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Acanthocephalans of marine and freshwater fishes from Taiwan with description of a new species

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Abstract: During an ichthyoparasitological survey in 2017–2019, six species of acanthocephalans were found among Taiwan's freshwater (Cypriniformes: Xenocyprididae, Cyprinidae) and marine fishes (Scombriformes: Scombridae, Trichiuridae; Anabantiformes: Channidae; Carangaria/misc: Latidae): *Micracanthorhynchina dakusuiensis* (Harada, 1938), *Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011, *Pallisentis rexus* Wongkham et Whitfield, 1999, *Longicollum* sp., *Bolbosoma vasculosum* (Rudolphi, 1819), and one new species, *Micracanthorynchina brevelemniscus* sp. n. All species are morphologically characterised and illustrated using light and scanning electron microscopy. The finding of *R. laterospinosus, P. rexus* and *B. vasculosum* is the first record for these species in Taiwan. *Micracanthorhynchina brevelemniscus* is similar to *Micracanthorhynchina motomurai* (Harada, 1935) and *M. dakusuiensis* in proboscis armature but differs from *M. motomurai* by larger eggs (53–59 × 15–16 µm vs 40 × 16 µm) and by the number of cement glands (6 vs 4) and from *M. dakusuiensis* by shorter body length (2.2–2.9 mm vs 4.0 mm in males and 2.9–4.1 mm vs 7.6 mm in females), by the location of the organs of the male reproductive system (from level of the posterior third of the proboscis receptacle in *M. brevelemniscus* vs in the posterior half of the trunk in *M. dakusuiensis*), and by length of lemnisci (lemnisci shorter than the proboscis receptacle vs lemnisci longer than the proboscis receptacle). Phylogenetic analyses of almost complete 18S rRNA gene revealed paraphyly of the family Rhadinorhynchidae suggested in previous studies. *Micracanthorhynchina dakusuiensis* and *M. brevelemniscus* formed a strongly supported cluster, which formed the earliest diverging branch to the rest of the rhadinorhynchids and transvenids.

Keywords: Acanthocephala, taxonomy, molecular phylogeny, comparative morphology, host specificity

This article contains supporting figure (Supplementary Fig. 1) online at http://folia.paru.cas.cz/suppl/2023-70-021.pdf

The helminth fauna of the fishes of Taiwan comprises four major taxonomic groups, including the Acanthocephala, or thorny-headed worms (Kuntz 1967, Shih 2004, Bagherpour et al. 2011). Although some reports have been published (Shih et al. 2010, Cheng et al. 2022, Gao et al. 2022), taxonomic and genetic studies on fish parasites are limited and the actual species diversity of fish parasites in Taiwan is poorly known.

To date, 11 species of acanthocephalans are known in Taiwan's marine and freshwater fish. Nine species of acanthocephalans have been found in marine fish: *Brentisentis uncinus* Leotta, Schmidt et Kuntz, 1982 (Palaeacanthocephala: Illiosentidae) and *Gorgorhynchus satoi* (Morisita, 1937) (Palaeacanthocephala: Rhadinorhynchidae) from the tank goby *Glossogobius giurus* (Hamilton) (Gobiidae) and the spinycheek sleeper *Eleotris pisonis* (Gmelin) (Eleotridae); *Rhadinorhynchus pristis* (Rudolphi, 1802) from the blue mackerel *Scomber australasicus* Guvier (Scombridae); *Neorhadinorhynchus macrospinosus* Amin et Nahhas, 1994 (Palaeacanthocephala: Cavisomidae) from the rabbit fish mottled spinefoot *Siganus fuscescens* (Houttuyn) (Siganidae); *Neoechinorhynchus agilis* (Rudolphi, 1819) (Eoacanthocephala: Neoechinorhynchidae) from the flathead grey mullet *Mugil cephalus* Linnaeus (Mugilidae); *Neorhadinorhynchus nudus* (Harada, 1938) (Palaeacanthocephala: Cavisomidae) from the Japanese jack mackerel *Trachurus japonicus* (Temminck et Schlegel); *Longicollum alemniscus* (Harada, 1935) from the spotted scat *Scatophagus argus* (Linnaeus) (Scatophagidae), Russell's snapper *Lutjanus russelli* (Bleeker) (Lutjanidae), blackhead seabream *Acanthopagrus schlegelii* (Bleeker) (Sparidae), Japanese eel *Anguilla japonica* Temminck et Schlegel (Anguillidae), Amur catfish *Silurus asotus* Linnaeus (Siluridae), and Soleidae sp.; *Longicollum pagrosomi* Yamaguti, 1935 and *Filisoma mi-*

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crocanthi Harada, 1938 from the stripei *Microcanthus strigatus* (Cuvier) (Microcanthidae) (Harada 1935, Fukui and Morisita 1936, Petrochenko 1956, Leotta et al. 1982, Shin et al. 2010, Cheng et al. 2022).

Only two species of acanthocephalans have been recorded in the freshwater fish of Taiwan: the type species of the genus *Micracanthorhynchina* Strand, 1936, *Micracanthorhynchina motomurai* (Harada, 1935) from the freshwater minnow *Zacco platypus* (Temminck et Schlegel) and dark chub *Nipponocypris temminckii* (Temminck et Schlegel) (both Xenocyprididae), and *Micracanthorhynchina dakusuiensis* (Harada, 1938) from *N. temminckii* (see Harada 1935, 1938, Petrochenko 1956, Golvan 1969).

During a recent survey of fish parasites in Taiwan, acanthocephalans were found in various marine and freshwater fish. Based on morphological characters supplemented by molecular data (SSU rDNA, COI), one new species was described and its phylogenetic relationships to other species are discussed.

MATERIALS AND METHODS

Specimen collection and morphological examination

The specimens studied in the present work were collected by the present authors and their collaborators in Taiwan in 2017–2019 (Table 1). Newly collected acanthocephalans were obtained from the intestine of freshly killed fish. Acanthocephalans were washed in tap water, then relaxed in the refrigerator for 24 hours and fixed under slight pressure in 4% formaldehyde solution. For light microscopy, temporary slides mounted in Berlese's medium were prepared. Line drawings were made using a drawing tube of Leica DM 5000B light microscope (Leica Microsystems, Wetzlar, Germany).

All measurements in the text and tables are in micrometres (μm) unless otherwise stated. Trunk length does not include proboscis, neck and evaginated bursa. The width is given as the maximum in all cases. The ordinal number of the hook in the longitudinal row is indicated in brackets when describing the dimensions of the blades and the roots of the hooks. For scanning electron microscopy, specimens were dehydrated in an ethanol series and dried in hexamethyldisilazane (HMDS). Subsequently, the samples were sputter coated with gold and examined using a JEOL JSM 6510LA electron microscope (JEOL Ltd., Tokyo, Japan).

The scientific and common names of the fish host followed FishBase (Froese and Pauly 2023). Type and voucher specimens were deposited in the Helminthological collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (acronym IPCAS).

DNA sequencing

Worms isolated from the fish intestine were rinsed in saline (0.75%), and fixed and stored in 96% molecular grade ethanol. Total genomic DNA was extracted into 400 μl of 5% Chelex® sodium form solution (Merck, Darmstadt, Germany) in deionised water using the protocol of Blasco-Costa et al. (2016), except of overnight incubation. Almost complete nuclear gene for small subunit of ribosomal RNA (18S rRNA) was amplified using primers of Garey et al. (1996), and primers of Folmer et al. (1994) were employed to amplify partial mitochondrial gene for cytochrome c oxidase 1 (COI). PCR reactions were held in 25 μl volume using Takara Ex Taq polymerase (Takara Bio Inc., Shiga, Japan) according to manufacturer's instructions. Cycling conditions were identical for both genetic markers except for annealing and elongation steps (55 °C/40s and 72 °C/2 min for 18S rRNA gene; and 50 °C/30s and 72 °C/1 min for COI gene).

Results of PCR were verified by electrophoresis of 2 μl of the products in 1% agarose gel. The rest of amplicons were enzymatically purified (Werle et al. 1994) and Sanger sequenced with PCR primers. The 18S rRNA gene was also sequenced by internal 600R, 1270F and 1270R primers (Littlewood and Olson 2001). The sequences were generated by *de novo* assembly of five (18S) or two (COI) Sanger reads, the beginning and the end primer-complementary parts of assembled sequences were cut off, and the assembly was inspected for ambiguous bases. The final sequences were deposited to GenBank (Table 2).

Molecular phylogenetic analysis

The dataset for phylogenetic analyses was selected based on pairwise similarity of newly generated sequences with available sequences in GenBank using the BLASTn algorithm with default settings. The comparison revealed their close relatedness to Echinorhynchida and Polymorphida. Therefore, available 18S rRNA gene sequences of acanthocephalans of these two orders were include into initial phylogenetic analysis (see Supplementary Fig. 1). For subsequent analyses, only the isolates clustering with newly generated isolates into well-supported clades were chosen and concatenated with their COI gene sequences (see Fig. 9 and list of isolates in Table 2).

The two datasets were aligned separately using MAFFT v7.490 with employing algorithms E-INS-i and L-INS-i for 18S rRNA and COI markers, respectively (Katoh et al. 2002, Katoh and Standley 2013). The optimal nucleotide substitution models were calculated in ModelFinder (Chernomor et al. 2016, Kalyaanamoorthy et al. 2017) using AICc criterion as GTR + F + I + G (18S rRNA), TIM2 + F + I + G (COI, codon 1), TVM + F + I + G (COI, codon 2) and TN + F + G (COI, codon 3) for Echinorhynchida, and TVM + F + I + G (18S rRNA), TIM + F + I + G4 (COI, codon 1), TVM + F + G (COI, codon 2) and TIM2 + F + G (COI, codon 3) for Polymorphida.

Phylogenetic interrelationships were estimated in IQtree 2.0.5. using ultrafast bootstraping of 1,000 replicates, Bayesian-like transformation (aBayes) and Shimodaira–Hasegawa approximate likelihood ratio tests (SH-aLRT) (Anisimova et al. 2011, Hoang et al. 2018, Minh et al. 2020). The same methods with GTR + F + I + G model were used for initial phylogenetic analysis of 18S rRNA gene dataset.

RESULTS

Specimen collection and morphological examination

In the present work, a total of 53 individual fish belonging to nine species of six families were examined, in which six species of acanthocephalans of two classes, Palaeacanthocephala and Eoacanthocephala, were found, including one new species. Detailed descriptions of the new species and brief characterisations of the five other species found follow.

***Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011** Figs. 1, 2, Table 3

Morphological description (based on eight specimens: three males and five females). With characters of *Rhadinorhynchus* Lühe, 1911. Long trunk with single field of irregular circular rows of tegumental spines on anterior part (Fig. 2A). Posterior circles incomplete dorsally. Length of larger ventral spines 75–91 in males, 82–99 in females, smaller dorsal spines 65–85 in males, 68–74 in females. Proboscis long, almost cylindrical (Figs. 1A,B, 2D). Proboscis with 18 longitudinal rows of 21–22 hooks in each in males, 26–28 hooks in each in females. Ventral hooks larger than dorsal (Table 3). Hooks with simple roots directed posteriorly. Basal hooks longer than prebasal hooks, without roots, form a circle. Proboscis receptacle double-walled with cephalic ganglion in anterior third. Lemnisci elongate, ribbon-like, longer than proboscis receptacle. Genital pore subterminal in both sexes (Figs. 1A,D, 2E).

