [50]; García-Varela and Nadler [5,41].
Pomphorhynchus laevis	Pomphorynchidae	*Rutilus rutilus*	JX014223			Verweyen et al. [47].
Pomphorhynchus zhoushanensis	Pomphorynchidae	*Oplegnathus fasciatus*	KY490051		KY490047	Liang et al. [52].
Plagiorhynchus cylindraceus	Plagiorhynchidae		AF001839	AY829102	DQ089714	Near et al. [51]; García-Varela and Nadler [5,41].
Polymorphus brevis	Polymorphidae	*Nycticorax nycticorax*	AF064812	AY829105	DQ089717	García-Varela et al. [50]. García-Varela and Nadler [5,41].
Profilicollis altmani	Polymorphidae	*Enhydra lutris*	AF001838	AY829108	DQ089720	Near et al. [50]; García-Varela and Nadler [5,41].
Pseudoacanthocephalus lucidus	Pseudoacanthocephalidae	*Rana ornativentris*	LC129279			Nakao [42].
Pseudoacanthocephalus toshimai	Pseudoacanthocephalidae	*Rana pirica*	LC129278			Nakao [42].
Pseudocavisoma setoense	Cavisomidae	*Chromis notata*			LC835834	Kita et al. [55].
Rhadinorhynchus sp.	Rhadinorhynchidae	*Auxis thazard*	MN705828	MN705848	MN69268	Huston et al. [7].
Rhadinorhynchus carangis	Rhadinorhynchidae	*Trachinotus coppingeri*	MN705830	MN705850	MN692684	Huston et al. [7].
Rhadinorhynchus dorsoventrospinosus	Rhadinorhynchidae	*Decapterus kurroides*			MN267179	Chaudhary et al. [54].
Rhadinorhynchus decapteri	Rhadinorhynchidae	*Decapterus puntatus*			KJ590125	Braicovich et al. (Unpublished).
Rhadinorhynchus gerberi	Rhadinorhynchidae	*Trachinotus botla*	MN105739	MN105745	MN104897–898	Lisitsyna et al. [30].
Rhadinorhynchus hiansi	Rhadinorhynchidae	*Sarda orientalis*	MN203134		MN203136–137; MN203138	Amin et al. [56].
Rhadinorhynchus johnstoni	Rhadinorhynchidae	*Auxis thazard*	MN705827	MN705847	MN692680	Huston et al. [7].
Rhadinorhynchus mariserpentis	Rhadinorhynchidae	*Regalecus russelii*	MK014866	MK014867	MK012666	Steinauer et al. [57].
Rhadinorhynchus nudus	Rhadinorhynchidae	*Auxis thazard*	MG838943		PV266023; MG757445–447; MN692681; OR541110	Li et al. [58]; Ghanei-Motlagh et al. [27].
Rhadinorhynchus laterospinosus	Rhadinorhynchidae	*Auxis rochei*	MK457183		MK572742–744; OR625530–531; LC777823	Amin et al. [59].
Rhadinorhynchus lintoni	Rhadinorhynchidae	*Selar crumenophthalmus*	JX014224			Verweyen et al. [47].
Rhadinorhynchus pristis	Rhadinorhynchidae	*Nyctiphanes couchii*	JX061133		JQ061132	Gregory et al. [60].
Rhadinorhynchus pristis	Rhadinorhynchidae	*Alosa alosa*	KR349116			Bao et al. [61].
Rhadinorhynchus trachinoti	Rhadinorhynchidae	Fish family (Scianidae)	AY062433	AY829099	DQ089712	García-Varela et al. [50]. García-Varela and Nadler [5,41].
Rhadinorhynchus trachinoti	Rhadinorhynchidae	*Trachinotus rhodopus*	PQ549640	PQ549642	PQ541022–025	Grano-Maldonado et al. [17].
Rhadinorhynchus villalobosi	Rhadinorhynchidae	*Trachinotus rhodopus*			PQ374008–012	Martínez-Flores et al. [38].
Serrasentis nadakali	Rhadinorhynchidae		KC291715			Paul et al. (Unpublished)
Sclerocollum sp.	Transvenidae	*Zebrasoma velifer*			MN692689	Huston et al. [7].
Sclerocollum sp.	Transvenidae	*Siganus argenteus*			LC757485	Kita and Kajihara (Unpublished)
Sclerocollum australe	Cavisomidae	*Siganus argenteus*	MN705831	MN705851	MN692685–686	Huston et al. [7].
Sclerocollum robustum	Cavisomidae	*Siganus lineatus*	MN705832	MN705852	MN692687–688	Huston et al. [7].
Spinulacorpus biformis	Spinulacorpidae	*Pelates sexlineatus*	MN705829	MN705849	MN692682–683	Huston and Smales [8].
Transvena annulospinosa	Transvenidae	*Anampses neoguinaicus*	AY830153	AY829098	DQ089711	García-Varela and Nadler [5,41].
Transvena pichelinae	Transvenidae	*Thalassoma purpureum*	MN105737	MN105743	MN104895–896	Lisitsyna et al. [30].
Outgroup *Neoechinorhynchus saginatus*	Neoechinorhynchidae		AY830150	AY829091	DQ089704	García-Varela and Nadler [5,41].
Floridosentis mugilis	Neoechinorhynchidae	*Mugil cephalus*	AF064811	AY829111	DQ089723	García-Varela et al. [50]. García-Varela and Nadler [5,41].

with elliptic cephalic ganglion toward posterior end of proboscis receptacle (Figs. 1 A, B; 2C). Lemnisci equal, extending beyond proboscis receptacle and reaching anterior testis. Testes in overlapping tandem, with four pyriform cement glands, occupying more than half of trunk (Fig. 1 A and B). Säfftigen's pouch present. Vagina short (Fig. 1 F). Eggs elongated with polar prolongation (Fig. 1 E). Genital pore subterminal in both sexes (Fig. 1 F).

Species: *Darwinorhynchus bajacaliforniaensis* n. gen., n. sp.

Type host: *Hypsypops rubicundus* Girard, 1854, Pomacentridae (Garibaldi fish).

Site of infection: Small intestine (prevalence 62 %, (21/34)).

Type locality: Bahía de Todos los Santos, Baja California, Mexico

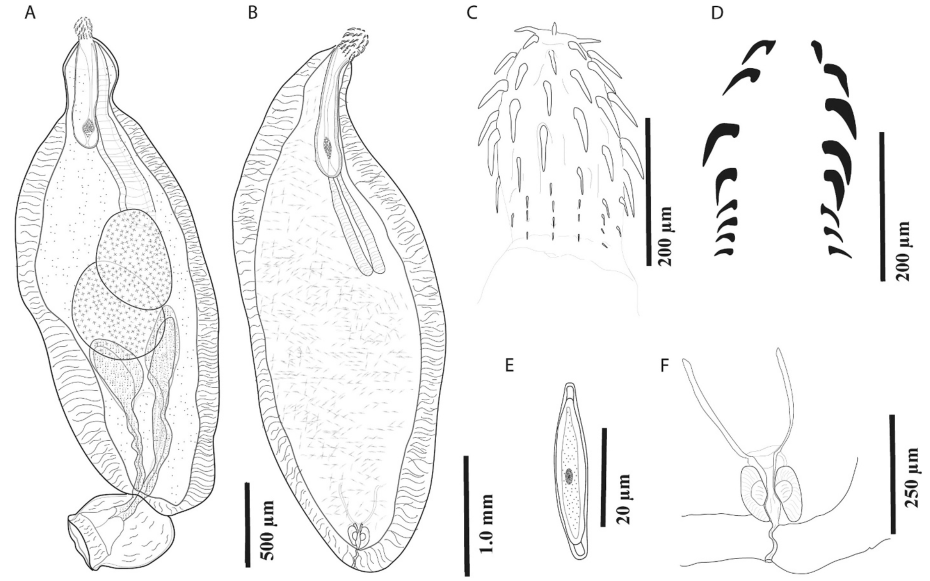

Fig. 1. Whole adult male of *Darwinorhynchus bajacaliforniaensis* n. gen., n. sp. from *Hypsypops rubicundus* from Bahía de Todos los Santos, Baja California, Mexico (**A**); Entire female, (**B**); Proboscis, (**C**); Hooks, (**D**); Egg, (**E**); Reproductive system (**F**).

