



Research paper

Welcome back to life: Validating the genus *Illiosentis* Van Cleave and Lincicome, 1939 (Leptorhynchoididae: Palaeacanthocephala), with the description of a new species from the pigfish (*Orthopristis chrysoptera*: Haemulidae) in Yucatán Peninsula, Mexico

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ABSTRACT

The haemulid fish *Orthopristis chrysoptera* commonly known as pigfish is distributed in the Western Atlantic coast, Caribbean Sea and Gulf of Mexico. Specimens of *O. chrysoptera* sampled off the coast of Sisal, Yucatán, in the Gulf of Mexico were infected with two species of acanthocephalans from the family Leptorhynchoididae. One of them was identified as *Dollfusentis bravoae* and the other was allocated into the genus *Illiosentis*. However, the taxonomic status of *Illiosentis* has been controversial since it has been proposed as synonym of *Tegorhynchus*. Here, sequences the small (SSU) and large (LSU) subunits from the nuclear DNA and cytochrome *c* oxidase subunit 1 (*cox 1*) from the mitochondrial DNA were generated and aligned with sequences from GenBank from other leptorhynchoidid species. Phylogenetic analyses inferred with the concatenated data set (SSU + LSU + *cox 1*) and *cox 1* data set along, revealed that isolates of *Tegorhynchus* sp. and *T. cetratus* from GenBank were nested in two independent clades, suggesting that the genus is paraphyletic, indicating that *Tegorhynchus* needs a taxonomic review. Specimens identified in this study as *Illiosentis* sp., formed an independent genetic lineage which is recognized herein as a new species, *Illiosentis kukulkani* n. sp. The new species is morphologically distinguished from the other five congeners by having a cylindrical proboscis armed with 20–21 longitudinal rows with 14 hooks each and by having a sensory papilla between 6 and 8 hooks from posterior region of the proboscis. Novel molecular evidence was also useful for testing the validity of the genus *Illiosentis*.

1. Introduction

Acanthocephalans of the class Palaeacanthocephala Meyer, 1931 use vertebrates (fishes, amphibians, reptiles, birds and mammals) and invertebrate malacostracans (crustaceans), to complete their life cycle and alternatively use fish, amphibians and reptiles as paratenic hosts (transport) to facilitate transmission to the appropriate definitive hosts [1–4]. Members of the family Leptorhynchoididae Witenberg, 1932 belong to the order Echinorhynchida, Southwell and Macfie, 1925 and have been extensively studied from a morphological, ecological and molecular point of view [2–15]. The family, Leptorhynchoididae contains approximately 85 species classified into 15 genera: *Brentisentis*

Leotta, Schmidt and Kuntz, 1982, *Dollfusentis* Golvan 1969, *Indorhynchus* Golvan, 1969, *Koronacantha* Monks and Pérez-Ponce de León, 1996, *Leptorhynchoides* Kostylev, 1924, *Metacanthocephalus* Yamaguti, 1959, *Metarhadinorhynchus* Yamaguti, 1959, *Pseudorhadinorhynchus* Akhmerov and Dombrovskaja-Akhmerova, 1941, *Tegorhynchus* Van Cleave, 1921, and *Telosentis* Van Cleave, 1923. Five additional genera are monotypic: *Dentitruncus* Sinzari 1955, *Goacanthus* Gupta and Jain 1980, *Neotegorhynchus* Lisitsyna, Xi, Orosová, Barčák and Oros 2002, *Paradentitruncus* Moravec and Sey, 1989 and *Pseudoleptorhynchoides* Salgado-Maldonado 1976 [9,14–18]. Adults of Leptorhynchoididae are intestinal parasites of a broad spectrum of marine, brackish and freshwater fishes distributed in tropical and temperate waters across the world [9,14–17].

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The 15 genera are morphologically distinguished by the proboscis shape, number of hooks on the proboscis, size and location of the posterior hooks, presence or absence of genital spines, structure of the reproductive system of male and female, location of somatic spines on the body, position of the cerebral ganglion, and position of the genital pore [9,11,14,15,17]. The classification of Leptorhynchoididae has been studied by combining morphological and molecular characteristics; new genera and species have been discovered and several taxonomic rearrangements and transferences have been proposed [8,9,14,15,17]. The taxonomic status of genera such as *Illiosentis* Van Cleave and Lincicome, 1939 and *Tegorhynchus* has been unstable. For instance, *Illiosentis* was originally proposed to accommodate *I. furcatus* Van Cleave and Lincicome, 1939, as a parasite of the southern kingfish (*Menticirrhus americanus*) from Louisiana, USA. Later, other six species (*I. cetratus* Van Cleave, 1945; *I. africanus* Golvan, 1956; *I. edmondsi* Golvan, 1960; *I. longispinus* Cable and Linderth, 1963, *I. heteracanthus* Cable and Linderth, 1963; *I. ctenorhynchus* Cable and Linderth, 1963) were added to genus and recognized by Golvan [19], in his classification scheme. However, some species originally classified in *Illiosentis*, later were transferred to other genera including *Tegorhynchus* and *Dollfusentis*, and these changes were accepted by other authorities [20,21]. Still, the proposal of the synonymy of *Illiosentis* with *Tegorhynchus* has been questioned [11,13,14,21].

Specimens of Leptorhynchoididae recently sampled from marine fish in waters of the Yucatán Peninsula allowed to further test the taxonomic status of these genera. Other species of Leptorhynchoididae were previously reported from that geographical area, including *Dollfusentis bravoae* Salgado-Maldonado, 1976 and *D. mayae* García-Varela, Sereno-Uribe, Solórzano-García and Pérez-Ponce de León 2024 [22]. In continuation with the survey work aimed at describing the diversity of marine fish helminths in the Gulf of Mexico, acanthocephalans were collected from the intestines of the Pigfish (*Orthopristis chrysoptera*) off the coast of Sisal, Yucatán. Two morphotypes were identified, one morphologically consistent with *D. bravoae* and one that showed a unique combination of morphological traits that was allocated in the genus *Illiosentis*. The main objectives of the current study were i) to characterize molecularly and morphologically a new species of *Illiosentis*; ii) to test the phylogenetic position of the new species within Leptorhynchoididae; iii) to use the novel molecular data to analyze the taxonomic status of the genus *Illiosentis*.