Male (based on three mature specimens with sperm). Trunk 7.16–7.43 mm long, 488–617 width at level of middle part of proboscis receptacle. Trunk spines extend to 1.04–1.42 mm ventrally and 207–715 dorsally. Length of larger ventral spines 75–91, larger dorsal spines 65–85. Length of proboscis 1.41–1.52 mm, width 163–333 anteriorly. Proboscis with 18 longitudinal rows of 21–22 hooks each. Proboscis receptacle 1.74–2.09 mm × 135–301. Length of neck 231–330 dorsally, 148–191 ventrally. Lemnisci 1.91–2.30 mm × 115–173. Distance between anterior edge of anterior testis and bottom of proboscis receptacle 0.98–1.22 mm. Testes two, elongate-oval, tandem. Anterior testis 0.83–1.02 mm × 344–392, longer than posterior testis. Posterior testis 701–924 × 232–378. Longer pair of cement glands 1.55–2.00 mm long, extends to posterior edge of posterior testis. Cement reservoir 221–446 × 197–240. Genital pore slit-like, opens on ventral side. Testes in posterior half of trunk, oblong, contiguous. Cement glands 4. Oval-clavate cement reservoir behind cement glands.

Female (based on two mature, egg-bearing specimens and three immature specimens). Trunk 9.43–19.12 mm long, 525–690 width at level of middle part of proboscis receptacle. Trunk spines extend to 1.48–2.58 mm ventrally and 215–420 dorsally. Length of larger ventral spines 82–99, larger dorsal spines 68–74. Length of proboscis 1.58–1.69 mm, width 221–310 anteriorly. Proboscis with 18 longitudinal rows of 26–28 hooks each. Proboscis receptacle 2.48–3.83 mm × 164–351. Length of neck 246–353 dorsally. Lemnisci 3.30–4.25 mm × 127–130. Length of female reproductive ducts in immature specimens 2.10–4.07 mm, reproductive system of mature females obscured by fusiform eggs. Eggs 83–85 × 16–19, with polar prolongations of middle membranes. Distance between gonopore and body edge 115–194. Female reproductive tract long, in immature specimens 2.1–4.1 mm long, in mature females hidden by eggs. Vagina with single muscular sphincter.

Hosts: skipjack tuna, *Katsuwonus pelamis* (Linnaeus), blue mackerel, *Scomber australasicus* Cuvier (both Scombridae), largehead hairtail, *Trichiurus lepturus* Linnaeus (Trichiuridae)

Site of infection: intestine.

Localities: East China sea off Northern (near the cities of Taipei and Yilan) and Western (Budai Harbor) Taiwan.

Infection rates: prevalence 38% (3/8), intensity 1–4 in *S. australasicus*; 20% (1/5), 1 in *K. pelamis*; 13% (1/8), 1 in *T. lepturus*

Molecular data: Two almost complete sequences of 18S rRNA gene (1,704 bp) and two partial sequences of mitochondrial COI gene (603 and 624 bp) of *Rhadinorhynchus laterospinosus* from *T. lepturus* and *S. australasicus* were deposited in the GenBank database (Accession Nos. OR625656, OR625657 for 28S and OR625530, OR625531 for COI).

Material: voucher (IPCAS A-134)

Remarks. *Rhadinorhynchus laterospinosus* was described from a single female collected from a trigger fish, *Balistes* sp. (Balistidae) from the northern Pacific coast of Vietnam in Halong Bay, Gulf of Tonkin (Amin et al. 2011). This species was also later found along the whole Pacific coast of Vietnam in *Alectis ciliaris* (Bloch) (Carangidae), *Auxis rochei* (Risso) (Scombridae), *Auxis thazard* (Lacépède) (Scombridae), *Leiognathus equula* (Forsskål) (Leiognathidae), *Lutjanus bitaeniatus* (Valenciennes) (Lutjanidae), *Megalaspis cordyla* (Linnaeus) (Carangidae), *Nuchequula flavaxilla* Kimura, Kimura et Ikejima (Leiognathidae), and *Tylosurus* sp. (Belonidae) (Amin et al. 2019).

Our findings of *R. laterospinosus* in three fish species of two families expand the list of hosts and confirm euryxenous specificity of the species to definitive hosts and also indicate its wider geographic range. The specimens we found are slightly different from those of the original description and subsequent morphological studies. In particular, all specimens found have a lemniscus slightly longer than the proboscis receptacle versus shorter than the proboscis receptacle, according to Amin et al. (2019), as well as larger eggs (83–85 × 16–19 μm versus 57–68 × 12–18 μm). We attribute these differences to intraspecific variability, especially since the authors of the species point to the variability of the species for most characters depending on the host (Amin et al. 2019).

***Micracanthorhynchina dakusuiensis* (Harada, 1938) Wang, 1951** Fig. 8E

Morphological description (based on 12 adult specimens: seven males and five females). Small worms, shared structures larger in females than in males. Trunk with a single field of circular rows of small tegumental spines on anterior part. First 10–18 rows of spines complete, next 6–12 rows incomplete dorsally. Length of longer spines 16–20. Proboscis with 12 longitudinal rows of 7–9 hooks each. Hook size does not differ ventrally and dorsally, decreases from anterior to posterior. Anterior 2–4 hooks roots with two manubria directed forward and sideways. Next hooks with simple roots, directed posteriorly, basal hooks without roots. Neck short, cylindrical, often not visible. Proboscis receptacle double-walled, clavate with cephalic ganglion in middle. Lemnisci saccular, longer than proboscis receptacle, less often only reach its bottom. Genital pore subterminal in both sexes.

Table 1. Parameters of the samples and number of helminths collected from eight species of freshwater and marine fishes in Taiwan in 2017–2019

Fish species	No	TBL*, cm (min–max)	Infected	No. of acanth. collected
Family Channidae				
Channa sp.	1	36	1	1
Family Latidae				
Lates calcarifer (Bloch)	2	23	1	1
Family Scombriidae				
Scomber australasicus Cuvier	8	32–40	3	6
Katsuwonus pelamis (Linnaeus)	5	30.5–33.5	2	3
Thunnus obesus (Lowe)	3	40–47	1	2
Family Trichiuridae				
Trichiuris lepturus Linnaeus	8	69–89	2	2
Family Xenocyprididae				
Candidia barbata (Regan)	15	6–11.9	1	2
Opsariichthys pachycephalus Günther	10	9.3–15	4	31

*Total body length

Male. Trunk 3.27–6.28 mm long, 0.69–1.39 wide. Proboscis 351–458 long, 139–183 wide, with 12 longitudinal rows of 7–8, 8 or 8–9 hooks each. Largest hook first, blade 41–69, root 22–49. Neck 53–98. Proboscis receptacle 652–821 × 132–197. Testes do not reach posterior edge of the lemniscus. Anterior testis 651–913 × 380–737. Posterior testis 566–737 × 328–725. Säeftigen's pouch 644–923 × 265–377. Organs of male reproductive system in posterior half of body.

Female. Trunk 4.42–6.28 mm long, 1.07–1.39 mm wide. Proboscis 428–493 × 191–201 with 12 longitudinal rows of 8 or 8–9 hooks each. Largest hook first, blade 45–66, root 28–29. Neck 55–92. Proboscis receptacle 663–940 × 291–330. Lemnisci 796–894 × 170–217. Eggs 60–63 × 15–17 with polar prolongations of middle membranes. Vagina with single muscular sphincter.

Host: *Opsariichthys pachycephalus* Günther, Cypriniformes, Xenocyprididae

Locality: Daja River near Taichung, Taichung City (24.1969N, 120.7469E) and Bei River near Meiziliao, New Taipei City (24.9625N, 121.7705E)

Site of infection: Intestine

Infection rates: Prevalence 20% (2/10), intensity of infection 1–2 in *O. pachycephalus*.

Material: voucher (IPCAS A-135)

Remarks. *Micracanthorhynchina dakusuiensis* was described from cyprinid fishes of the family Xenocyprididae, namely *Zacco platypus* and the dark chub *Nipponocypris temminckii* by Harada (1935, 1938). The specimens of *M. dakusuiensis* that we found correspond completely to the original description. The species was recently found in the yellow catfish *Tachysurus fulvidraco* (Richardson) (Siluriformes: Bagridae) collected from South Dongting Lake, Yuanjiang County, Hunan Province, China (Gao et al. 2022). Unfortunately, the authors did not provide a detailed description of the specimens found, nor did they indicate whether all worms were sexually mature, so it is not clear whether the reported body length (2.6–6.0 mm) refers to adults. The given morphological characteristics (formula of proboscis hooks, length of lemniscus), as well as a slightly blurred photo of the male correspond to both the original description and our specimens.

***Micracathorhynchina brevelemniscus* sp. n.** Figs. 3–5

Morphological description (based on 12 adult specimens: five males and seven females). With characters of the genus *Micracathorhynchina* Strand, 1936. Small worms, shared structures larger in females than in males. Trunk with a single field of circular rows of the small tegumental spines on anterior part. First 10–12 rows of spines complete, next 6–8 rows incomplete dorsally. Length of longer ventral spines 16–26, longer dorsal spines 13–22 (Fig. 4D). Surface tegument in middle part of body flat with micropores (Fig. 4E). Proboscis cylindrical or slightly clavate, curved to ventral. Proboscis with 12 (in four male and seven female) or 13 (in one male) longitudinal rows of 8–9 hooks each (Figs. 3C, 4C, 5A). Hooks size does not differ ventrally and dorsally, decreases from anterior to posterior (Figs. 3C, 4C). Anterior 3–4 hooks roots with two manubria directed forward and sideways. Next hooks with simple roots, directed posteriorly, basal hooks without roots. Neck short, cylindrical, often not visible. Proboscis receptacle double-walled, long, clavate posteriorly with cephalic ganglion in middle. Lemnisci saccular, shorter than proboscis receptacle. Genital pore subterminal in both sexes (Figs. 3A,B, 4A,F, 5B).

Male. Trunk 2.16–2.90 mm long, 564–787 wide. Longer ventral spines 16–26, longer dorsal spines 13–18. Proboscis 339–424 long, 164–173 wide, with 12–13 longitudinal rows of 8–9 or 9 hooks each. Length of hook blades: 47–56 (1); 47–54 (2); 40–49 (3); 36–43 (4); 29–37 (5); 27–32 (6); 27–32 (7); 19–27 (8); 21–22 (9). Length of hook roots: 16–37 (1); 31–36 (2); 28–36 (3); 25–31 (4); 20–30 (5); 17–24 (6); 20–22 (7); 14–15 (8). Neck 76–79. Proboscis receptacle 747–813 × 142–165. Lemnisci 347–439 × 146–204. Testes two, elongate-oval, tandem. Anterior testis 343–685 × 369–388, longer than posterior testis. Posterior testis 298–532 × 265–527. Cement glands clavate, 705–976 long. Cement reservoir 280–370 × 164–192. Säeftigen's pouch clavate, 310–561 × 142–321. Genital pore slit-like, subterminal. Evaginated bursa 433 × 430. Organs of male reproductive system from level posterior third of proboscis receptacle, 80% in posterior trunk. Testes oval, contiguous. Cement glands six. Oval cement reservoir behind cement glands.