(31° 48′ N, 116° 46′ W).

Type-material: CNHE: 12,425 (holotype); 12,426 (allotype); 12,427 (paratype).

Representative DNA sequences: PX139052–053 (SSU); PX139055–056 (LSU); PX132612–613 (cox 1).

Etymology: The specific epithet refers to the state of Baja California, northern Mexico, where the type host was collected.

Darwinorhynchus bajacaliforniaensis n. gen., n. sp. (Figs. 1–2).

General (based on 18 mounted specimens).

Sexual dimorphism evident, females larger than males. Trunk aspinose, cylindrical, anterior trunk wall without sclerotised plates. Proboscis claviform with 12 longitudinal rows of hooks; each row with 7–8 hooks. Hooks differ in size, apical and basal hooks smaller than medial hooks. Neck short. Proboscis receptacle double-walled, with ganglion toward posterior end of proboscis receptacle. Presence of a sensory pore at the proboscis base. Lemnisci tubular, extend beyond proboscis receptacle. Genital pore subterminal in both sexes.

Male (based on 10 mounted specimens and 2 for SEM). Trunk cylindrical, aspinose, 2565 mm long (2223–2818) × 920 (608–1160) wide. Proboscis 278 (239–312) × 131 (106–171). Proboscis with 12 longitudinal rows of hooks; each row with 7–8 hooks, the first four apical hooks length; 1: 47 (43–52); 2: 56 (53–61); 3: 63 (61–67); 4: 63 (59–67); medial hooks, 5: 56 (50–62); 6: 34 (29–42); basal hooks, 7: 23 (20–25); 8: 18 (16–23). Neck, 166 (128–198) × 240 (208–257). Proboscis receptacle, 701 (589–785) × 126 (95–165). Lemnisci 1164 long (969–1349), reaching the anterior border of anterior testis. Testes two, oval, overlapping. Anterior testis 524 (433–642) × 353 (281–461). Posterior testis 495 (340–606) × 376 (300–454). Cement glands 4, in two pairs, pyriform. Copulatory bursa everted, cylindrical, 506 (399–606) × 382 (300–454).

Female (based on 8 mounted specimens). Trunk cylindrical, aspinose, 2688 mm long (2042–3190) × 1134 (889–1356). Proboscis 293 (259–332) × 143 (120–164). Proboscis with 12 longitudinal rows of hooks; each row with 7–8 hooks, the first four apical hooks length; 1: 38 (33–41); 2: 58 (55–60); 3: 67 (62–73); 4: 63 (57–73); medial hooks, 5: 29 (24–40); 6: 21 (17–27); basal hooks, 7: 18 (15–24); 8: 15 (14–18). Neck, 166 (104–222) × 260 (238–312). Proboscis receptacle, 736 (559–841) × 159 (140–200). Reproductive system obscured. Eggs elongated with polar prolongation, 50 (48–54) × 12 (11–13).

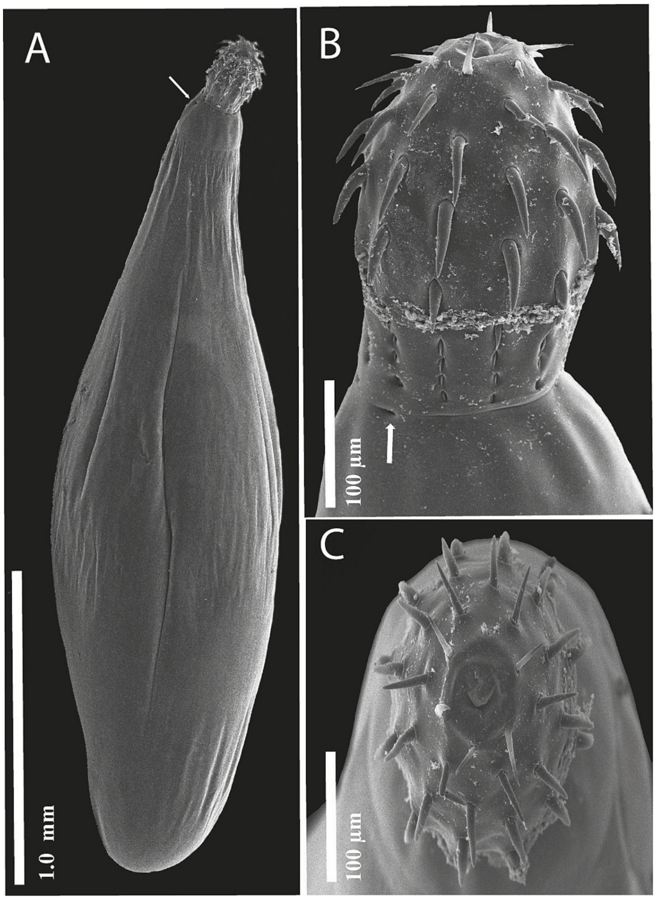

Fig. 2. Scanning electron micrographs of *Darwinorhynchus bajacaliforniaensis* n. gen., n. sp. from *Hypsypops rubicundus* from Bahía de Todos los Santos, Baja California, Mexico. Adult male, entire worm (**A**); Proboscis (**B, C**). Arrow indicates a sensory pore.

3.2. Remarks

Darwinorhynchus bajacaliforniaensis n. gen. n. sp. represents the first species from the family Transvenidae associated with a pomacentrid fish from the Northeast Pacific. The new genus is distinguished from the other five genera in the Transvenidae namely: *Transvena* Pichelin and Cribb, 2001, *Trajectura* Pichelin and Cribb, 2001, *Pararhadinorhynchus* Johnston and Edmons, 1947, *Sclerocollum* Schmidt and Paperna, 1978 and *Paratrajectura* Amin, Heckmann and Ali, 2018 by having an aspinose, cylindrical trunk, a short neck, presence of a sensory pore at the proboscis base and by having four pyriform cement glands. In contrast, the genera *Pararhadinorhynchus* and *Paratrajectura* are characterized by having two elongated cement glands, whereas the genera *Transvena* and *Trajectura* have two pyriform cement glands [7,18,26]. In addition, *Darwinorhynchus* n. gen., resembles *Sclerocollum* in have four cement glands [7,26]. However, *Darwinorhynchus* n. gen., differs from *Sclerocollum* in the shape of the cement glands, pyriform in *Darwinorhynchus* n. gen., vs pyriform or tubular in *Sclerocollum,* as well as in the proboscis shape, claviform in *Darwinorhynchus* n. gen., vs cylindrical in *Sclerocollum,* presence of sclerotised plates on the anterior trunk wall of *Sclerocollum* vs absence of sclerotised plates in *Darwinorhynchus* n. gen., and in the shape of the lemnisci, coiled in *Sclerocollum* vs tubular in *Darwinorhynchus* n. gen [7,26]. Finally, the species of *Sclerocollum* are distributed in Australian waters and in the Red Sea associated mainly with fishes from the family Siganidae. Although occasionally adult worms have been found in fishes from the families Balistidae, Lutjanidae, Acanthuridae and Chaetodontidae [26 and references therein], whereas *Darwinorhynchus* n. gen., is distributed in the Northeast Pacific, Mexico.