2. Material and methods

2.1. Host collection and morphological study

Four specimens of the Pigfish (*O. chrysoptera*) were obtained from the commercial capture of fisherman from off the coast of Sisal, Yucatán (21° 08' 1.5" N, 90° 07' 55.9" W), in February 2025. Acanthocephalans were removed from the intestines of their definitive hosts, washed in a 0.85% saline solution, placed in distilled water at 4 °C overnight, and subsequently fixed in 70% ethanol. Some specimens 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 (CNHE, 12586–12589). Acanthocephalans were initially identified by conventional morphological criteria. Measurements of the specimens are presented in micrometers unless otherwise stated, with the mean followed by range in parentheses. For scanning electron microscopy (SEM), specimens were dehydrated through an ethanol series, critical point dried with CO₂, sputter coated with gold, and examined with a Hitachi Stereoscan Model S-2469N scanning electron microscope operating at 15 kV at the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM).

2.2. DNA sequencing and phylogenetic analyses

Ten specimens identified as *Illiosentis* sp., plus four specimens identified as *Dollfusentis bravoae* were individually digested overnight at 56 °C in a solution containing 20 mM NaCl, 100 mM Na₂ 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' [5,6]. A near complete fragment from 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' [5,6]. Finally, the cytochrome c oxidase subunit 1 (*cox 1*) from the mitochondrial DNA was amplified using the forward primer 5'-AGTTC-TAATCATAA(R)GATAT(Y)GG-3' and reverse primer 5'-TAAACTT-CAGGGTGACCAAAAAATCA-3' [23]. The amplification reactions were performed with MyTaq DNA Polymerase following the manufacturer's instructions. PCR amplifications were performed in a total volume of 12.5 µl containing 2 µl of each primer, 10 pmol/µl, 1.5 µl buffer 10× and 0.25 µl of Taq polymerase. 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). Newly generated sequences were aligned with published sequences for other acanthocephalans from family Leptorhynchoididae retrieved from the GenBank dataset (Table 1). Two alignments were performed. The first contained three molecular markers (SSU, LSU and *cox 1*), the second contained only *cox 1*. Both alignments were constructed using the software SeaView v.4 [24] and adjusted manually with the software Mesquite [25]. The phylogenetic analyses of each data set was performed using maximum likelihood (ML) and Bayesian inference (BI) methods. The ML analysis was carried out with RAxML version 7.04 [26], and Bayesian inference analyses were performed with MrBayes version 3.2.7 [27] using the Cyberinfrastructure with Phylogenetic Research (CIPRES) Science Gateway v3.3 online interface [28]. To support each node, 10,000 bootstrap replicates were run with ML. Bayesian inference analyses include Markov chain Monte Carlo (MCMC) searches with two simultaneous runs for 10 million generations, sampling every 1000 generations with a heating parameter value of 0.2 and a "burn-in" of 25%. Trees were visualized in FigTree v. 1.4.0 [29]. Genetic divergence among taxa was estimated using uncorrected 'p' distances with the software MEGA version 11 [30].

Table 1

Summary of the taxa from Leptorhynchoididae and sequences used in the phylogenetic analyses. Sequences in bold were obtained in this study.

Genus	Species Number	Distribution	Host family	Environment	Sequences			Resource
					SSU	LSU	Cox 1	
<i>Brentisentis</i>	3	Asia	Eleotridae Gobiidae	Brackish Marine Freshwater				Leotta et al. [16].
<i>Dentitruncus</i>	1	Europe	Salmonidae	Marine	JX460863		OQ569921	Irena et al. [42].
<i>Dollfusentis</i>	7	America						Gibson and Wayland [18].
<i>D. bravoae</i>		America	Gerreidae Haemulidae	Brackish Marine	MK282759; OR886453	MK282754; OR886456	MK294060; OR883559–60; MK294060–64; PZ464625–28	Keidel et al. [37] García-Varela et al. [22].
<i>D. lenti</i>			Haemulidae	Marine	MK282745		MK294053–59	This study
<i>D. mayae</i>			Haemulidae	Marine	OR886452	OR886455	OR883550–53	Keidel et al. [37] García-Varela et al. [22].
<i>D. chandleri</i>		America	Sciaenidae	Marine			DQ320484–93	Unpublished
<i>Goacanthus</i>	1	Asia						Gibson and Wayland [18].
<i>Illiosentis</i>	6	America, Asia		Marine				Gibson and Wayland [18].
<i>Illiosentis</i> sp.		America			AY830158	AY829092	DQ089705	García-Varela and Nadler, [5,6].
<i>Illiosentis kukulkani</i> n. sp.		America	Haemulidae	Marine	PZ464638–639	PZ464640–641	PZ464615–24	This study
<i>Indorhynchus</i>	5	Asia	Arridae	Marine				Gibson and Wayland [18].
<i>Koronacantha</i>	2	America		Marine				Monks et al. [11].
<i>K. mexicana</i>			Carangidae Labridae		AY830157	AY829095	DQ089708;	García-Varela and Nadler, [5,6]; García-Varela et al. [2].
<i>K. pectinaria</i>			Haemulidae		AF092433	AY829094	DQ089707	García-Varela and Nadler [5,6]
<i>Leptorhynchoides</i>	10	America	Centrarchidae	Freshwater	AF001840	AY829093	DQ089706	Gibson and Wayland [18].
<i>L. thecatus</i>		Europe	Acipenseridae	Marine				Near et al. [43];
<i>Metacanthocephalus</i>	6	Asia	Pleuronectidae	Marine	LC730868	LC730868	LC730869–70	García-Varela and Nadler, [5].
<i>M. ovicephalus</i>		Antartica						Gibson and Wayland [18].
<i>Metarhadinorhynchus</i>	15	Asia	Carangidae Serranidae Synodontidae Scianidae Mullidae Lateolabridae	Marine				Kita et al. [9].
<i>Neotegorhynchus</i>	1	Asia	Cyprinidae	Brackish	MK411443		MK411446	Gibson and Wayland [18].
<i>N. cyprini</i>								García-Varela and González Oliver [44].
<i>Paradentitruncus</i>	1	Asia	Ariidae	Marine				Unpublished
<i>Pseudoleptorhynchoides</i>	1	America	Centropomidae	Marine	EU090950	EU090951	EU090949	
<i>P. lamothei</i>			Ariidae	Brackish				
<i>Pseudorhadinorhynchus</i>	18	Asia	Anguillidae	Freshwater		PP455316		
<i>P. samogainsis</i>			Cyprinidae	Marine				
			Gasterosteidae					
			Gobiidae					
			Salmonidae					
<i>Tegorhynchus</i>	7	America	Gerreidae	Marine				Gibson and Wayland [18].
		Australia	Mullidae					
		Asia	Labridae					
<i>T. cetratus</i>		America	Scianidae	Marine	ON180689	OR166425	ON184030–31	Amin et al. [33].
<i>Tegorhynchus</i> sp.		Asia	Labridae	Marine	OQ942221	OR166369		Bennett et al. [45].
<i>Telosentis</i>	6	Australia	Atherinidae	Marine				Gibson and Wayland [18].
		Asia	Anguillidae	Brackish				
		America	Scianidae					
		Europe	Lutjanidae					