Female. Trunk 2.93–4.11 mm long, 563–857 wide. Longer ventral spines 21–26, longer dorsal spines 18–22. Proboscis 428–433 × 154–201, with 12 longitudinal rows of 8, 8–9 or 9 hooks each. Length of hook blades: 41–58 (1); 55–65 (2); 49–58 (3); 41–50 (4); 36–45 (5); 31–46 (6); 23–38 (7); 21–33 (8); 19–31 (9). Length of hook roots: 24–35 (1); 32–45 (2); 31–38 (3); 27–36 (4); 27–34 (5); 20–32 (6); 18–30 (7); 14–24 (8). Neck 59–77. Proboscis receptacle 816–976 × 149–230. Lemnisci 296–745 × 115–225. Eggs 53–59 × 15–16, with polar prolongations of middle membranes. Female reproductive tract long. Vagina with single muscular sphincter.

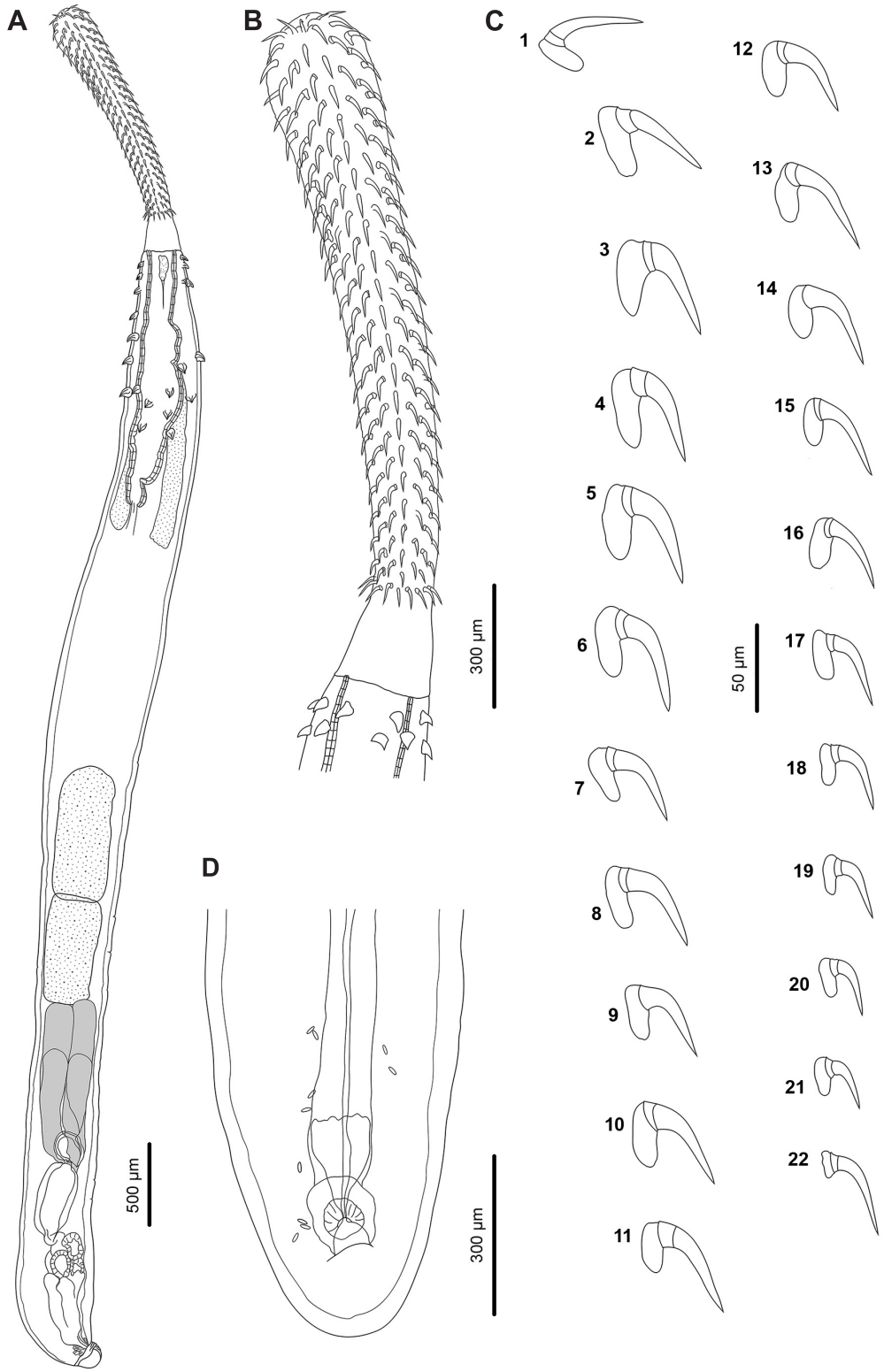

Fig. 1. Line drawing of *Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011 from *Scomber australasicus* Cuvier. **A** – total view of male; **B** – proboscis of male; **C** – hooks of one longitudinal row of proboscis; **D** – posterior end of female.

Type host: *Opsariichthys pachycephalus* Günther, Cypriniformes, Xenocyprididae

Other hosts: *Onychostoma alticorpus* (Oshima), *Candidia barbata* (Regan), both Cypriniformes, Xenocyprididae

Type locality: Daja River near Taichung, Taichung City (24.1969N, 120.7469E)

Other locality: Tamsui River near Meiziliao, New Taipei City (24.9625N, 121.7705E)

Site of infection: Intestine

Infection rates: Prevalence 30% (3/10), intensity 5–11 in *O. pachycephalus*; prevalence 6% (1/15), intensity 2 in *C. barbata*; prevalence 1/1, intensity 1 in *O. alticorpus*.

Table 2. Sequence data included in the phylogenetic analyses

Species	Host (Locality)	18S	COI	References
Dataset 1				
Micracanthorhynchina brevelemniscus sp. n.	*Opsariichthys pachycephalus* (TWN)	**OR625654**	**OR625528**	**this study**
Micracanthorhynchina brevelemniscus sp. n.	*Opsariichthys pachycephalus* (TWN)	**OR625655**	**OR625529**	**this study**
Micracanthorhynchina dakusuiensis (Harada, 1938) Ward, 1951	*Tachysurus fulvidraco* (CHN)	OP133175	OP131911	Gao et al. 2022
Neorhadinorhynchus nudus (Harada, 1938) Yamaguti, 1939	*Auxis thazard* (CHN)	MG838944	MG838934	Li et al. 2019
Pararhadinorhynchus sodwanensis Lisitsyna, Kudlai, Cribb et Smith, 2019	*Pomadasys furcatus* (ZAF)	MN105738	N/A	Lisitsyna et al. 2019a
Pararhadinorhynchus sp.	*Siganus fuscescens* (CHN)	HM545903	N/A	Wang et al. unpublished
Rhadinorhynchus biformis Smales, 2014	*Helotes sexlineatus* (AUS, Qld)	MN705829	MN692682	Huston et al. 2020
Rhadinorhynchus decapteri[1] (Braicovich, Lanfranchi, Farber, Marvaldi, Luque et Timi, 2014) Huston, Cribb et Smales, 2020	*Decapterus punctatus* (BRA)	KJ590123	KJ590125	Braicovich et al. 2014
Rhadinorhynchus carangis Yamaguti, 1939	*Trachinotus coppingeri* (AUS, Qld)	MN705830	MN692684	Huston et al. 2020
Rhadinorhynchus gerbera Lisitsyna, Kudlai, Cribb et Smith, 2019	*Trachinotus botla* (ZAF)	MN105739	MN104898	Lisitsyna et al. 2019a
Rhadinorhynchus hiansi Soota et Bhattacharya, 1981	*Sarda orientalis* (VNM)	MN203133	MN203136	Amin et al. 2020
Rhadinorhynchus johnstoni Golvan, 1969	*Auxis thazard* (AUS, Qld)	MN705827	MN692680	Huston et al. 2020
Rhadinorhynchus laterospinosus Amin, Heckmann et Ha, 2011	*Auxis rochei* (VNM)	MK457183	MK572741	Amin et al. 2019
Rhadinorhynchus laterospinosus	*Trichiurus lepturus* (TWN)	**OR625656**	**OR625530**	**this study**
Rhadinorhynchus laterospinosus	*Scomber australasicus* (TWN)	**OR625657**	**OR625531**	**this study**
Rhadinorhynchus mariserpentis[1] (Steinauer, Garcia-Vedrenne, Weinstein et Kuris, 2019) Huston, Cribb, Smales, 2020	*Regalecus russelii* (JAP)	MK012666	MK014666	Steinauer et al. 2019
Rhadinorhynchus sp.	Fish (Sciaenidae) (N/A)	AY062433	DQ089712	García-Varela et al. 2002 García-Varela and Nadler 2005
Rhadinorhynchus pristis (Rudolphi, 1802) Lühe, 1911	*Nyctiphanes couchii* (ESP)	JQ061133	N/A	Gregori et al. 2012
Rhadinorhynchus sp.	*Auxis thazard* (AUS, Qld)	MN705828	MN692681	Huston et al. 2020
Sclerocollum australe Pichelin, Smales et Cribb, 2016	*Siganus argenteus* (AUS, Qld)	MN705831	MN692685	Huston et al. 2020
Sclerocollum robustum (Edmonds, 1964) Schmidt et Paperna, 1978	*Siganus lineatus* (AUS, Qld)	MN705832	MN692687	Huston et al. 2020
Sclerocollum sp.	*Zebrasoma velifer* (AUS, Qld)	MN705834	MN692689	Huston et al. 2020
Transvena annulospinosa Pichelin et Cribb, 2001	*Anampses neoguinaicus* (N/A)	AY830153	DQ089711	García-Varela and Nadler 2005, 2006
Transvena pichelinae Lisitsyna, Kudlai, Cribb, Smith, 2019	*Thalassoma purpureum* (ZAF)	MN105737	MN104896	Lisitsyna et al. 2019a
Dataset 2				
Andracantha gravida (Alegret, 1941) Schmidt 1975	*Phalacrocorax auritus* (MEX)	EU267802	EU267822	García-Varela et al. 2009
Andracantha leucocarboi Presswell, García-Varela et Smales, 2017	*Leucocarbo chalconotus* (NZL)	N/A	MF527023	Presswell et al. 2017
Andracantha phalacrocoracis (Yamaguti, 1939) Schmidt, 1975	*Zalophus californianus* (USA, Cal)	N/A	MK119254	Lisitsyna et al. 2019b
Andracantha sigma (Yamaguti, 1939) Schmidt, 1975	*Eudyptula minor* (NZL)	N/A	MF527034	Presswell et al. 2017
Andracantha sp.	*Osmerus dentex* (JAP)	N/A	LC465333	Sasaki et al. 2019
Bolbosoma balaenae (Gmelin, 1790) Porta, 1908	*Balaenoptera physalus* (ITA)	MZ047225	MZ047276	Santoro et al. 2021
Bolbosoma caenoforme (Heitz, 1920) Meyer, 1932	*Salvelinus malma* (RUS)	KF156879	KF156891	Malyarchuk et al. 2014
Bolbosoma nipponicum Yamaguti, 1939	*Callorhinus ursinus* (USA, Ala)	ON358429	ON359908	Ru et al. 2022
Bolbosoma sp.	*Homo sapiens* (JAP)	N/A	LC377776	Kaito et al. 2019
Bolbosoma turbinella (Diesing, 1851) Porta 1908	*Eschrichtius robustus* (USA, Cal)	JX442166	JX442189	García-Varela et al. 2013
Bolbosoma vasculosum (Rudolphi, 1819) Porta, 1908	*Thunnus obesus* (TWN)	**OR625658**	**OR625532**	**this study**
Corynosoma australe Johnston, 1937	*Zalophus californianus* (USA, Cal)	MK119255	MK119245	Lisitsyna et al. 2019b
Corynosoma enhydri Morozov, 1940	*Enhydra lutris* (N/A)	AF001837	DQ089719	García-Varela and Nadler 2006
Corynosoma evae Zdzitowiecki, 1984	*Notothenia coriiceps* (ATA)	ON890394	ON881147	Hernández-Orts et al. 2022
Corynosoma hannae[2] Zdzitowiecki, 1984	*Phocarctos hookeri* (NZL)	JX442168	JX442191	García-Varela et al. 2013
Corynosoma magdaleni Montreuil, 1958	*Phoca hispida* (FIN)	EU267803	EF467872	García-Varela and Pérez-Ponce de León 2008
Corynosoma nortmeri Waindok, Lehnert, Siebert, Pawliczka et Strube, 2018	*Phoca vitulina* (NoSe)	N/A	MF001278	Waindok et al. 2018
Corynosoma semerme[3] (Forssell, 1904) Lühe, 1905	*Callorhinus ursinus* (USA, Ala)	JX442169	JX442192	García-Varela et al. 2013
Corynosoma strumosum (Rudolphi, 1802) Lühe, 1904	*Phoca vitulina* (USA, Cal)	EU267804	EF467870	García-Varela et al. 2009; García-Varela and Pérez-Ponce de León 2008
Corynosoma validum Van Cleave, 1953	*Callorhinus ursinus* (USA, Ala)	JX442170	JX442193	García-Varela et al. 2013
Corynosoma villosum Van Cleave, 1953	*Callorhinus ursinus* (USA)	N/A	MK119251	Lisitsyna et al. 2019b
Gorgorhynchus lepidus Van Cleave, 1940	*Syacium papillosum* (MEX)	N/A	MK937568	Vidal-Martínez et al. 2019
Gorgorhynchoides bullock Cable et Mafarachisi, 1970	*Eugerres plumiere* (N/A)	AY830154	DQ089715	García-Varela and Nadler 2005, 2006
Gorgorhynchoides gnathanodontos Smales, 2014	*Gnathanodon speciosus* (AUS, Qld)	MN705839	MN692697	Huston et al. 2020
Gorgorhynchoides quenslandensis Smales, 2014	*Seriola lalandi* (AUS, Qld)	MN705838	MN692695	Huston et al. 2020
Gorgorhychoides sp.	*Pseudocaranx dentex* (AUS, Qld)	MN705840	KC291715	Huston et al. 2020
Serrasentis nadakali George et Nadakal, 1978	(N/A)	KC291715	KC291712	Paul et al., unpublished
Serrasentis sagittifer (Linton, 1889) Van Cleave 1923	*Lethrinus laticaudis* (WAUS)	MF426933	MF134302	Barton et al. 2018
Outgroup for both datasets				
Metacanthocephaus ovicephalus	*Pseudopleuronectes schrenki* (JAP)	LC730868	LC730869	Kita et al. 2023
Neotegorhynchus cyprini	*Cyprinus carpio* (CHN)	MK411441	MK411444	Lisitsyna et al. 2022
Pseudoleptorhynchoides lamothei	*Ariopsis guatemalensis* (N/A)	EU090950	EU090949	García-Varela and Gonzalez-Oliver 2008