Class: Palaeacanthocephala Meyer, 1931.

Order: Echinorhynchida Southwell and Macfine, 1925.

Family: Cavisomidae Meyer, 1932.

Genus: *Caballerorhynchus* Salgado-Maldonado, 1977.

Species: *Caballerorhynchus lamothei* Salgado-Maldonado, 1977.

Morphological identification of C. lamothei.

The acanthocephalans recovered from the intestines of the striped mojarra (*E. plumieri*) were obtained from the type host and locality (Sontecomapan, Veracruz, Gulf of Mexico) and showed similar morphological characteristics compared with those assigned to *C. lamothei* by Salgado-Maldonado [19], including *i*) an elongated, cylindrical, aspinose trunk *ii*) a small claviform proboscis, *iii*) proboscis hooks arranged in 6 longitudinal rows of 3 hooks per row, *iv*) a double-walled proboscis receptacle (Fig. 3A,B), and *v*) four tubular cement glands in males.

3.3. Phylogenetic analysis

The combined alignment of the SSU + LSU consisted of 72 taxa and 4,909 sites. The phylogenetic trees inferred with the combined dataset, place the two species analysed herein in two independent clades. The species *C. lamothei* from Cavisomidae was placed in an independent basal branch together with species of Rhadinorhynchidae Lühe, 1912, Spinulacorpidae Huston and Smales, 2020 and Transvenidae with moderate bootstrap support (70 %) and Bayesian posterior probability (0.8) support values (Fig. 4). The new two isolates of *D. bajacaliforniaensis* n. gen., n. sp., were nested inside a clade formed with species from the genera *Paratrajectura*, *Transvena, Pararhadinorhynchus* and *Sclerocollum* from Transvenidae with strong bootstrap (90 %) and Bayesian posterior probability (0.9) support values (Fig. 4). Our phylogenetic analyses revealed that other genera from Cavisomidae such as *Filisoma* Van Cleave 1928 and the species *Pararhadinorhynchus magnus* Ha, Amin, Ngo, Heckmann, 2018 from Transvenidae were placed in an independent clade, suggesting that Cavisomidae and Transvenidae are paraphyletic. A concatenated alignment was built with sequences of the SSU + LSU+ cox 1 and consisted of 72 taxa and 5, 564 sites. The phylogenetic tree inferred with the concatenated data set also place the two species (*C. lamothei* and *D. bajacaliforniaensis* n. gen, n. sp.) in two independent clades. This tree confirmed that *D. bajacaliforniaensis* n. gen., n. sp., represents a new genus from Transvenidae (Fig. 5), because it was placed inside a clade formed by *Paratrajectura*, *Transvena, Pararhadinorhynchus* and *Sclerocollum* from Transvenidae. In addition, *C. lamothei* was placed in a basal branch together with the species *Spinulacarpus biforme* (Smales, 2014) Huston and Smales, 2020 from Spinulacorpidae.

The cox 1 alignment for the two species analysed herein included 655 sites and 60 sequences. The phylogenies inferred with the ML and BI methods yielded that the two isolates representing *C. lamothei* from Cavisomidae was placed in a clade with moderate bootstrap (83 %) and Bayesian posterior probability (0.9) support values (Fig. 6). The new two isolates of *D. bajacaliforniaensis* n. gen., n. sp., were placed in a clade together with species from the genus *Sclerocollum* from Transvenidae with strong bootstrap (99 %) support and Bayesian posterior probability (1.0) (Fig. 6). The cox 1 tree also placed other genera from *Cavisomidae* such as *Filisoma* and *Pseudocavisoma* Golvan and Houin, 1964 and *Paratrajectura* and *Transvena* from Transvenidae in independent clades suggesting that Cavisomidae and Transvenidae are paraphyletic (Fig. 6).

4. Discussion

The classification of the 15 families from Echinorhynchida has started to be analysed by combining morphological and molecular characteristics and modifying and updating the classification at the family level [4–11]. The reproductive system of males, such as the number, shape, structure and organization of cement glands, has been used as the main taxonomic criterion to classify families from Echinorhynchida [3,4]. In the present study, two species, *C. lamothei* from Cavisomidae as well as *D. bajacaliforniaensis* n. gen., n. sp., from Transvenidae, are characterized by having four cement glands. The

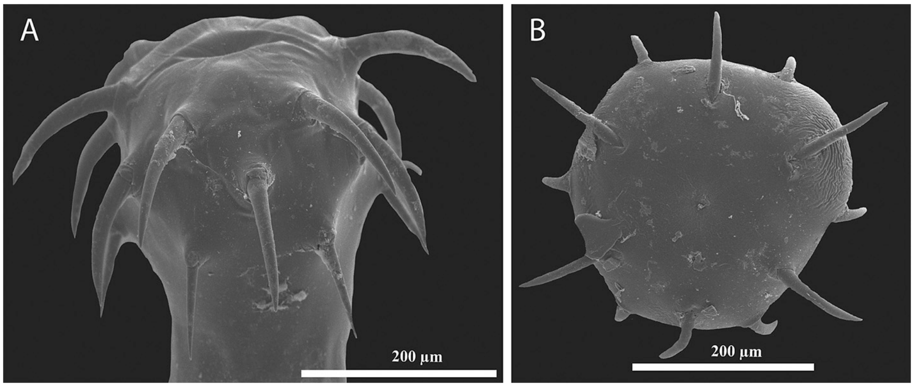

Fig. 3. Scanning electron micrographs of the proboscis of *Caballerorhynchus lamothei* from *Eugerres plumieri* from Sontecomapan, Veracruz, Mexico (**A, B**).