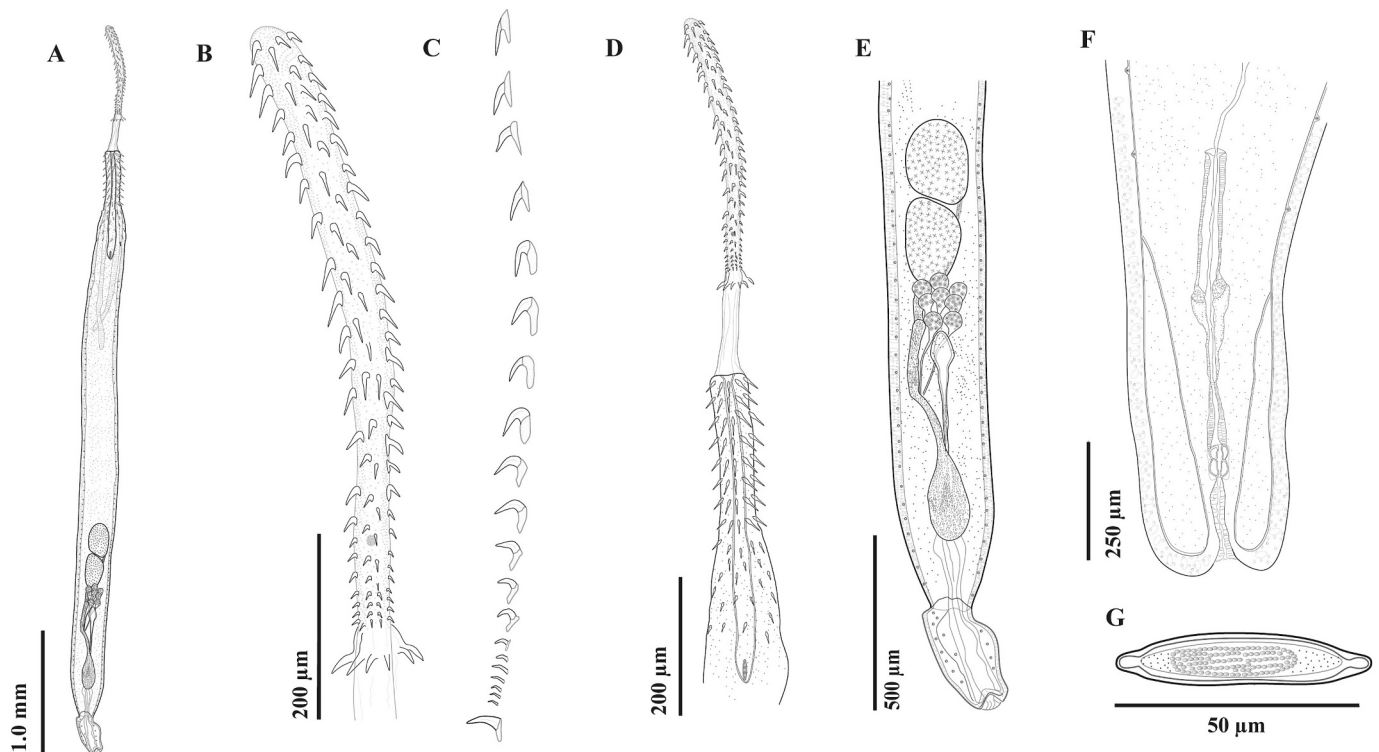


Fig. 1. Whole adult male of *Illiosentis kukulkani* n. sp. ex *Orthoprists chrysoptera* from off the coast of Sisal, Yucatán, Mexico (A); Entire male, (B); Proboscis, (C); Hooks, (D); Anterior region male (E); Posterior region male, (F) Reproductive system female, (G). Egg.

3. Results

3.1. Taxonomy

Class: Palaeacanthocephala Meyer, 1931.

Order: Echinorhynchida Southwell and Macfane, 1925.

Family: Leptorhynchoididae Witenberg, 1932.

Genus: *Illiosentis* Van Cleave and Lincome, 1939.

Species: *Illiosentis kukulkani* n. sp.

(Figs. 1 and 2)

Type host: pigfish, *Orthoprists chrysoptera* (Linnaeus, 1766).

Site of infection: Small intestine (prevalence 33%, (2/4)).

Type locality: off the coast of Sisal, Yucatán (21° 08' 1.5" N, 90° 07' 55.9" W).

Type-material: CNHE: 12586 (holotype); 12587 (allotype); 12588–89 (paratype).

Representative DNA sequences: PZ464638–PZ464639 (SSU); PZ464640–PZ464641 (LSU); PZ464615–PZ464624 (cox 1).