[1] originally assigned to the genus *Gymnorhadinorhynchus*, but transferred to *Rhadinorhynchus* (Huston et al. 2020)
[2] originally identified as *Corynosoma obtuscens* (see Hernández-Orts et al. 2022).
[3] originally identified as *Corynosoma australe* (see Lisitsyna et al. 2019b).

Abbreviations: Ala – Alaska, ATA – Antarctica, AUS – Australia, BRA – Brasil, Cal – California, CHN – China, ESP – Spain, FIN – Finland, ITA – Italy, JAP – Japan, MEX – Mexico, NoSe – North Sea, NZL – New Zealand, Qld – Queensland, RUS – Russia, TWN – Taiwan, USA – United States of America, VNM – Vietnam, WAUS – Western Australia, ZAF – South Africa KC291712

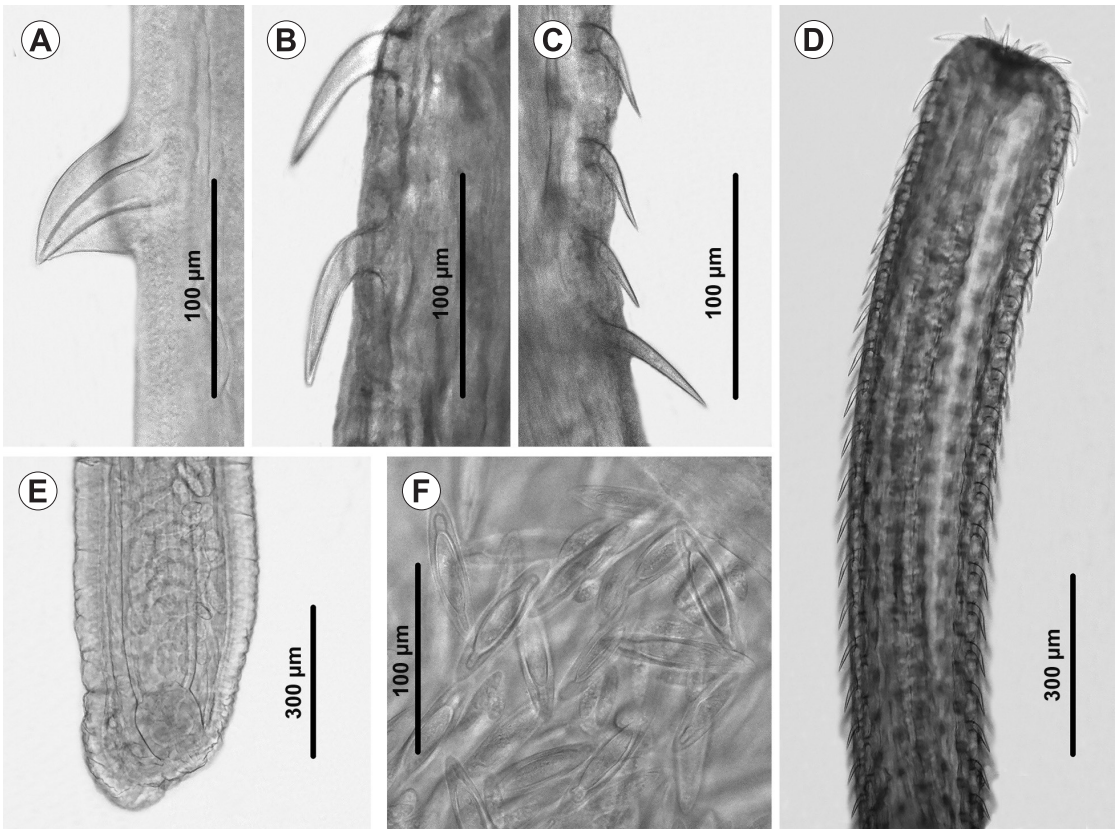

Fig. 2. Light microscope photographs of *Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011 from *Scomber australasicus* Cuvier. **A** – somatic spine; **B** – middle hooks of proboscis; **C** – basal hooks of proboscis; **D** – proboscis of male; **E** – posterior end of immature female; **F** – eggs.

Table 3. Measurements of the ventral and dorsal proboscis hooks of male and female specimens of *Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011.

Hook No. from anterior	♂ (n = 3)				♀ (n = 5)			
	ventral		dorsal		ventral		dorsal	
	blades	roots	blades	roots	blades	roots	blades	roots
1	68	37	58	39	67	38	57	27
2	69	38	69–70	38–61	57–75	40–42	68–74	42
3	49–62	33–44	67–68	31–48	68–76	49–53	72–75	47–48
4	51–63	38–45	62–66	36–47	66–72	51–50	71–76	41–44
5	66–69	44–49	63–67	38–44	65–76	40–50	71–72	43–49
6	64	36–56	65–68	34–42	63–67	43–46	69–72	47–48
7	64–67	39–46	65–67	43–47	65–74	42–49	71–72	43–47
8	67	45–47	68	37–41	66–71	48–57	60–72	44–46
9	68–71	42–53	64–65	34–52	68–76	45–46	73	39–42
10	67–68	39–58	65–68	38–40	69–77	46–59	73–74	44–45
11	63–66	37–54	64–65	37–39	70–78	47–51	73–79	37–42
12	63–66	37–44	68	35	69–73	50–53	72–79	39–42
13	65–66	31–51	64	39	73–76	44–53	70–81	38–39
14	63–66	31–49	63	38	74–78	46–54	73–76	32–41
15	63	50	62	39	72–80	44–53	66–76	32–44
16	64	44	60	35	70–82	38–53	65–78	31–36
17	62	42	55	35	66–81	40–53	60–79	32–38
18	60	43	53	38	65–80	36–51	62–77	34–44
19	54	39	37–48	19–29	61–79	40–56	55–78	30–40
20	43–49	21–29	38–47	19–26	64–83	40–46	54–72	33–36
21	48–52	29–31	43–46	14–25	63–79	36–44	48–69	27–37
22	60–64	–	55–56	–	60–76	38–43	42–67	28–37
23					54–74	35–39	30–66	32–34
24					53–68	31–37	30–57	26–33
25					48–67	23–29	44–61	25–32
26					40–85	23–31	45–74	23–35
27					59	20	46–68	28–32
28					73		70	

Type material: Holotype (IPCAS A-133), nine paratypes (IPCAS A-133); one hologenophore (IPCAS A-133)

Molecular data: Two almost complete sequences of 18S rRNA gene (1,699 bp) and two partial sequences of mitochondrial COI gene (624 & 655 bp) of *Micracanthorhynchina brevelemniscus* sp. n. from *O. pachycephalus* were deposited in the GenBank database (Accession Nos. OR625654, OR625655 for 28S, OR625528, OR625529 for COI).

Etymology: The species is named after a morphological feature, namely the lemniscus, which is shorter than the proboscis receptacle.

Remarks. Two of the 13 known species of the genus *Micracanthorhynchina* cannot be considered valid (Amin 2013, Smales 2015). In particular, *Micracanthorhynchina indico* Farooqi, 1980 should be considered a species *inquirenda*, as it has been insufficiently and incorrectly described (see Amin and Sey 1996, Smales 2014). The name *Micracanthorhynchina sajori* (Belous, 1952) cannot be considered valid either, because acanthocephalans under this name have not been described. Belous (1952) described specimens from the Japanese halfbeek *Hyporhamphus sajori* (Temminck et Schlegel) under the name *Bolbosentis hyporhamphi* Belous, 1952, not *Bolbosentis sajori* Belous, 1952. Petrochenko (1956) later proved that *B. hyporhamphi* is identical with *Micracanthocephalus* (=*Micracanthorhynchina*) *hemiramphi* Baylis, 1944, which was previously described from Lutke's halfbeak *Hemirhamphus lutkei* Valenciennes and is its synonym. Ward (1951) later transferred the species to the genus *Micracanthorhynchina*. The error was not noticed and the name was kept in the species list of the genus until now (Golvan 1969, Amin 2013, Smales 2014). In view of the foregoing, we consider 11 species of the genus *Micracanthorhynchina*, parasites of marine and freshwater fishes in Southeast Asia, Australia and New Zealand (Amin and Sey 1996, Amin 2013, Smales 2014).