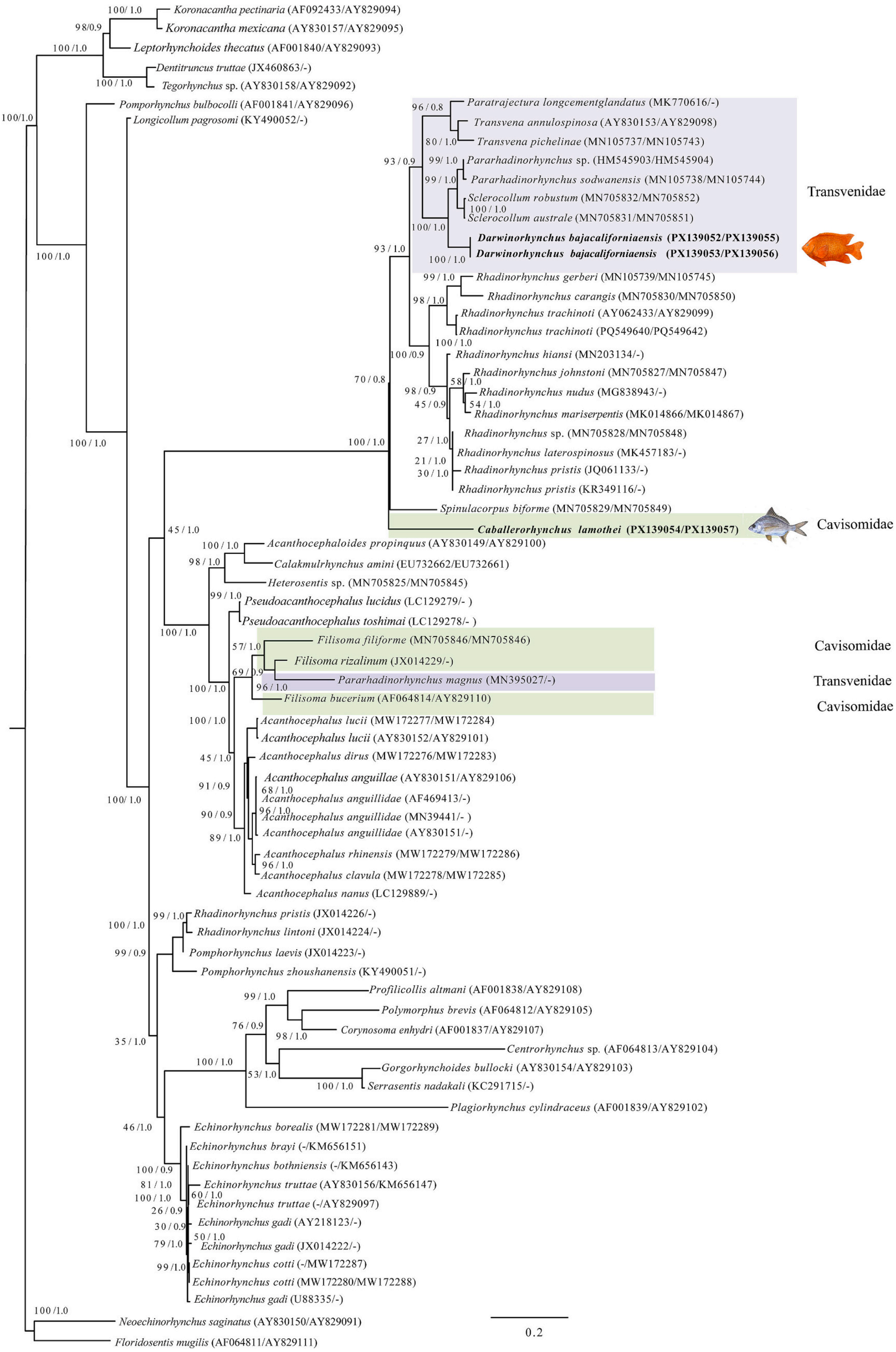

Fig. 4. Phylogenetic tree using maximum likelihood (ML) and consensus Bayesian obtained with the small and large (SSU + LSU) subunits of ribosomal DNA data set. Numbers near internal nodes show ML bootstrap percentages/ Bayesian posterior probabilities.

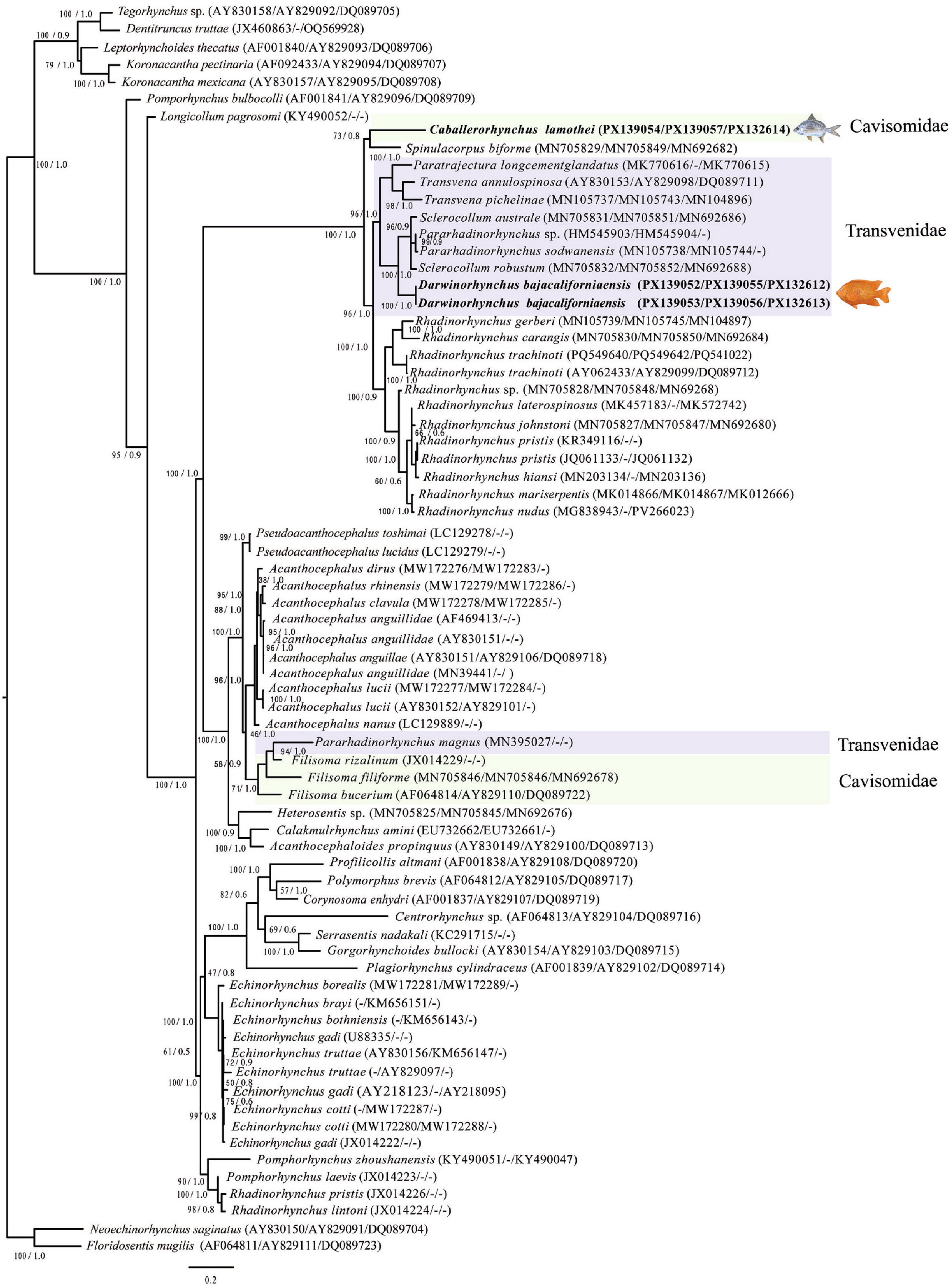

Fig. 5. Phylogenetic tree using maximum likelihood (ML) and consensus Bayesian obtained with the small and large (SSU + LSU+ cox 1) subunits of ribosomal DNA and cytochrome *c* oxidase subunit 1 from the mitochondrial DNA data set. Numbers near internal nodes show ML bootstrap percentages/ Bayesian posterior probabilities.