Etymology: The specific epithet refers to Kukulcán which represents the feathered serpent god in the Mayan civilization.

General:

Sexual dimorphism evident, females larger than males. Trunk elongated cylindrical, covered with spines on the anterior region of trunk, extending to level of 3/4 of proboscis receptacle length in both sexes (Fig. 1A). Anterior spines larger than posterior spines. Proboscis long, cylindrical, covered with 20–21 longitudinal rows with 14 hooks each, decreasing in size towards posterior end, with a transition to minute hooks and a ring of seven hooks in the posterior region of the proboscis (Fig. 1B, C; Fig. 2A, B). Sensory papillae located between 6 and 8th proboscis hook (Fig. 1B, D). Neck smooth (Fig. 2A). Proboscis receptacle double-walled. Cerebral ganglion located at base proboscis receptacle. Lemnisci tubular, elongate, longer than proboscis receptacle. Gonopore terminal in both sexes (Figs. 1A and 2E).

Male (based on 4 mounted specimen and 1 for SEM). Trunk, 4.1 mm long (3.5–4.8) × 404 (358–452) wide. Anterior trunk spines large 48

(47–50), decreasing in size; medial trunk spines 29 (43–23); posterior trunk spines 12 (8–18) (Fig. 2A, C). Proboscis 822 (789–878) × 78 (58–94), with 20–21 longitudinal rows with 14 hooks each. Apical hooks (first 9–10, rows of hooks) 35 (32–37) long, middle hooks (11–16, rows of hooks) 28 (21–35) long, basal hooks (17–25, row of hooks) 9 (6–12) (Fig. 2A, B). Ring of seven hooks in the posterior region of the proboscis 35 (30–40). Neck 283 × 85. Proboscis receptacle 1.2 mm (0.9–1.4) × 104 (78–137). Lemnisci of different size, 1.5 mm (1.4–1.7) long × 49 (41–63) wide (Fig. 1A–C). Testes ovoid in tandem, anterior 300 (264–329) × 197 (161–258), posterior 301 (263–357) × 175 (170–182). Seminal vesicle oval, elongated. Cement glands pyriform, eight in number (Fig. 1A, E) Saeftigen's pouch pyriform (Fig. 2D). Copulatory bursa well-developed, 279 long (207–348) × 230 (204–260) wide (Fig. 1E).

Female (based on 6 gravid mounted specimens). Trunk 7.4 mm long (5.3–9.5 mm) × 425 wide (339–511). Anterior trunk spines longer 53 (50–58), decreasing in size, middle spines 33 (24–47), posterior spines 19 (18–21). Proboscis 875 (749–1002) × 96 (83–109), with 20–21 longitudinal rows with 14 hooks each. Apical hooks (first 9–10, rows of hooks) 37 (33–45) long, middle hooks (11–16, rows of hooks) 25 (20–28) long, basal hooks (17–25, row of hooks) 10(8–13). Ring of seven hooks in the posterior region of the proboscis 49 long. Neck 330 (303–357) × 99 (95–103). Proboscis receptacle 1.3 mm (1.2–1.4) × 98 (73–123). Gonopore terminal. Mature eggs elongated ($n = 20$), with polar prolongations 50 (46–55) long × 14 (12–16) wide (Fig. 1F, G).

3.2. Remarks

Illiosentis kukulkani n. sp. represents the sixth species described of the genus *Illiosentis*, which contains *I. africanus*, *I. cetratus*, *I. furcatus*, *I. heteracanthus*, and *I. holospinus* which are associated mainly with marine fishes in the Americas (four species), one in Africa and other in Asia [18,31–35]. The new species can be readily differentiated from the other five congeners species by the number of hooks in the proboscis. *Illiosentis kukulkani* n. sp. possesses of 20–21 longitudinal rows of hooks