The specimens of *M. brevelemniscus* have characteristics that are fully consistent with the generic diagnosis for *Micracanthorhynchina* (see Petrochenko 1956, Golvan 1969, Amin and Sey 1996). Of the 11 valid species of the genus, only two species are similar to *M. brevelemniscus*, i.e. by the proboscis armature. These are acanthocephalans from freshwater fishes in Taiwan, the type species of the genus, *Micracanthorhynchina motomurai* and *M. dakusuiensis*.

Micracanthorhynchina brevelemniscus, however, differs in several characters from these two species of the genus. *Micracanthorhynchina brevelemniscus* differs from *M. motomurai* in having larger eggs (53–59 × 15–16 µm in *M. brevelemniscus* versus 40 × 16 µm in *M. motomurai*) and in the number of the cement glands (six in *M. brevelemniscus* versus four in *M. motomurai*). *Micracanthorhynchina brevelemniscus* can be distinguished from *M. dakusuiensis* by Harada (1938) the shorter body length (2.16–2.90 mm versus 4.00 mm in males and 2.93–4.11 mm versus 7.60 mm in females), by the location of the organs of the male reproductive system (from level of the posterior third of proboscis receptacle in *M. brevelemniscus* versus in posterior half of the trunk in *M. dakusuiensis*) and by the length of the lemnisci (lemnisci shorter than proboscis receptacle in *M. brevelemniscus* versus lemnisci longer than proboscis receptacle in *M. dakusuiensis*).

Bolbosoma vasculosum (Rudolphi, 1819) Porta, 1908

Figs. 5–7

Morphological description (based on two immature female). Trunk cylindrical, 8.13–8.66 mm long, 789–968 wide. Anterior part cylindrical 488–580 long, further enlarged extension 764–964 long. Spines of two fields in anterior cylindrical 299–346 long with spines in 46 longitudinal rows in 8–9 spines each 31–38 long and further extension 318–491 long with spines in 62–70 in 7–8 spines each 40–44 long. Distance between fields 189–234. Genital spines absent. Surface of tegument with micropores only in region of neck (Fig. 7E). Proboscis oval, 751–682 × 508–519 with 16 longitudinal rows in 7–9 hooks each. Anterior 4–5 hooks large with simple heavy roots directed backwards. Blades of hooks length: 60–80 (1); 75–84 (2); 77–92 (3); 81–94 (4); 70–94 (5). Roots of hooks length: 38–60 (1); 57–66 (2); 66–81 (3); 81–101 (4); 57–76 (5). Largest hooks fourth. Blades next hooks narrower, roots decrease to basal. Basal hooks without roots. Length of hook blades: 69–83 (6); 75–81 (7); 69–79 (8); 71 (9). Length of hook roots: 46–50 (6); 45–59 (7); 42–43 (8). Proboscis receptacle double-walled, 1.45–1.97 mm × 452–489 with cephalic ganglion in middle. Neck prominent, 659–866 long. Lemnisci shoe-like, 0.89–1.31 mm long, attached in distal part of neck, at a distance of 141–216 from its posterior edge; they extend beyond bottom of proboscis receptacle. Female reproductive tract 0.62–1.20 mm long. Vagina with two muscular sphincters. Genital pore terminal (Figs. 5G; 6A).

Hosts: Bigeye tuna, *Thunnus obesus* (Lowe), Scombridae and Largehead hairtail, *Trichiurus lepturus* Linnaeus, Trichiuridae

Locality: East China sea off Western Taiwan (fish market in Dongshi harbour, Budai harbor).

Site of infection: Intestine.

Infection rates: Prevalence 33% (1/3), intensity of infection 2 in *T. obesus*; prevalence of infection 13% (1/8), intensity of infection 1 in *T. lepturus*.

Molecular data: The almost complete sequence of 18S rRNA gene (1,702 bp) and the partial sequence of mitochondrial COI gene (627 bp) of *B. vasculosum* from *T. obesus* were deposited in the GenBank database (Accession Nos. OR625658 for 28S and OR625532 for COI)

Material: voucher (IPCAS A-136)

Remarks. *Bolbosoma vasculosum* was described based on immature specimens from fish (Rudolphi 1819). Later, immature acanthocephalans were found under this name in the intestines of various fishes, such as Black scabbard fish *Aphanopus carbo* Lowe and Oceanic horse mackerel *Trachurus picturatus* (Bowdich) in the Mediterranean Sea (Costa et al. 2000), from Savalai hairtail *Lepturacanthus savala* (Cuvier) in Indonesia (Verweyen et al. 2011), and in the intestine of marine mammals, namely cachalot *Physeter macrocephalus* Linnaeus in Indonesia (Pendergraph 1971), Cuvier's beaked whale *Ziphius cavirostris* Cuvier from the western Mediterranean Sea (Fernández et al.

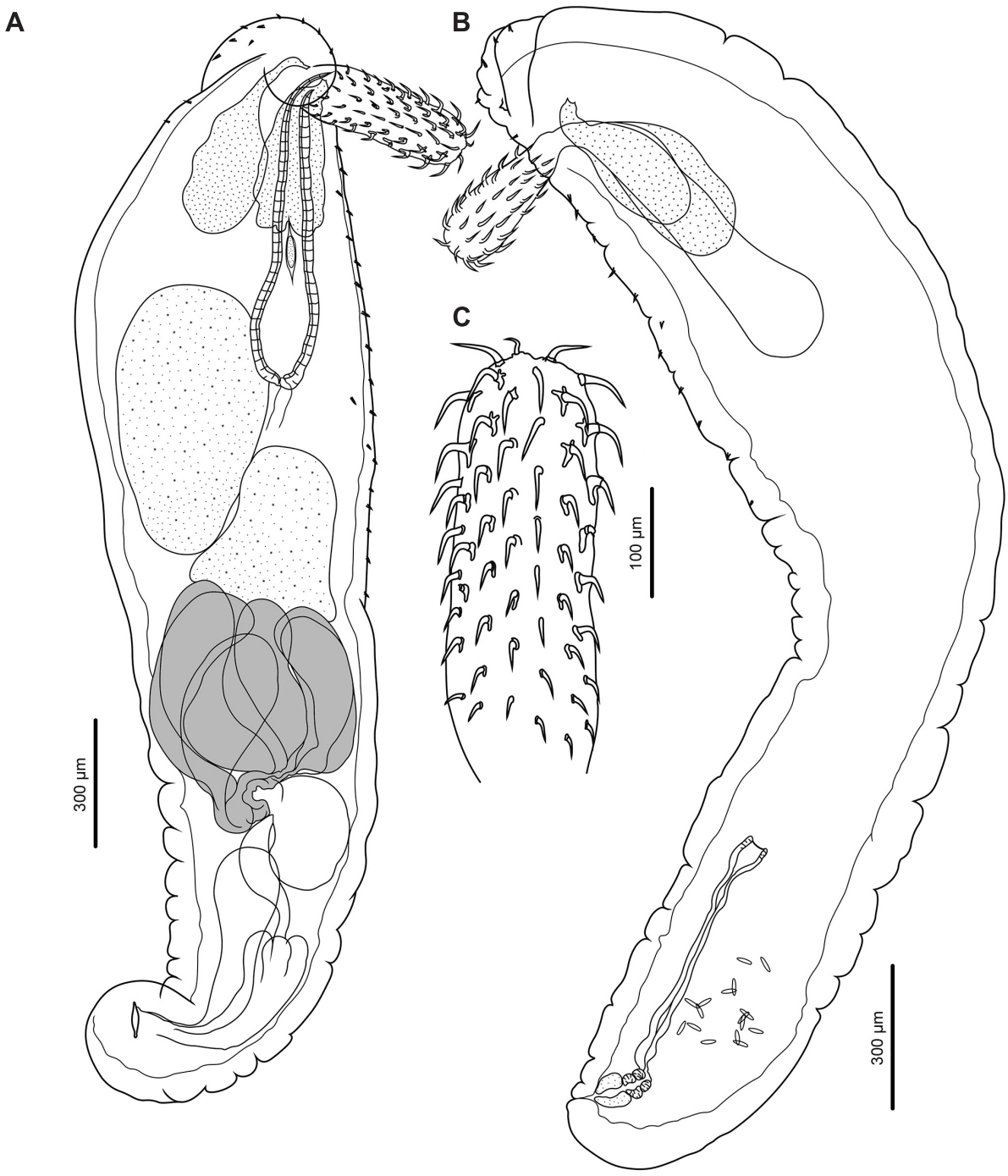

Fig. 3. Line drawing of *Miracanthorhynchina brevelemniscus* sp. n. from *Opsariichthys pachycephalus* Günther. **A** – total view of male (holotype); **B** – proboscis of male; **C** – total view of female.

2004), Striped dolphins *Stenella coeruleoalba* (Meyen) in the western Mediterranean Sea (Mateu et al. 2014).

In three cases, *B. vasculosum* was found in mature state, from marine mammals Cape fur seal, *Arctocephalus pusillus pusillus* (Schreber) in Southwest Africa (Halajian et al. 2020) and in the intestines of fish. Williams and Bunkley-Williams (1996) found one specimen in King mackerel, *Scomberomorus cavalla* (Cuvier), in Puerto Rico and also Harada (1935) found three specimens of *Bolbosoma thunni* Harada, 1935 (synonym of *B. vasculosum* according to 1958) with developing acanthors in the Atlantic bluefin tuna *Thunnus thynnus* (Linnaeus) in Japan.

Pallisentis rexus Wongkham et Whitfield, 1999

Fig. 8 A–D

Short description (based on one specimen). Trunk without posterior part and without internal organs, but proboscis preserved, sex unknown (Fig. 8A). The main diagnostic characteristics in the anterior part of the body make it possible to reliably identify the species. Proboscis 154 × 288 with four circular rows in 12 hooks each (Fig. 8A,B). Length of hook