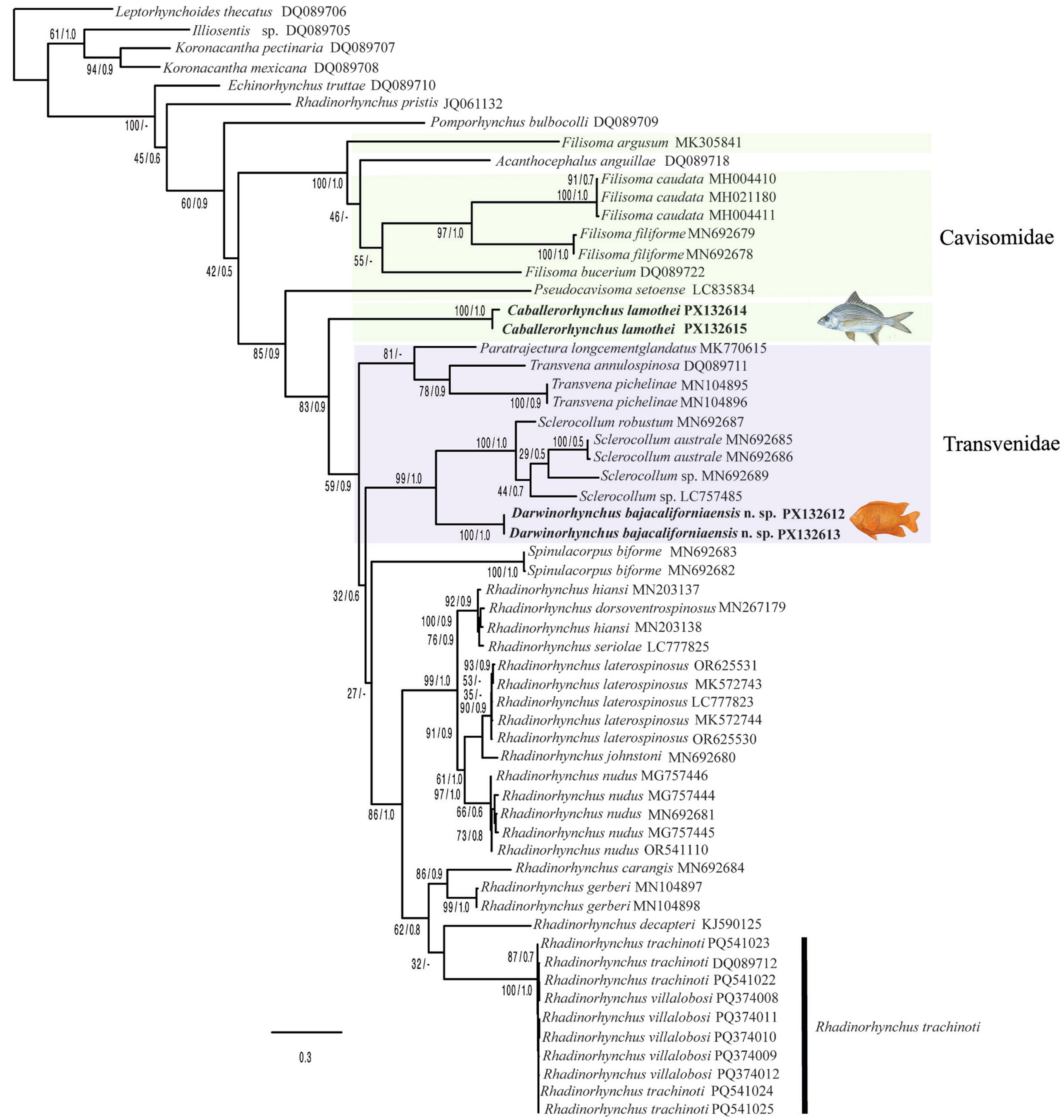

Fig. 6. Phylogenetic tree using maximum likelihood (ML) and consensus Bayesian obtained with the cytochrome *c* oxidase subunit 1 from the mitochondrial DNA dataset. Numbers near internal nodes show ML bootstrap percentage values/ Bayesian posterior probabilities.

phylogenetic analyses inferred with the combined (SSU + LSU) and concatenated (SSU + LSU+ cox 1) datasets of two nuclear and one mitochondrial molecular marker placed the two species analysed in independent clades, suggesting that the number of cement glands is a homoplastic characteristic that should be considered with caution when classifying echinorhynchids.

Phylogenetic analyses inferred with the combined (SSU + LSU) and (SSU + LSU+ cox 1) concatenated datasets also revealed the paraphyly of Cavisomidae, which was represented by *Caballerorhynchus* (*C. lamothei*) and three species from *Filisoma*. However, the species *P. magnus* (MN395027, SSU) from Transvenidae was nested within the genus *Filisoma*, suggesting that *P. maguns* could be considered as a member of Cavisomidae. In addition, the phylogenetic analyses inferred with the concatenated (SSU + LSU+ cox 1) dataset placed *C. lamothei* from Cavisomidae as a sister of *S. biforme* from Spinulacorpidae, a parasite found in marine fishes (Tetrapontidae) from Queensland, Australia [8], which suggests that *C. lamothei* should be transferred to the family Spinulacorpidae.

The cox 1 tree also confirmed the paraphyly of Cavisomidae, which is in agreement with the findings of a previous phylogenetic study [27].

The current evidence also indicates that *C. lamothei* does not belong to Cavisomidae and should be assigned an independent family or transferred to a previous family. However, the addition of other genera from Cavisomidae is indispensable for identifying the systematics of *C. lamothei* and other members of the family Cavisomidae. The species *C. lamothei* was described from the striped mojarra from Sontecomapan, Veracruz, in the Gulf of Mexico [19], and since then, it has been reported in marine and brackish fishes from the Gulf of Mexico [12].

In this study, we recognized that the acanthocephalans from the Garibaldi from the Mexican northeastern Pacific belong to a new genus and species described herein as *D. bajacaliforniaensis*, which was previously reported as *Pararhadinorhynchus* sp. from the same host and locality [28]. The taxonomic history of the family Transvenidae has been rather complex; it was created by Pichelin and Cribb [4] to accommodate the following three species: *Transvena annulospinosa* Pichelin and Cribb 2001, *Trajectura perinsolens* Pichelin and Cribb 2001, and *Trajectura ikedai* (Machida, 1992) Pichelin and Cribb 2001, from marine fishes in the Australian Pacific Sea. In the same study, these authors reviewed the taxonomy of the genus *Pararhadinorhynchus* and transferred it to the family Transvenidae with its four previously described species due to having two cement glands [4]. More recently, two other species of *Pararhadinorhynchus*, i.e., *P. magnus* from Vietnam in the Pacific Ocean and *P. sodwanensis* Lisitsyna, Kudlai, Cribb and Smith, 2019, from South Africa were described [29,30]. Amin et al. [18] described the genus *Paratrajectura* to accommodate a new species (*P. longcementglandatus*) from marine fishes from the Arabian Gulf, Iraq. More recently, Huston et al. [7], in their review of acanthocephalans from Australian marine fishes, transferred the genus *Sclerocollum* (with four cement glands) with four described species from Cavisomidae to Transvenidae. With the addition of *D. bajacaliforniaensis* n. gen., n. sp., the family contains 15 species classified into six genera. The current evidence suggests that *D. bajacaliforniaensis* n. gen., n. sp., could have a restricted distribution because the host, the Garibaldi fish, is found along the eastern Pacific coast from Monterey Bay, California, where it reaches Baja California, Mexico. This marine fish inhabits rocky reefs and kelp forests and feeds mainly on fishes, macroinvertebrates (polychaetes, molluscs and crustaceans) and kelp [31,32]. In addition, the current record in the Americas extends the geographical range of transvenid acanthocephalans from the Indian Ocean and the Arabian Gulf to the northeastern Pacific in the Americas.