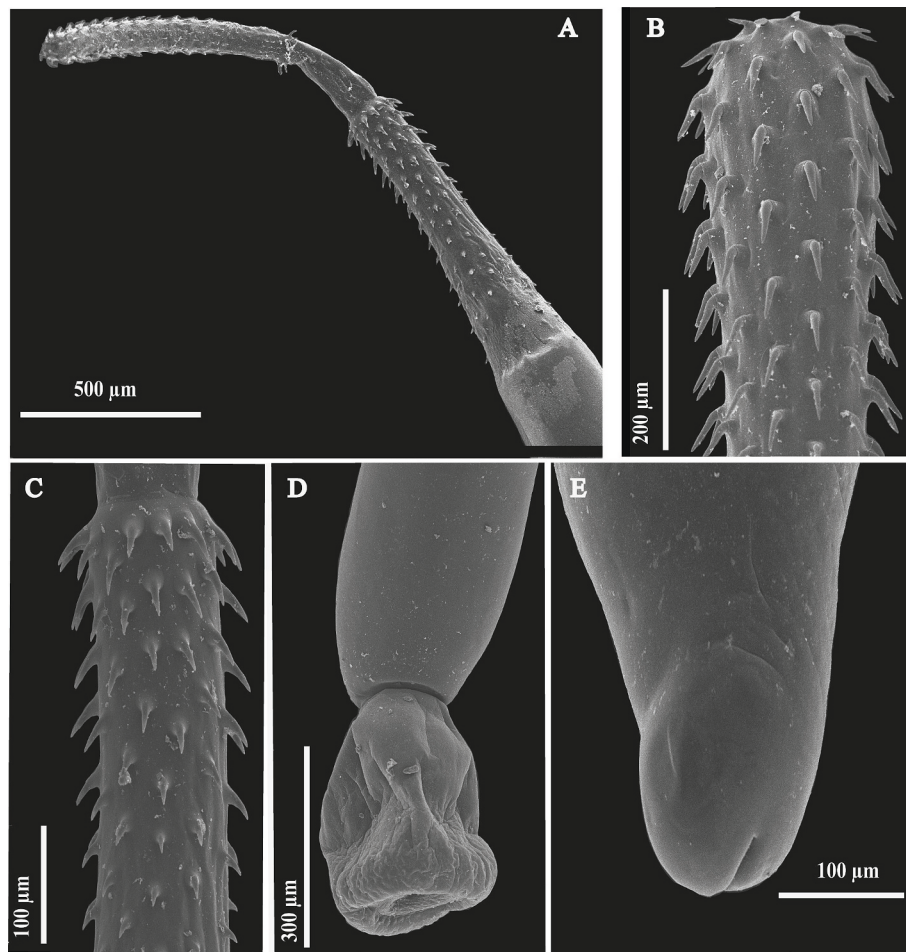


Fig. 2. Scanning electron micrographs of *Illiosentis kukulkani* n. sp. ex *Orthopristis chrysoptera* from off the coast of Sisal, Yucatán, Mexico (A) Adult male, anterior region; (B) Proboscis; (C) anterior trunk; (D) Adult male, posterior region; (E) Adult female, posterior region.

Table 2

Comparative metrical data for males and females of species of *Illiosentis*. Measurements are in micrometers.

Species name	<i>I. kukulkani</i> n. sp. Present study	<i>I. furcatus</i> Van Cleave and Lincicome [31].	<i>I. cetratus</i> Amin et al. [14].	<i>I. heteracanthus</i> Amin and Dailey [32].	<i>I. africanus</i> Golvan [34].	<i>I. holospinus</i> Amin and Sey [21].
Host family	Haemulidae	Sciaenidae	Sciaenidae	Gerreidae and Albulidae	Albulidae	Paralichthyidae and Leiognathidae
Distribution	Gulf of Mexico (Mexico)	Gulf of Mexico (USA)	North Pacific (USA)	Caribbean (Curacao, Turks and Caicos Islands)	Africa (Senegal)	Asia (Arabian Gulf, Kuwait)
Proboscis hooks						
Rows	14	14 (12–15)	14	14	14	14
Longitudinal rows	20–21	26–33	18–23	26–29	30–34	29–32
Sensory papillae	Between hooks 6–8	Between hooks 11–13	Between hooks 7–9	Between hooks 9–11	Hook 10	Between hooks 1–2
Male						
Trunk (mm)	3.5–4.8 (4.1) × 358–452 (404)	4.0–9.8 × 320–520	15.6–21.3 (18.3) × 520–870	5.2–11.8 (7.5) × 760–1200 (800)	–	3.13–8.58 (6.1) × 231–561 (412)
Proboscis (mm)	789–878 (822) × 58–94 (78)	1.06–2.97	0.95–1.25 (1.17) × 0.24–0.27 (0.26)	1.12–1.8 (1.3) × 0.1–0.2 (0.14)	2.82–3.0 × 0.24–0.38	1.15–1.48 (1.3) × 99–132 (108)
Proboscis receptacle (mm)	0.9–1.4 (1.2) × 78–137 (104)	–	2.20–2.90 (2.57) × 0.25–0.35 (0.30)	1.2–1.8 (1.6) × 0.12–0.23 (0.17)	1.8–2.0	1.8–2.9 (2.3) × 99–198 (142)
Anterior testis (mm)	264–329 (300) × 161–258 (197)	–	1.0–1.55 (1.26) × 0.22–0.35 (0.27)	0.53–1.4 (0.83) × 0.26–0.61 (0.37)	–	325–676 (546) × 143–286 (214)
Posterior testis (mm)	263–357 (301) × 170–182 (175)	–	0.87–1.17 (0.99) × 0.22–0.32	0.42–1.26 (0.65) × 0.28–0.56 (0.37)	–	273–702 (455) × 156–286 (214)
Female						
Trunk (mm)	5.3–9.5 (7.4) × 339–511 (425)	5.6–21.5 × 350–620	21.3–30.7 (25.3) × 0.52–0.87 (0.71)	7.0–19.5 (11.7) × 0.80–1.6 (1.04)	–	7.4–19.1 (13.0) × 429–900 (643)
Proboscis (mm)	0.74–1.02 (0.87) × 0.83–0.10 (0.96)	–	1.20–1.50 (1.34) × 0.26–0.35 (0.31)	1.05–1.82 (1.47) × 0.11–0.28 (0.17)	–	1.3–1.8 (1.5) × 99–165 (128)
Proboscis receptacle (mm)	1.2–1.4 (1.3) × 0.73–0.12 (0.98)	–	2.50–3.30 (2.87) × 0.27–0.35 (0.32)	1.40–1.9 (1.5) × 0.12–0.19 (0.15)	–	2.4–3.6 (2.8) × 132–231 (187)
Eggs	46–55 (50) × 12–16 (14)	67–74 × 8–10	62–78 × 13–18	48–64 (56) × 9–16 (14)	75 × 18	93–105 (98) × 20–25 (22)

in the proboscis, whereas *I. furcatus* (Type species) possesses 26–33, *I. cetratus* possesses 18–23 hooks, *I. heteracanthus* 26–29, *I. africanus* has 30–34 longitudinal rows of hooks and *I. holospinus* possesses 29–32 hooks (Table 2). Additionally, *Illiosentis kukulkani* n. sp. can be differentiated by having smaller eggs, of 50 (46–55) long $\times$ 14 (12–16) wide vs 67–74 $\times$ 8–10 in *I. furcatus*; 62–78 $\times$ 13–18 in *I. cetratus*; 56 (48–64) $\times$ 14 (9–16) in *I. heteracanthus*; 75 $\times$ 18 in *I. africanus* and 93–105 $\times$ 20–25 in *I. holospinus* (Table 2). Moreover, a morphological trait that can be used to differentiate the species of *Illiosentis* is the position of the sensory papillae in the proboscis hooks. For instance, in *Illiosentis kukulkani* n. sp., the sensory papillae is placed between the hooks 6–8 from posterior proboscis, whereas in *I. furcatus* the papillae is placed between the hooks 11–13; between hooks 7–9 in *I. cetratus*; between hooks 9–11 in *I. heteracanthus*; in the hook 10 in *I. africanus* and between hooks 1–2 in *I. holospinus* (Table 2).