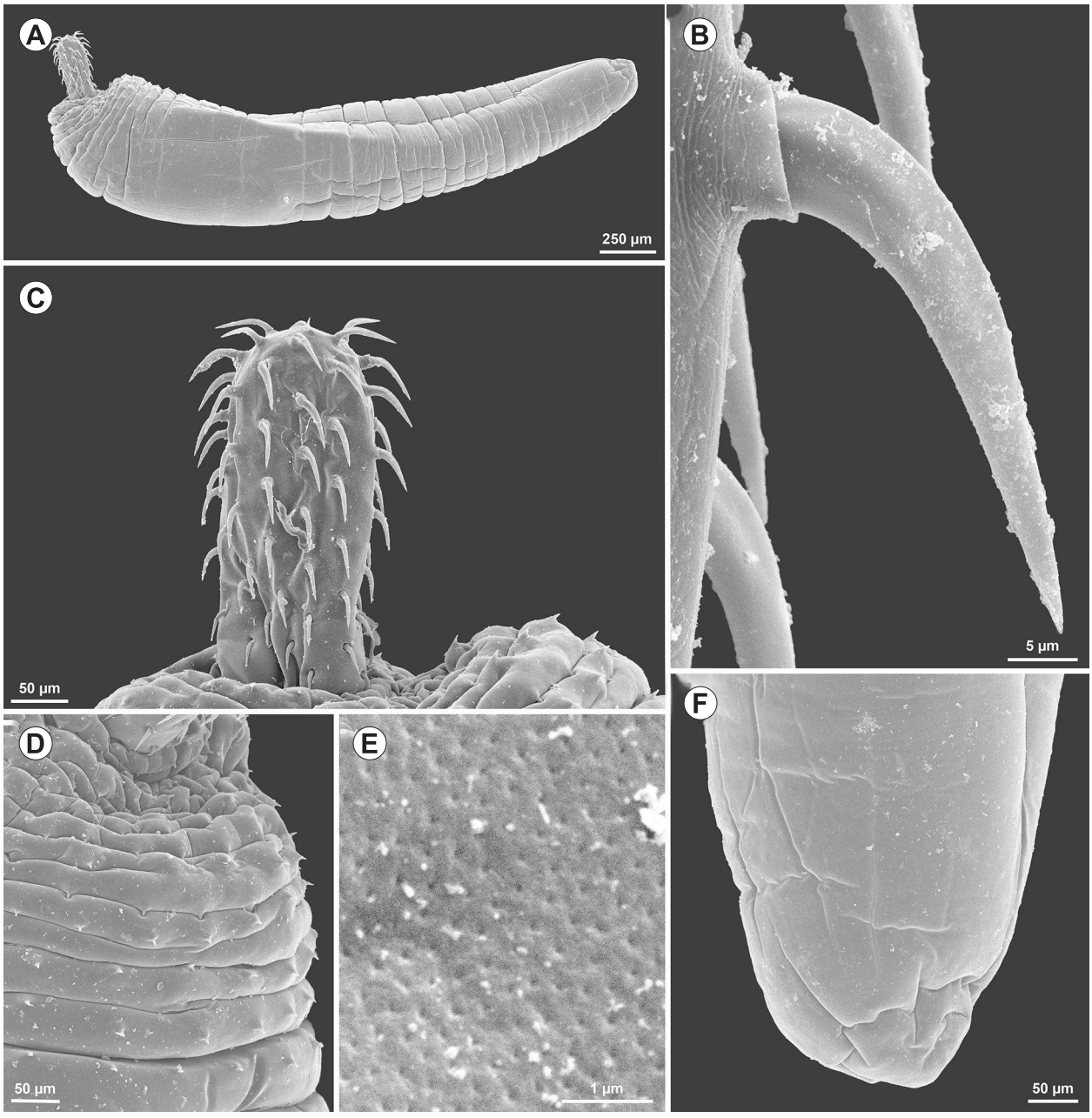

Fig. 4. Scanning electron micrographs of *Micracanthorhynchina brevelemniscus* sp. n. from *Opsariichthys pachycephalus* Günther. **A** – total view of female; **B** – hook; **C** – proboscis; **D** – spines on anterior part of trunk; **E** – micropores in the tegument in the middle part of the body; **F** – posterior end of female.

blades: 85; 75; 52–53; 36–39. Length of hook roots: 61; 53; 39–41; 28. Roots of hooks of third circular row complex, with anterior and posterior processes. Roots of hooks of other circular rows with simple posterior processes. Proboscis receptacle 535 × 136. Neck 277 × 147. Anterior part of trunk 205 wide, with spines 26–32 long with 12 circular rows in 20 each (Fig. 8C). Posterior part of trunk 244–282 wide with spines 35–41 long with 10 in a circular row (Fig. 8D).

Host: *Channa* sp. (Channidae)
Locality: East China sea off Northern Taiwan (near Taipei City)
Site of infection: Intestine
Infection rates: Prevalence, 1/1, intensity of infection 1.
Material: voucher (IPCAS A-137)

Remarks. *Pallisentis rexus* (Eoacanthocephala, Quadrigyridae) was described from the freshwater snakehead fish, *Channa striata* (Bloch), in the Chiang Mai basin, Thailand (Wongkham and Whitfield 1999). The main diagnostic characteristics in the anterior part of the body make it possible to reliably identify the species. No other host species and no other geographic location were previously reported.

***Longicollum* sp.** Fig. 8

Short description. Pomphorhynchidae, with characters of the genus *Longicollum* Yamaguti, 1935. Trunk 5.13 mm long with an extension in anterior part (Fig. 8E), 1.11 mm wide, and narrowed, 555 wide, in posterior cylindrical part. Proboscis club-shaped (Fig. 8F), 489 long, 357 wide in anterior

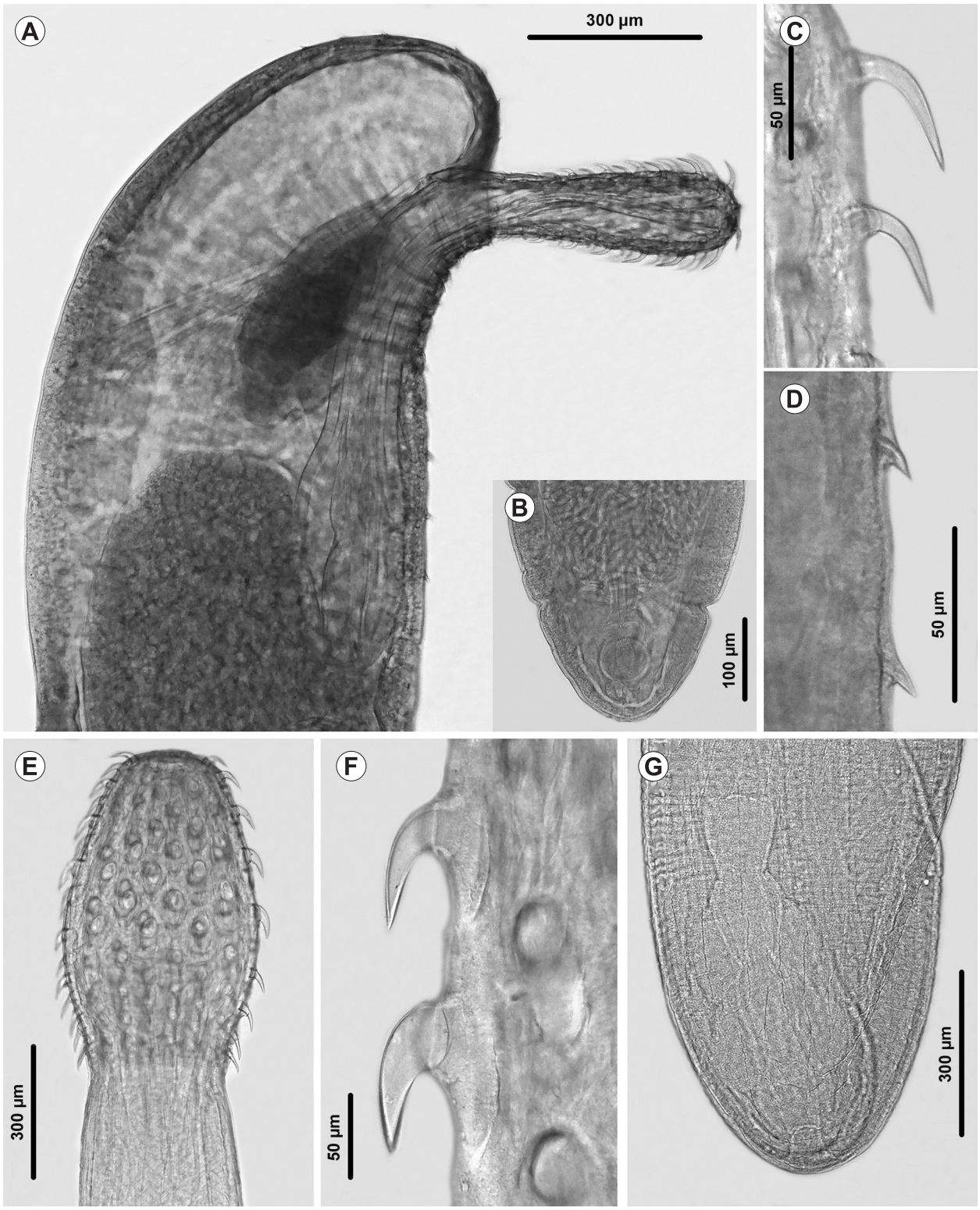

Fig. 5. Light microscope photographs of *Micracanthorhynchina brevelemniscus* sp. n. from *Opsariichthys pachycephalus* Günther (A–D) and *Bolbosoma vasculosum* (Rudolphi, 1819) from *Thunnus obesus* (Lowe) (E–G). **A** – anterior part of male; **B** – posterior end of female; **C** – hooks of proboscis; **D** – tegumental spines; **E** – proboscis; **F** – hooks of proboscis; **G** – posterior end of female.

part and 256 wide in posterior part, with 12 longitudinal rows in 12 hooks each. Hooks small, 24–28 long in anterior part and 22–24 long in posterior proboscis part. Neck 4.89 mm. Proboscis receptacle 6.40 mm × 73–137. Lemnisci extend beyond bottom of proboscis receptacle, swollen under it. Ducts of reproductive system 1.32 mm long. Genital pore terminal.

Host: Barramundi, *Lates calcarifer* (Bloch), Latidae.
Locality: East China sea off Western Taiwan (Budai Harbour)
Site of infection: Intestine.
Infection rates: Prevalence 50% (1/2), intensity of infection 1.
Material: voucher (IPCAS A-138)

Remarks. The specimen belonging to *Longicollum* sp. resembles *Longicollum alemniscus* (Harada, 1935) Fukui et Morisita 1938, the only specimen of the genus found in fish (see above) from Taiwan, in the formula of the proboscis armature (12 × 12 in *Longicollum* sp. versus 11 × 11 in *L. alemniscus*), the length of proboscis hooks (24–28 µm in *Longicollum* sp. versus 16–24 µm in *L. alemniscus*), but differs in the length of the lemnisci (extend beyond the bottom of the proboscis receptacle in *Longicollum* sp. versus do not extend to the bottom of the proboscis receptacle in *L. alemniscus*) (Golvan 1969). However, we cannot assign this worm with certainty to a particular species and leave the name as *Longicollum* sp.