The diversity of helminth parasites in marine fishes along the Mexican Pacific has started to be documented on the basis of morphological and molecular characteristics. To date, eight species of echinorhynchids have been documented, namely, *Filisoma bucerium* Van Cleave 1940; *Echinorhynchus gadi* Zoega in Müller, 1776; *Koronacantha mexicana* Monks & Perez-Ponce de León, 1996; *K. pectinaria* (Van Cleave, 1940); *Pomphorhynchus rocci* Cordonnier & Ward, 1967; *Pseudoleptorhynchoides lamothei* Salgado-Maldonado, 1976; and *Rhadinorhynchus trachinoti* Grano-Maldonado, Sereno-Uribe, Hernández Payán, Pérez-Ponce de León, & García-Varela 2025, plus *D. bajacaliforniaensis* n. gen., n. sp. [12,17]. In addition, our phylogenetic analyses inferred with nuclear and mitochondrial molecular markers supported the close relationships among Cavisomidae, Spinulacorpidae, Transvenidae and Rhadinorhynchidae. Notably, cox 1 is a molecular marker with a high rate of substitution, which is suitable for determining the phylogenetic relationships among species, detecting complexes of cryptic species or performing population studies of acanthocephalans [33–37]. For example, our cox 1 tree placed in a single clade five isolates of *R. trachinoti*, from the Gafftopsail pompano (*Trachinotus rhodopus* Gill) and from the mysid crustaceans (*Metamysidopsis frankfiersi* Hendrickx and Payán), plus five isolates of a putative species (*Rhadinorhynchus villalobosi* Martínez-Flores, García-Prieto and Oceguera-Figueroa, 2025), from the Pacific Coast of Mexico, showing a very low genetic divergence ranging from 0 to 0.2 %. The phylogenetic analyses inferred with cox 1, in combination with the low genetic divergence and morphological evidence suggest that all the isolates are conspecific and belong to *R. trachinoti* (see Fig. 6 [17,38]) and therefore, *R. villalobosi* is considered a synonym of *R. trachinoti*.

CRediT authorship contribution statement

Rogelio Aguilar-Aguilar: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Marcelo Tonatiuh González-García:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Martín García-Varela:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Consent to participate

All the listed authors have made significant contributions to the study and agreed to participate.

Consent for publication

All authors have read and agreed to the published version of the manuscript.

Ethical approval

The sampling in this work complies with the current laws and animal ethics regulations of México. Specimens were collected under the Cartilla Nacional de Colector Científico (FAUT 0202) issued by the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT), to M.G.V.

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Declaration of competing interest

No conflict of interest exists among the authors.

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References

[1] O.M. Amin, Classification of the Acanthocephala, Folia Parasitol. 60 (2013) 273–305, https://doi.org/10.14411/fp.2013.031.

[2] D. Gibson, M. Wayland, World List of marine Acanthocephala. Echinorhynchida, Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=20286, 2025.

[3] W.L. Bullock, Morphological features as tools and as pitfalls in acanthocephalan systematics, in: G.D. Schmidt (Ed.), Problems in Systematics of Parasites, University Park Press, Baltimore, Maryland and Manchester, England, 1969, pp. 9–45.

[4] S. Pichelin, T.H. Cribb, The status of the Diplosentidae (Acanthocephala: Palaeacanthocephala) and a new family of acanthocephalans from Australian wrasses (Pisces: Labridae), Folia Parasitol. 48 (2001) 289–303, https://doi.org/10.14411/fp.2001.047.

[5] M. García-Varela, S.A. Nadler, Phylogenetic relationships of Palaeacanthocephala (Acanthocephala) inferred from SSU and LSU rDNA gene sequences, J. Parasitol. 91 (2005) 1401–1409, https://doi.org/10.1645/GE-523R.1.

[6] L.R. Smales, A new acanthocephalan family, the Isthmosacanthidae (Acanthocephala: Echinorhynchida), with the description of *Isthmosacanthus*

fitzroyensis n. g., n. sp. from threadfin fishes (Polynemidae) of northern Australia, Syst. Parasitol. 82 (2012) 105–111, https://doi.org/10.1007/s11230-012-9348-9.

[7] D.C. Huston, T.H. Cribb, L.R. Smales, Molecular characterisation of acanthocephalans from Australian marine teleosts: proposal of a new family, synonymy of other and transfer of taxa between orders, Syst. Parasitol. 97 (2020) 1–23, https://doi.org/10.1007/s11230-020-09932-6.

[8] D.C. Huston, L.R. Smales, Proposoal of *Spinulacorpus biforme* (Smales, 2014) n. g., n. comb. and the Spinulacorpidae n. fam. to resolve paraphyly of the acanthocephalan family Rhadinorhynchidae Lühe, 1912, Syst. Parasitol. 97 (2020) 477–480, https://doi.org/10.1007/s11230-020-09923-7.

[9] M. García-Varela, A, González-Oliver, the systematic position of *Leptorhynchoides* (Kostylew, 1924) and *Pseudoleptorhynchoides* (Salgado-Maldonado, 1976), inferred from nuclear and mitochondrial DNA gene sequences, J. Parasitol. 94 (2008) 959–962, https://doi.org/10.1645/GE-1420.1.

[10] M. García-Varela, L. Andrade-Gómez, First steps to understand the systematics of Echinorhynchidae Cobbold, 1876 (Acanthocephala), inferred through nuclear gene sequences, Parasitol. Int. 81 (2021) 102264, https://doi.org/10.1016/jparint.2020.102264.

[11] Y. Kita, S.F. Hiruta, M. Sasaki, H. Kajihara, Systematic position of the genus *Metacanthocephalus* Yamaguti, 1959 (Palaeacanthocephala: Echinorhynchida) inferred from molecular evidence, with a redescription of *Metacanthocephalus ovicephalus* (Zhukov, 1960), Parasitol. Int. 94 (2023) 102731, https://doi.org/10.1016/j. parint. 2023. 102731.

[12] L. García-Prieto, M. García-Varela, B. Mendoza-Garfias, G. Pérez-Ponce de León, Checklist of the Acanthocephala in wildlife vertebrates of Mexico, Zootaxa 2419 (2010) 1–50, https://doi.org/10.11646/zootaxa.2419.1.1.

[13] R. Rosas-Valdez, J.J. Morrone, M. García-Varela, Molecular phylogenetics of *Floridosentis* Ward, 1953 (Acanthocephala: Neoechinorhynchidae) parasites of mullets (Osteichthyes) from Mexico, using 28S rDNA sequences, J. Parasitol. 98 (2012) 855–862, https://doi.org/10.1645/GE-2963.1.

[14] R. Rosas-Valdez, J.J. Morrone, C.D. Pinacho-Pinacho, O. Domínguez-Domínguez, M. García-Varela, Genetic diversification of acanthocephalans of the genus *Floridosentis* Ward, 1953 (Acanthocephala: Neoechinorhynchidae), parasites of mullets from the Americas, Infect. Genet. Evol. 85 (2020) 104535, https://doi.org/10.1016/j.meegid.2020.104535.

[15] A. Martínez-Aquino, J.G. García-Teh, F.S. Ceccarelli, M.L. Aguirre-Macedo, V. M. Vidal-Martínez, Integrative taxonomy of Serrasentis gibsoni n. sp. (Acanthocephala: Isthmosacanthidae) from flatfishes in the Gulf of Mexico, J. Helminthol. 97 (e96) (2023) 1–17, https://doi.org/10.1017/S0022149X23000822.

[16] M. García-Varela, A.L. Sereno-Uribe, B. Solórzano-García, G. Pérez-Ponce de León, The white grunt, *Haemulon plumierii* (Lacepède, 1801) as paratenic and definitive host of two acanthocephalan species, with the description of a new species of *Dollfusentis* (Palaeacanthocephala: Leptohynchoididae) from the Yucatán peninsula, Mexico, J. Helminthol. 98 (2024) e31, https://doi.org/10.1017/S0022149X24000105.

[17] M.I. Grano-Maldonado, A.L. Sereno-Uribe, J.C. Hernández Payán, G. Pérez-Ponce de León, M. García-Varela, Linking adults and cystacanths of a new species of *Rhadinorhynchus* Lühe, 1911 (Acanthocephala: Rhadinorhynchidae) from the Pacific coast of Mexico by using morphological and molecular data, Syst. Parasitol. 102 (2025), https://doi.org/10.1007/s11230-024-10205-9.