3.3. Phylogenetic analysis

The concatenated alignment (SSU + LSU + *cox 1*) consisted of 22 taxa and 5351 sites. The phylogenetic tree inferred with the concatenated dataset place the two species (*D. bravoae* and *Illiosentis kukulkani* n. sp.) in two independent clades. The two samples described as *Illiosentis kukulkani* n. sp., formed an independent clade and were the sister taxa to *Illiosentis* sp. (originally reported as *Illiosentis* sp. and transferred to *Tegorhynchus*) (AY830158/AY829092/DQ089705), sampled from marine fish in the Caribbean Sea, with moderate bootstrap support (81%) and Bayesian posterior probability (0.9) support values (Fig. 3). Phylogenetic analyses revealed that three isolates of *Tegorhynchus cetratus* (OR166425 / OR166369 / ON180689 and ON184031) from the California kingcroaker (*Menticirrhus undulatus*) from California, USA were placed in two independent clades, suggesting that the isolates correspond to two separate species. An isolate identified as *Tegorhynchus* sp. (OQ942221) from the scarlet wrasse (*Pseudolabrus miles*) from New Zealand was placed in another unresolved branch suggesting that the genus is paraphyletic (see Fig. 3). Interestingly, genera such as *Koronacantha* (with two species) from the Pacific coast of Mexico, and *Dollfusentis* (with three species) from the Gulf of Mexico, formed two independent clades with strong bootstrap and Bayesian posterior probability support values (Fig. 3).

A second alignment was built with sequences of the *cox 1* and consisted of 64 taxa and 655 sites. The phylogenetic tree also placed the two species obtained in the present study in two independent clades and confirmed that the 10 new isolates of *Illiosentis kukulkani* n. sp., represented a new species as the sister taxa to an isolate of *Illiosentis* sp. (DQ089705) with strong bootstrap support (100%) and Bayesian posterior probability (1.0) support values (Fig. 4). The new four isolates of *D. bravoae* were placed within a clade formed by other 10 isolates of *D. bravoae* from the Gulf of Mexico and Caribbean Sea, with strong nodal support (Fig. 4). In addition, two isolates of *T. cetratus* (ON184030–31), from the California kingcroaker (*Menticirrhus undulatus*) from California, USA were yielded as an independent clade. Finally, the two species of *Koronacantha*, the four species of *Dollfusentis* and the two isolates of *Metacanthocephalus ovicephalus* (LC730869–70) (Zhukov, 1960) Golvan, 1969 from dark flounder (*Pseudopleuronectes obscurus*) from Japan formed three independent clades supporting their taxonomic status (Fig. 4).

The uncorrected genetic distance estimated among the 10 isolates of *Illiosentis kukulkani* n. sp., with the *cox 1* ranged from 0.0 to 0.7% and among the four isolates of *D. bravoae* ranged from 0.1 to 0.3%; the genetic distances between the newly sequenced four isolates of *D. bravoae* and other isolates available in GenBank ranged between 0.0 and 6%. Finally, the genetic distances among genera from Leptorhynchoididae analysed herein ranged from 18.0 to 28.0%.

4. Discussion

The specimens obtained from the Pigfish (*O. chrysoptera*), from off the coast of Sisal, Yucatán, belong to two species. One of them represented an undescribed species for which the name *Illiosentis kukulkani* n. sp., was coined. Currently, the genus *Illiosentis* contains species that infect mainly tropical marine fishes of six families, i.e., Haemulidae, Sciaenidae, Gerreidae, Albulidae, Paralichthyidae and Leiognathidae distributed worldwide. The second species recorded in this study was identified as *D. bravoae*. This species has been previously recorded in the burro grunt, *Pomadasys croco*, the stripped mojarra, *Eugerres plumieri*, and the white grunt, *Haemulon plumieri*, in localities across the Gulf of Mexico and Caribbean Sea of Mexico [22,36,37]. The species was previously reported from off the coast of Sisal [22], and its presence in the Pigfish, *O. chrysoptera* represents a new host record. Current data indicates that this species is a specific parasite of haemulids and gerroids [22].

Moreover, the life cycle of some members of *Illiosentis*, *Tegorhynchus* and *Leptorhynchoides* have been described in certain detail. Current evidence shows that adult worms live and sexually reproduce in the digestive tracts of marine and freshwater fishes that serve as definitive hosts. Eggs are expelled into the environment with the faeces of the host. After the ingestion of the eggs by marine and freshwater amphipods of the genera *Lepidactylus*, *Haustorius* and *Hyaella*, which serves as the intermediate hosts, the parasites develop into acanthor, acanthella and cystacanth in the hemocoel. Finally, the infected amphipods are ingested by definitive hosts to complete their life cycle [1,20,38,39]. Alternatively, paratenic hosts (fishes) play a main role in the transmission of the acanthocephalans to the appropriate definitive hosts, as is the case of *Leptorhynchoides thecatus* an acanthocephalan that have been reported in approximately 50 fish species from North America [40].

The phylogenetic analyses revealed that *Illiosentis kukulkani* n. sp., was retrieved as the sister taxa of *Illiosentis* sp.; this unidentified species was sampled in the Caribbean Sea [5]. Interestingly, the *cox 1* tree also revealed that the isolates of *Tegorhynchus* sp. and those of *T. cetratus* were recovered in two independent clades, suggesting that the genus is paraphyletic, or that the later species was probably misidentified. The taxonomic history of both genera *Illiosentis* and *Tegorhynchus* has been rather complex. For instance, *Illiosentis* was established by Van Cleave and Lincicome [31] to accommodate *I. furcatus* from specimens sampled in Louisiana, USA, whereas *Tegorhynchus* was erected to accommodate *Tegorhynchus brevis*, from near the Juan Fernandez Island in Chile [41]. In two previous studies, Monks et al. [11] and Monks and Pulido-Flores [13], examined the type-material of *Tegorhynchus brevis* and other species belonging to Leptorhynchoididae, and suggested the transference of *T. pectinarium* to the genus *Koronacantha* and additionally, provided new morphological evidence in support of the diagnosis of *T. brevis*, as the type species of that genus and recognized the validity of the both genera, *Tegorhynchus* and *Illiosentis*. Morphologically, both genera differ in several traits for example, size of the trunk, shorter and robust in *Tegorhynchus* vs elongated in *Illiosentis*; size and shape of basal hooks on the proboscis slightly curved in *Tegorhynchus* and enlarged in *Illiosentis*; lemnisci longer that proboscis receptacle reaching midbody in *Tegorhynchus* vs lemnisci longer than proboscis receptacle and not reaching midbody in *Illiosentis* [11].