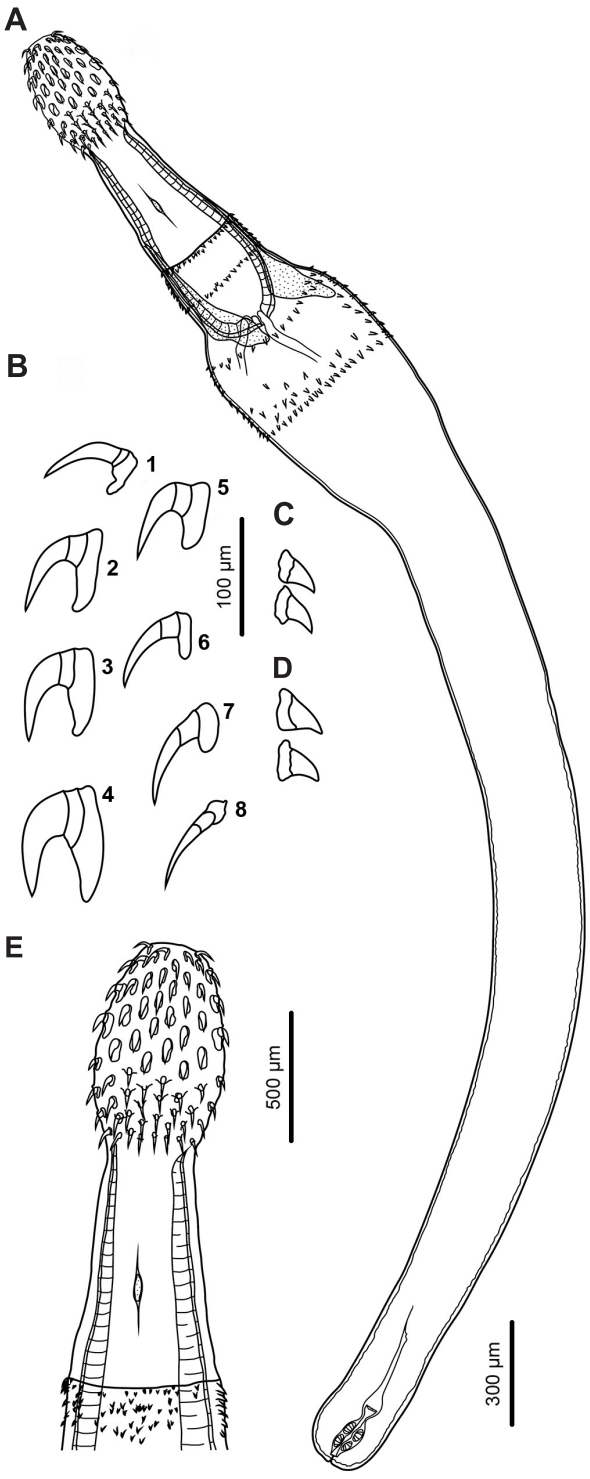

Fig. 6. Line drawing of *Bolbosoma vasculosum* (Rudolphi, 1819) from *Thunnus obesus* (Lowe). **A** – total view of female; **B** – hooks of one longitudinal row of proboscis; **C** – tegumental spines of anterior field of proboscis; **D** – tegumental spines of posterior field of proboscis; **E** – proboscis of female.

The pairwise similarity of newly generated sequences

The BLASTn comparison of newly generated 1,699–1,704 bp long sequences of the 18S rRNA gene with the data available in Genbank showed (i) 99.7–100% pairwise similarity of *R. laterospinosus* with *Rhadinorhynchus* spp. and *Neorhadinorhynchus nudus* (Acc. nos. MN705827, MN203133, MK457183–5, KR349116–7, MG838936–45) (Rhadinorhynchidae, Echinorhynchida), (ii) 99.8% pairwise similarity of *Micracanthorhynchina brevelemnicsus* with *M. dakusuiensis* (Acc. no. OP133175) (Rhadinorhynchidae, Echinorhynchida), and (iii) 99.1–99.5% pairwise similarity of *B. vasculosum* with *Bolbosoma* spp. (Acc. nos. JX014225, JX442166, MZ047218–27, JX442167) (Polymorphidae, Polymorphida).

The length of the new partial COI sequences was 603–655 bp. The pairwise similarity between two isolates of *R. laterospinosus* ex *S. australasicus* (Scombriformes, Scombridae) and *T. lepturus* (Scombriformes, Trichiuridae), respectively, both from the East China Sea off Taiwan, and *R. laterospinosus* ex *A. rochei* (Scombriformes, Scombridae) from the South China Sea off Vietnam, was 99.5%, suggesting their conspecificity. The highest calculated pairwise similarity of the partial COI sequences of *B. vasculosum* was only 83.1–83.4%, but similar to the 18S rRNA gene, *Bolbosoma* spp. and *Corynosoma strumosum* (Rudolphi, 1902) (Acc. nos. ON359908–9, KF156891, JX442190, EF467870) were identified as its closest taxa. The BLASTn analysis of the newly generated sequences of *M. brevelemniscus* did not provide any useful data, because the only available COI isolate of this genus was the mitochondrial genome of *M. dakusuiensis* (Acc. No. OP131911), which was excluded from the BLASTn search as an unverified sequence. Nevertheless, a partial COI sequence was extracted from the mitochondrial genome and used in our phylogenetic analyses. The pairwise similarity between the sequence of *M. dakusuiensis* and two isolates of *M. brevelemniscus* was calculated as 83.2–83.5% by MAFFT.

Molecular phylogenetic analysis

The initial phylogenetic analysis of the 18S rRNA dataset, which involved isolates from the orders Echinorhynchida and Polymorphida (Fig. S1), showed that the cluster of *M. dakusuiensis* and *M. brevelemniscus* formed a long branch with a strongly supported sister relationship to a clade of *Rhadinorhynchus* spp., including two newly sequenced isolates of *R. laterospinosus* (all Rhadinorhynchidae), *Pararhadinorhynchus* spp., *Sclerocollum* spp. and *Transvena* spp. (all Transvenidae), and *N. nudus* (Cavisomidae). The isolate of *B. vasculosum* nested to a highly

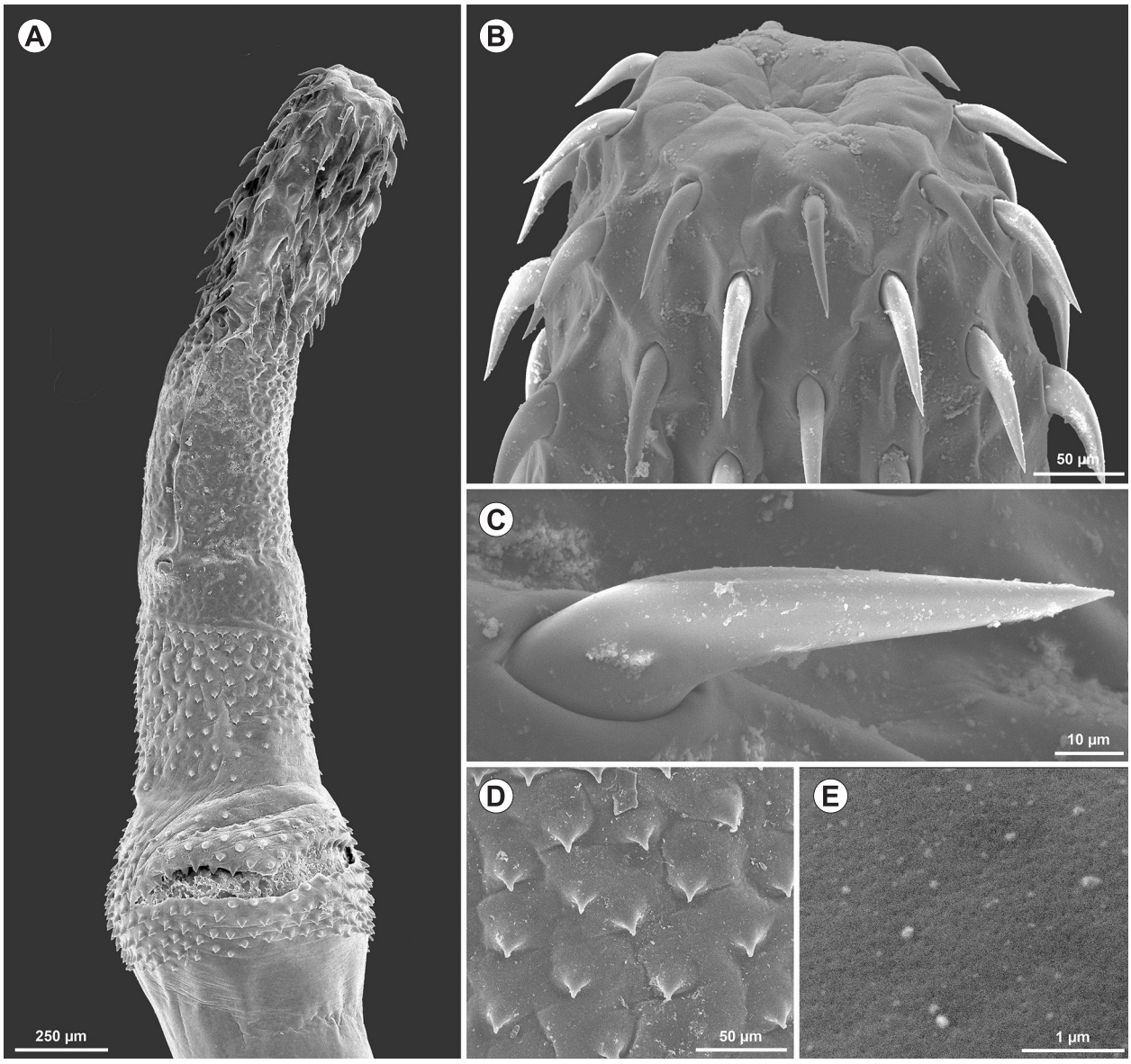

Fig. 7. Scanning electron micrographs of *Bolbosoma vasculosum* (Rudolphi, 1819) from *Thunnus obesus* (Lowe). **A** – anterior body; **B** – apical part of proboscis; **C** – hooks on proboscis in detail; **D** – somatic spines in anterior field, **E** – micropore in the tegument of the neck region.

supported clade containing *Bolbosoma* spp. (Polymorphidae). These results provided a background for subsequent analyses of the 18S rRNA+COI datasets.

In the phylogenetic analysis of the concatenated dataset of species of the families Rhadinorhynchidae and Transvenidae (Fig. 9A), *M. brevelemniscus* clustered with *M. dakusuiensis,* supporting the monophyly of *Micracanthorhynchina.* Newly generated isolates of *R. laterospinosus* from the East China Sea off Taiwan formed a well-supported clade with *R. laterospinosus* from the South China Sea off Vietnam, which was a sister group to the lineage of *Rhadinorhynchus johnstoni* Golvan, 1969.

The type species of the genus, *Rhadinorhynchus pristis* clustered with *Rhadinorhynchus hiansi* Soota et Bhattacharya, 1981, but its relationship with *R. laterospinosus* + *R. johnstoni* was poorly supported. It is worth noting that the position of *N. nudus* within the isolates of the genus *Rhadinorhynchus* and the position of *Rhadinorhynchus biformis* Smales, 2014, as a sister branch to a clade containing the two above-mentioned genera, as well as *Pararhadinorhynchus* spp., *Sclerocollum* spp., and *Transvena* spp. rendered the genus *Rhadinorhynchus* to be paraphyletic.

The phylogenetic analysis of the second concatenated dataset involving *B. vasculosum* (Fig. 9B) placed this currently polymorphid species into a highly supported clade of *Bolbosoma* spp., where it grouped with *B. vasculosum* from Java and an unidentified *Bolbosoma* sp. isolated from a human bowel. Species of *Bolbosoma*, including *B. vasculosum* from Taiwan, formed a sister branch to a monophyletic clade consisting of species of *Andracantha* Schmidt, 1975, and all these isolates clustered with three species of the genus *Corynosoma* Lühe, 1904, which appeared to be paraphyletic.