[18] O.M. Amin, R.A. Heckmann, A.H. Ali, The finding of Pacific transvenid acanthocephalan in the Arabian Gulf, with the description of *Paratrajectura longcementglandatus*, n. gen., n sp. from perciform fishes and emendation of Transvenidae, J. Parasitol. (2018) 294–299.

[19] G. Salgado-Maldonado, Acantocefalos de peces I. Descripción de *Caballerorhynchus lamothei*, gen., nov., sp, nov., Acanthocephala: Fessisentidae, parásitos de *Diapterus olisthostomus* de Sontecomapan, Veracruz, México, An. Inst. Biol. UNAM 29 (1977) 493–501.

[20] O. Folmer, M. Black, W. Hoeh, R. Lutz, R. Vrijenhoek, DNA primers for the amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates, Mol. Mar. Biol. Biotechnol. 3 (1994) 294–299.

[21] J.D. Thompson, D.G. Higgins, T.J. Gibson, CLUSTALW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice, Nucleic Acids Res. 22 (1994) 4673–4680, https://doi.org/10.1093/nar/22.22.4673.

[22] D. Posada, jModelTest: phylogenetic model averaging, Mol. Biol. Evol. 25 (2008) 1253–1256, https://doi.org/10.1093/molbev/msn083.

[23] A. Stamatakis, RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models, Bioinformatics 22 (2006) 2688–2690.

[24] F. Ronquist, M. Teslenko, P. Van Der Mark, D.L. Ayres, A. Darling, S. Hohna, B. Larget, L. Liu, M.A. Suchard, J.P. Huelsenbeck, MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space, Syst. Biol. 61 (2012) 539–542, https://doi.org/10.1093/sysbio/sys029.

[25] A. Rambaut, A.J. Drummond, Tracer v1.4. http://beast.bio.ed.ac.uk/Tracer, 2007.

[26] S. Pichelin, L.R. Smales, T.H. Cribb, A review of the genus *Sclerocollum* Schmidt & Paperna, 1978 (Acanthocephala: Cavisomidae) from rabbitfishes (Siganidae) in the Indian and Pacific Oceans, Syst. Parasitol. 93 (2016) 101–114, https://doi.org/10.1007/s11230-015-9609-5.

[27] R. Ghanei-Motlagh, J.S. Hernández-Orts, M.D. Fast, M. El-Matbouli, M. Saleh, Morphology and molecular phylogeny of *Rhadinorhynchus nudus* (Harada, 1938) (Acanthocephala: Rhadinorhynchidae) from *Euthynnus affinis* (Scombridae) in the Persian Gulf off Iran, Syst. Parasitol. 102 (2025) 34, https://doi.org/10.1007/s11230-025-10225-z.

[28] R. Aguilar-Aguilar, Little-known members of the kelp forest: Helminth parasites of the Garibaldi Damselfish *Hypsypops rubicundus* (Teleostei: Pomacentridae) from Bahía de Todos Santos, Baja California, Mexico, with the description of *Opegaster gorgonio* sp. nov. (Trematoda: Opecoelidae), Mar. Biodivers. (2026) (in press).

[29] N.V. Ha, O.M. Amin, H.D. Ngo, R.A. Heckmann, Descriptions of acanthocephalans, *Cathayacanthus spinitruncatus* (Rhadinorhynchidae) male and *Pararhadinorhynchus magnus* n. sp. (Diplosentidae), from marine fish of Vietnam, with notes on *Heterosentis holospinus* (Arhythmacanthidae), Parasite 25 (2018) 12, https://doi.org/10.1051/parasite/2018032.

[30] O.I. Lisitsyna, O. Kudlai, T.H. Cribb, N.J. Smit, Three new species of acanthocephalans (Palaeacanthocephala) from marine fishes collected off the East Coast of South Africa, Folia Parasitol. 66 (2019) 012, https://doi.org/10.14411/fp.2019.012.

[31] J.T. Claisse, C.A. Blanchette, J.E. Dugan, J.P. Williams, J. Freiwald, D.J. Pondella, N.K. Schooler, D.M. Hubbard, K. Davis, L.A. Zahn, C.M. Williams, J.E. Caselle, Biogeographic patterns of communities across diverse marine ecosystems in southern California, Mar. Ecol. 39 (2018), https://doi.org/10.1111/maec.12453 (S1).

[32] C.M. Williams, Spatial and Habitat Variation in Life History of the Garibaldi, *Hypsypops rubicundus*, Including Validation of Annual Growth Increments California, State Polytechnic University, Pomona, 2021.

[33] M.L. Steinauer, B.B. Nickol, G. Ortí, Cryptic speciation and patterns of phenotypic variation of variable acanthocephalan parasite, Mol. Ecol. 16 (2007) (2007) 4097–4109, https://doi.org/10.1111/j.1365-294X.2007.03462.x.

[34] F.J. Alcántar-Escalera, M. García-Varela, E. Vázquez-Domínguez, G. Pérez Ponce de León, Using DNA barcoding to link cystacanths and adults of the acanthocephalan *Polymorphus brevis* in Central Mexico, Mol. Ecol. Resour. 13 (2013) 1116–1124, https://doi.org/10.1111/1755-0998.12090.

[35] C.D. Pinacho-Pinacho, M. García-Varela, A.L. Sereno-Uribe, G. Pérez Ponce de León, A hyper-diverse genus of acanthocephalans revealed by tree-base and non-tree-base species delimitation methods: ten cryptic species of *Neoechinorhynchus* in middle American freshwater fishes, Mol. Phylogenet. Evol. 127 (2018) 30–45, https://doi.org/10.1016/j.ympev.2018.05.023.

[36] M.J. Perrot-Minnot, M. Špakulová, R. Wattier, P. Kotlík, S. Düsen, A. Ayogdu, C. Tougard, Contrasting phylogeography of two Western Palaeartic fish parasites despite similar life cycle, J. Biogeogr. 45 (2018) 101–115, https://doi.org/10.1111/jbi.13118.

[37] M. García-Varela, A. López-Jiménez, M.T. González-García, A.L. Sereno-Uribe, L. Andrade-Gómez, Contrasting the population genetic structure of a specialist (*Hexaglandula corynosoma*: Acanthocephala: Polymorphidae) and generalist parasite (*Southwellina hispida*) distributed sympatrically in Mexico, Parasitol (2023) 1–11, https://doi.org/10.1017/S0031182023000033.

[38] G. Martínez-Flores, L. García-Prieto, A. Oceguera-Figueroa, *Rhadinorhynchus villalobosi* sp. n. (Acanthocephala: Rhadinorhynchidae) from the gafftopsail pompano *Trachinotus rhodopus* (Carangiformes: Carangidae) from Pacific coast in Mexico, Folia Parasitol. 72 (2025) 007, https://doi.org/10.14411/fp.2025.007.

[39] O.M. Amin, R.H. Heckmann, Z. Fiser, V. Zaksek, H. Herlyn, R. Kostanjsek, Description of *Acanthocephalus anguillae balkanicus* subsp. n. (Acanthocephala: Echinorhynchidae) from *Proteus anguinus* Laurenti (Amphibia: Proteidae) and the cave ecomorph of *Asellus aquaticus* (Crustacea: Asellidae) in Slovenia, Folia Parasitol. 66 (2019) 015, https://doi.org/10.14411/fp.2019.015.

[40] H. Herlyn, O. Piskurek, J. Schmitz, U. Ehlers, H. Zischer, The syndermata phylogeny and the evolution of acanthocephalan edoparasitism as inferred from 18S rDNA sequence, Mol. Phylogenet. Evol. 26 (2003) 155–164.