The phylogenetic tree inferred with the *cox 1* gene in the present study further support the validity of *Tegorhynchus* and *Illiosentis* as two independent clades. However, the status of *I. cetratus* remains controversial. The two isolates sequenced for *cox 1* nested in a separated clade from sequences of the new species of *Illiosentis* provided in this study casting doubts on the validity of the synonymy of *I. cetratus* with *Tegorhynchus*. Sequences of other representative species of both genera are required to test further hypothesis about the systematic position of the three species allocated in *Tegorhynchus* and the six species of *Illiosentis*. The 10 sequenced specimens with *cox 1* unequivocally showed they are nested as the sister taxa of an isolate of *Illiosentis* sp. from the Caribbean

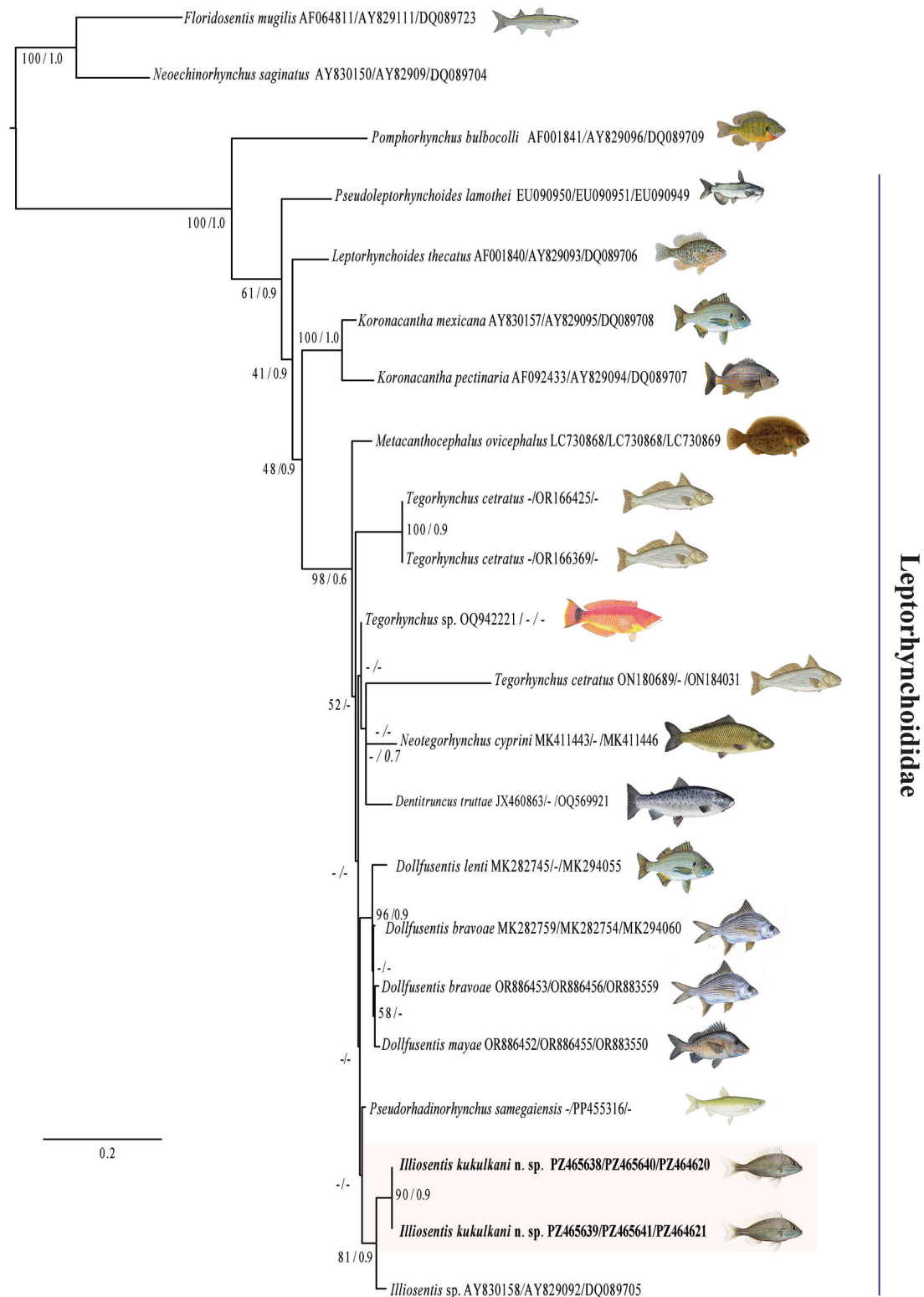


Fig. 3. Phylogenetic tree using maximum likelihood (ML) and consensus Bayesian obtained with the small and large (SSU + LSU + *cox 1*) subunits of ribosomal DNA and cytochrome oxidase subunit I (*cox 1*) from mitochondrial DNA. Numbers near internal nodes show ML bootstrap percentages/ Bayesian posterior probabilities.

Sea, within the Leptorhynchoididae. The four newly *cox 1* sequences of *D. bravoae* were nested in a clade formed for other 12 isolates of that species reported from several host species across the Gulf of Mexico and Caribbean Sea, indicating conspecificity.

Likewise, the intraspecific genetic divergence detected among the 10 *cox 1* isolates of *Illiosentis kukulkani* n. sp., was very low, ranging from

0.0 to 0.7%. This intraspecific genetic variation level is relatively similar to that observed among isolates of other species of leptorhynchoidids. For instance, the genetic divergence among isolates of *Dentitruncus truttae* Sinazar, 1955 from two fish species in Croatia ranged between 0.1 and 1.1% [42]; the divergence among isolates of *L. thecatus* (Linton, 1891) Kostylev, 1924, a parasite of freshwater fishes in eastern North

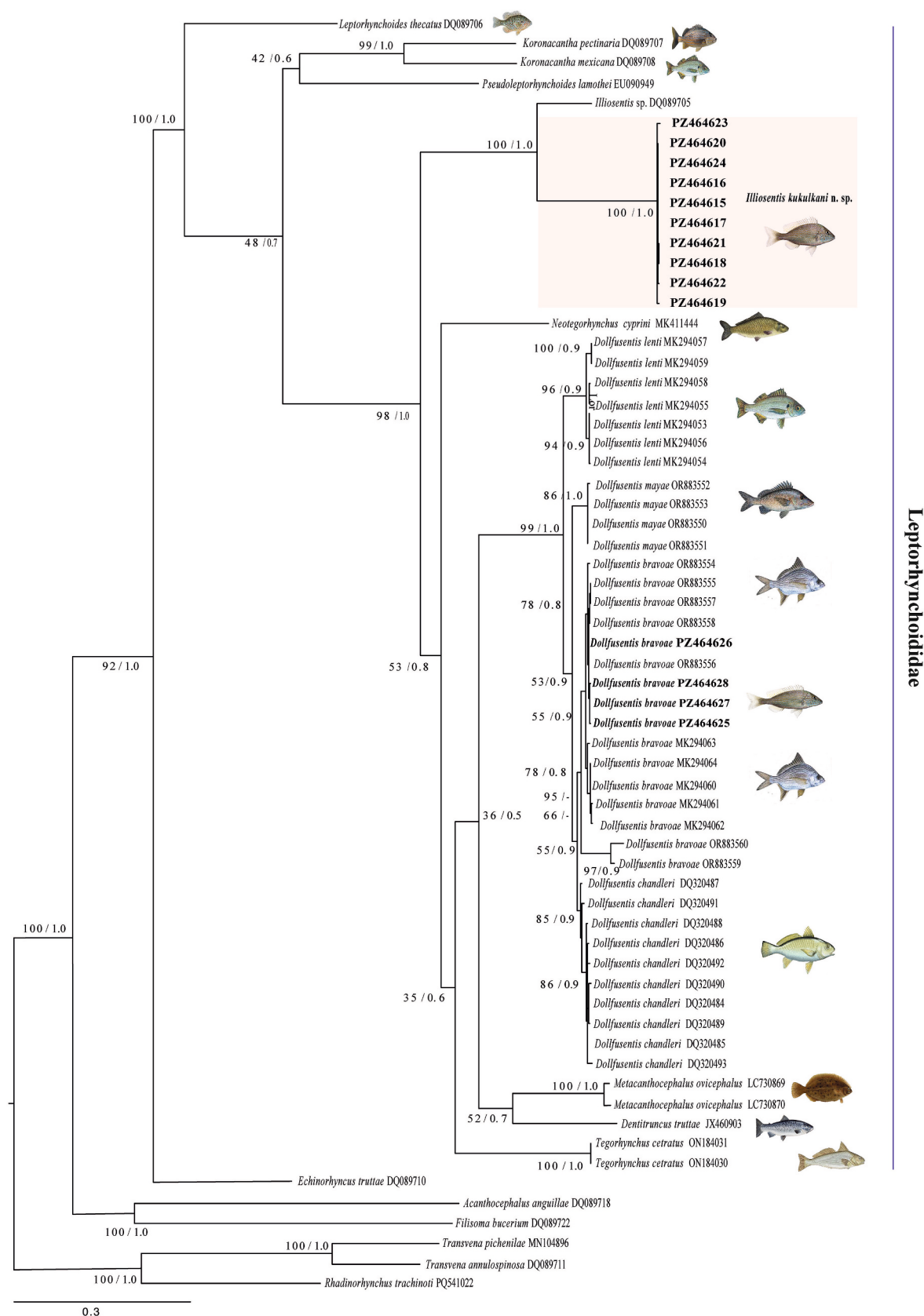


Fig. 4. Phylogenetic tree using maximum likelihood (ML) and consensus Bayesian obtained with the cytochrome oxidase subunit I (cox 1) from mitochondrial DNA. Numbers near internal nodes show ML bootstrap percentages/ Bayesian posterior probabilities.

America ranged from 0.4 to 2.8% [40]; among four isolates of *D. mayae* from the white grunt in Gulf of Mexico the divergence varied from 0.0 to 0.04%; whereas among 10 isolates of *D. chandleri* Golvan, 1969 it varied from 0.02 to 2.0% [22]; finally, among two isolates of *Metacanthocephalus ovicephalus* (Zhukov, 1960) from two flounder fish species in Japan the divergence ranged from 0.0 to 0.9% [9].

To conclude, the integrative taxonomic approach followed in the present study, combining information of nuclear and mitochondrial genes, along with morphological and geographical evidence, allowed the description of a new species and provided further support on the recognition of the genus *Illiosentis* within Leptorhynchoididae. Five of the 16 valid genera accepted in the classification scheme of Leptorhynchoididae are monotypic, showing a substantial amount of autapomorphic characters. Still the combination of morphological and molecular characters is required to fully understand the species composition and classification of this group of acanthocephalans.

CRedit authorship contribution statement

Martín García-Varela: Funding acquisition, Conceptualization. **Marcelo T. González-García:** Validation, Methodology, Formal analysis. **Leopoldo Andrade-Gómez:** Validation, Investigation. **Gerardo Pérez-Ponce de León:** Visualization, Validation, Project administration, Methodology, Funding acquisition, Conceptualization.

Ethical approval

Fish specimens were collected from the commercial capture by fisherman.

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Declaration of competing interest

The authors declare there are no conflicts of interest.

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