[41] M. García-Varela, S.A. Nadler, Phylogenetic relationships of Syndermata based on small subunit (SSU) and large subunit (LSU) of rRNA and cytochrome oxidase subunit I genes sequences, Mol. Phylogenet. Evol. 40 (2006) 61–72, https://doi.org/10.1016/j.ympev.2006.02.010.

[42] M. Nakao, *Pseudoacanthocephalus toshimai* sp. nov. (Palaeacanthocephala: Echinorhynchidae), a common acanthocephalan of anuran and urodelan amphibians in Hakkaido, Japan with a finding of its intermediate host, Parasitol. Int. 65 (2016) 323–332, https://doi.org/10.1016/j.parint.2016.03.011.

[43] V.S. Irena, V. Damir, K. Damir, D. Zrinka, G. Emil, C. Helena, T. Emin, Molecular characterization and infection dynamics of *Dentitruncus truttae* from trout (*Salmo trutta* and *Oncorhynchus mykiss*) in Krka River, Croatia, Vet. Parasitol. 197 (2013) 604–613, https://doi.org/10.1016/j.vetpar.2013.07.014.

[44] I. Vardić Smrzlić, B. Čolić, D. Kapetanović, S. Šariri, T. Mijošek, V.F. Marijić, Phylogeny and genetic variability of rotifer's closest relatives Acanthocephala: an example from Croatia, Hydrobiol 851 (2024) 2845–2860, https://doi.org/10.1007/s10750-023-05372-7.

[45] M.T. Wayland, J.K. Vainio, D.I. Gibson, E.A. Herniou, D.T. Littlewood, R. Väinölä, The systematics of *Echinorhynchus* Zoega in Müller, 1776 (Acanthocephala, Echinorhynchidae) elucidated by nuclear and mitochondrial sequence data from eight European taxa, Zookeys 484 (2015) 25–52, https://doi.org/10.3897/zookeys.484.9132.

[46] G. Giribet, M.V. Sorensen, P. Funch, R.M. Kristensen, W. Sterrer, Investigation into the phylogenetic position of Micrognathozoa using four molecular loci, Cladistic 20 (2004) 1–13, https://doi.org/10.1111/j.1096-0031.2004.00004.x.

[47] L. Verweyen, S. Klimpel, H.W. Palm, Molecular phylogeny of the Acanthocephala (class Palaeacanthocephala) with a paraphyletic assemblage of the orders Polymorphida and Echinorhynchida, PLoS One 6 (12) (2011) e28285, https://doi.org/10.1371/journal.pone.0028285.

[48] V.V. Aleshin, I.A. Milyutina, O.S. Kedrova, N.S. Vladychenskaya, N.B. Petrov, Phylogeny of nematoda and cephalorhyncha derived from 18S rDNA, J. Mol. Evol. 47 (1998) 597–605.

[49] V.S. Costa Fernandes, O. Amin, J.N. Borges, C.P. Santos, A New species of the Acanthocephalan genus *Filisoma* (Cavisomidae) from Perciform Fishes in Rio de

Janeiro, Brasil, Acta Parasitol. 64 (2019) 176–186, https://doi.org/10.2478/s11686-018-00019-3.

[50] M. García-Varela, G. Pérez-Ponce de León, P. de la Torre, M.P. Cummings, S. S. Sarma, J.P. Laclette, Phylogenetic relationships of Acanthocephala based on analysis of 18S ribosomal RNA gene sequences, J. Mol. Evol. 50 (2000) 532–540, https://doi.org/10.1007/s002390010056.

[51] T.J. Near, J.R. Garey, S.A. Nadler, Phylogenetic relationships of the Acanthocephala inferred from 18S ribosomal DNA sequences, Mol. Phylogenet. Evol. 10 (1998) 287–298, https://doi.org/10.1006/mpev.1998.0569.

[52] L. Liang, H.X. Chen, O.M. Amin, Y. Yang, Morphological variability and molecular characterization of *Pomphorhynchus zhoushanensis* sp. nov. (Acanthocephala: Pomphorhynchidae), with comments on the systematic status of *Pomphorhynchus* Monticelli, 1905, Parasitol. Int. 66 (2017) 693–698, https://doi.org/10.1016/j.parint.2017.05.010.

[53] M. Sharifdini, O.M. Amin, R.A. Heckmann, The Molecular profile of Paratrajectura longcementglandatus Amin, Heckmann Et Ali, 2018 (Acanthocephala: Transvenidae) from percid fishes in the marine waters of Iran and Iraq, Helminthologia 25 (2020) 1–11, https://doi.org/10.2478/helm-2020-0007.

[54] A. Chaudhary, O.M. Amin, R. Heckmann, H.S. Singh, The molecular phylogeny of *Pararhadinorhynchus magnus* Ha, Amin, Ngo, Heckmann, 2018 (Acanthocephala: Rhadinorhynchidae) from *Scatophagus argus* (Linn.) (Scatophagidae) in Vietnam, Acta Parasitol. 65 (2020) 610–619, https://doi.org/10.2478/s11686-020-00191-5.

[55] Y. Kita, M. Nitta, H. Kajihara, Systematics of *Pseudocavisoma* (Acanthocephala: Echinorhynchida): assessment of familial affiliation, establishment of a new species, and complementary redescription of the type species based on syntypes, Syst. Parasitol. 101 (2024) 73, https://doi.org/10.1007/s11230-024-10201-z.

[56] O.M. Amin, R.A. Heckmann, S. Dallarés, M. Constenla, N. Van Ha, Morphological and molecular description of Rhadinorhynchus hiansi Soota and Bhattacharya, 1981 (Acanthocephala: Rhadinorhynchidae) from marine fish off the Pacific coast of Vietnam, J. Parasitol. 106 (2020) 56–70.

[57] M.L. Steinauer, A.E. Garcia-Vedrenne, S.B. Weinstein, A.M. Kuris, Acanthocephalan parasites of the oarfish, *Regelecus russelii* (Regalecidae), with a description of a new species of *Gymnorhadinorhynchus* (Acanthocephala: Gymnorhadinorhynchidae), J. Parasitol. 105 (2019) 124–132, https://doi.org/10.1645/17-53.

[58] L. Li, H.X. Chen, Y. Yang, Morphological and molecular study of Neorhadinorhynchus nudus (Harada, 1938) (Acanthocephala: Cavisomidae) from Auxis thazard Lacepede (Perciformes: Scombridae) in the South China Sea, Acta Parasitol. 25 (2018) 479–485, https://doi.org/10.1515/ap-2018-0057.

[59] O.M. Amin, R.A. Heckmann, S. Dallarés, M. Constenla, N.V. Ha, Morphological and molecular description of *Rhadinorhynchus laterospinosus* Amin, Heckmann & Ha, 2011 (Acanthocephala, Rhadinorhynchidae) from marine fish off the Pacific coast of Vietnam, Parasite 26 (2019) 14, https://doi.org/10.1051/parasite/2019015.

[60] M. Gregori, F.J. Aznara, E. Abollo, A. Roura, A.F. González, S. Pascual, *Nyctiphanes couchii* as intermediate host for *Rhadinorhynchus* sp. (Acanthocephala, Echinorhynchidae) from NW Iberian Peninsula waters, Dis. Aquat. Org. 105 (2013) 9–20, https://doi.org/10.3354/dao02611.

[61] M. Bao, A. Roura, M. Mota, D.J. Nachón, C. Antunes, F. Cobo, K. MacKenzie, S. Pascual, Macroparasites of allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*) of the Western Iberian Peninsula Rivers: ecological, phylogenetic and zoonotic insights, Parasitol. Res. 114 (2015) 3721–3739, https://doi.org/10.1007/s00436-015-4601-1.