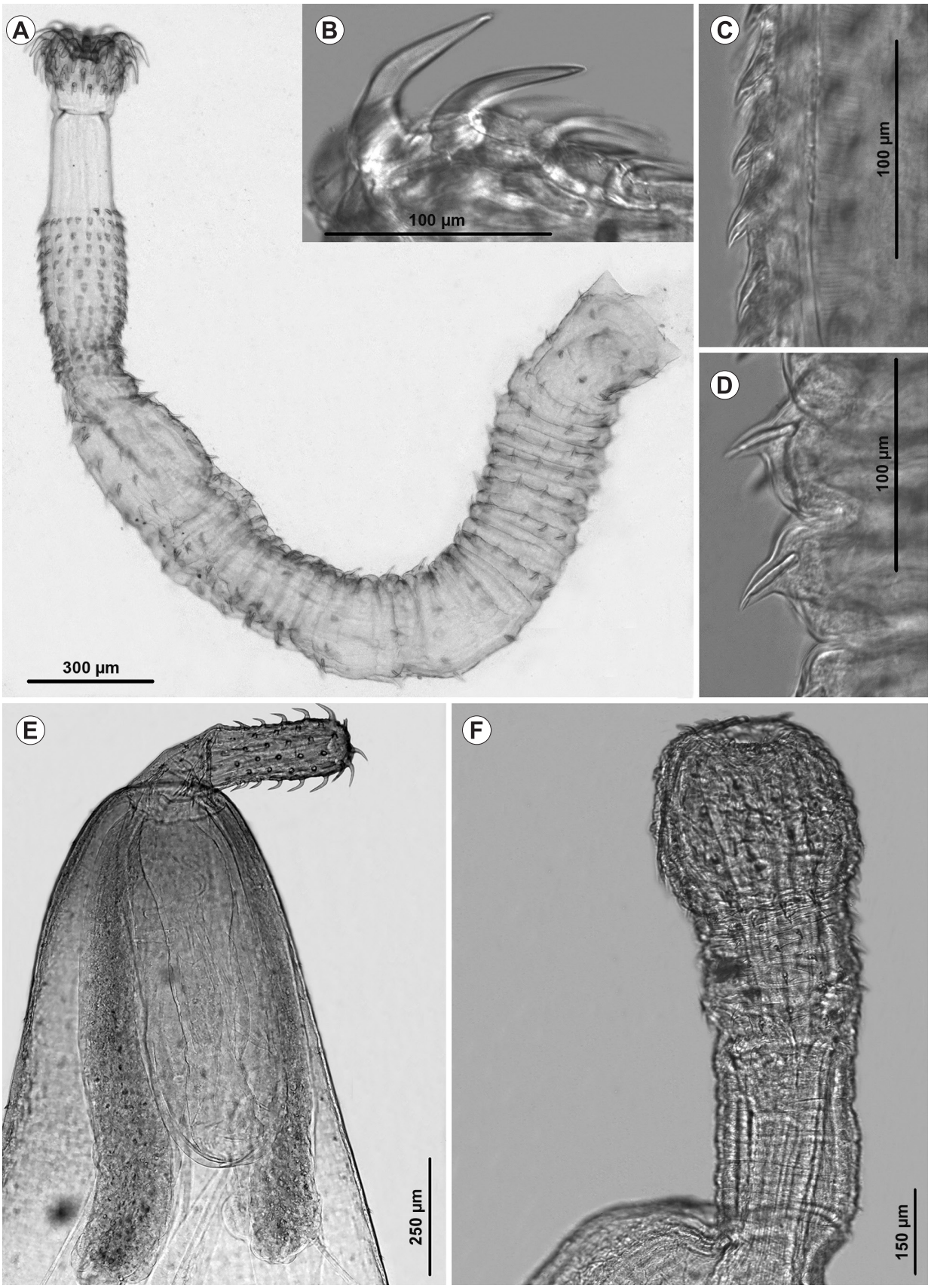

Fig. 8. Light microscope photographs of *Pallisentis rexus* Wongkham et Whitfield, 1999 of *Channa* sp. (A–D), *Micracanthorhynchina dakusuiensis* (Harada, 1938) of *Opsariichthys pachycephalus* Günther (E) and *Longicollum* sp. from *Lates calcarifer* (Bloch) (F). **A** – total view; **B** – hooks of proboscis; **C** – anterior trunk spines; **D** – median trunk spines; **E** – anterior part of female; **F** – proboscis.

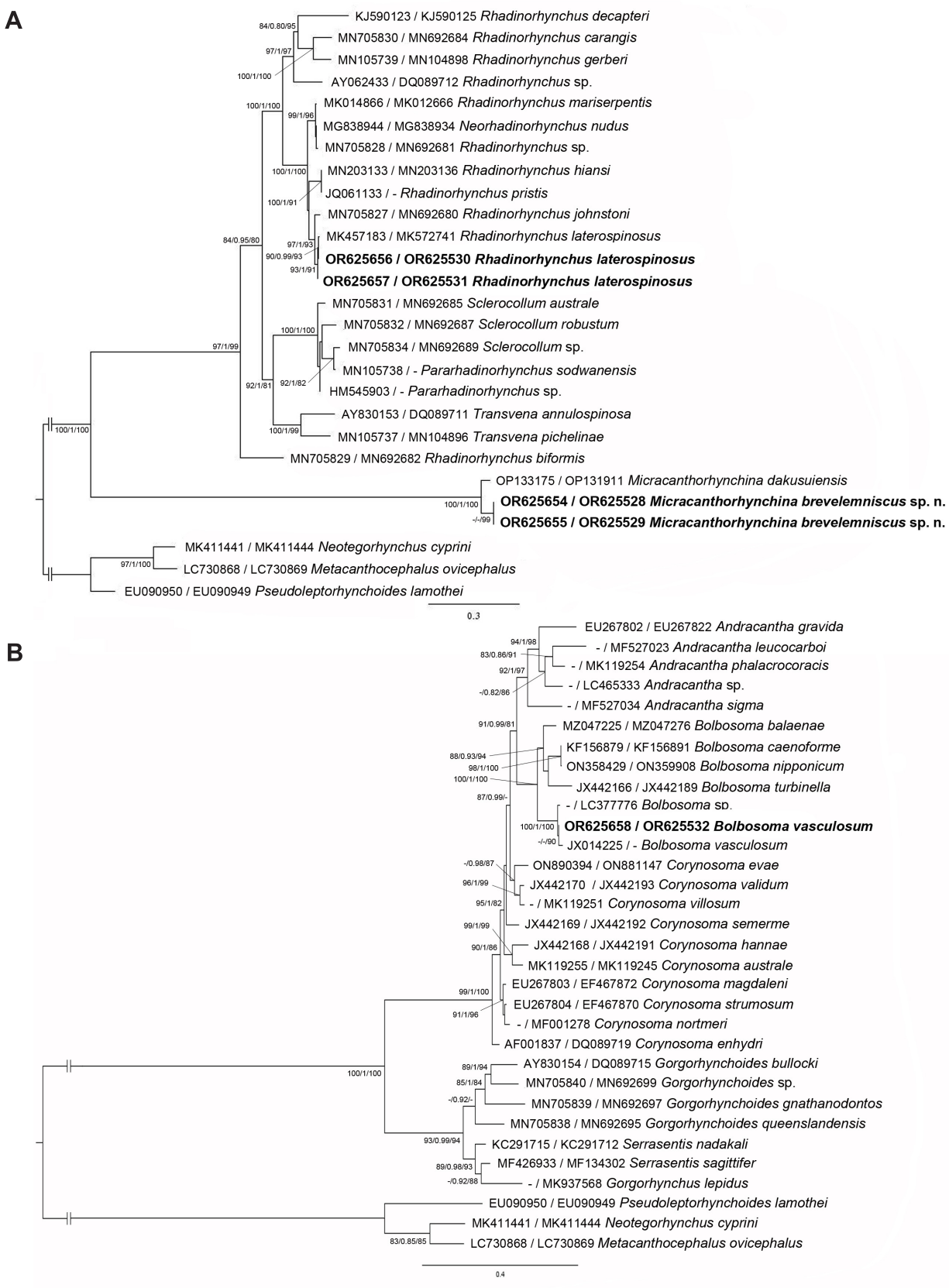

Fig. 9. Phylogenetic interrelationships within the families Rhadinorhynchidae + Transvenidae (A) and a part of Polymorphidae (B) inferred using ultrafast bootstraping (UFBoot) approach on concatenated datasets of almost complete 18S rRNA and partial COI genes. A – the isolates of *Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011 from East China Sea off Taiwan were closely related with *R. laterospinosus* from South China Sea off Vietnam, and *Micracanthorhynchina brevelemniscus* sp. n. clustered with isolates of *M. dakusuiensis* (Harada, 1938) from China, B – the isolate of *Bolbosoma vasculosum* (Rudolphi, 1819) nested within a clade of *Bolbosoma* spp. The values near the nodes indicate SH-aLRT (> 80), aBayes (> 0.80), UFBoot (> 80) supports. Scale bars indicate number of substitutions per site.

DISCUSSION

Our study adds five species to the list of acanthocephalans found in Taiwanese fishes. Thus, to date, there are 16 species of acanthocephalans in Taiwanese fishes. Of the species we found, only *Micracanthorhynchina dakusuiensis* was previously known from Taiwan. Judging from the individual finds, *M. dakusuiensis* does not have strict host specificity. The species was described from cyprinoids (Harada 1935), and our material is also from cyprinoids of the family Xenocyprididae. Recently *M. dakusuiensis* was found in yellow catfish *Tachysaurus fulvidraco* (Siluriformes, Bagridae) in mainland China (Gao et al. 2022).

In morphological characterisation of the acanthocephalans found in fish in Taiwan, we focused on some details of the morphology of worms that have recently received close attention. In particular, thanks to the use of a scanning microscope, we found micropores on the surface of the tegument of *Micracanthorhynchina brevelemniscus* sp. n. and *Bolbosoma vasculosum*. The diameter and position of the micropores are not the same in different species. For example, in *Rhadinorhynchus dorsoventrospinosus* Amin, Heckmann et Ha 2011, the micropores are located in the anterior part of the body (Amin et al. 2011), while in *Cathayacanthus spinitruncatus* Amin, Heckmann et Ha, 2014 the micropores are located in the middle part of the body (Amin et al. 2014). Micropores in the tegument of *M. brevelemniscus* are present only in the middle part of the body and in *B. vasculosum* only on the neck. This feature of tegument morphology has been shown for acanthocephalans of many taxonomic groups (Amin et al. 2009, 2011, 2014, 2017, 2021).

Mature *B. vasculosum* have been found only a few times in marine mammals (Halajian et al. 2020) and in fishes (Harada 1935, Williams and Bunkley-Williams 1996). Immature worms of this species are found in marine mammals (Pendergraph 1971, Costa et al. 2000, Fernández et al. 2004, Mateu et al. 2014), and also in the intestines of fish (Costa et al. 2000, Verweyen et al. 2011; present study). Findings of cystacanths of *B. vasculosum* are also known in the body cavity of various fishes (Costa et al. 2000, Klimpel et al. 2006). In this case, fish are paratenic hosts and can be a source of infection for definitive hosts, perhaps piscivorous marine mammals. Obviously, additional research is needed to resolve all the contradictions associated with this species.

Our phylogenetic analyses revealed that the newly generated isolates of the genus *Rhadinorhynchus* are conspecific with isolates of *Rhadinorhynchus laterospinosus*, but they also revealed the paraphyly of the family Rhadinorhynchidae suggested in previous studies (Amin et al. 2019, Lisitsyna et al. 2019a, Huston et al. 2020, Gao et al. 2022). This systematic incongruence was partially resolved by Huston et al. (2020) by (i) transferring two species of the genus *Gymnorhadinorhynchus* Braicovich, Lanfranchi, Farber, Marvaldi, Luque et Timi, 2014 (Gymnorhadinorhynchidae) to the genus *Rhadinorhynchus*, and (ii) proposing to consider the genus *Sclerocollum* Schmidt et Paperna, 1978 as a taxon of the Transvenidae, thus making this family monophyletic. Nevertheless, the topology of *Rhadinorhynchus biformis* as a sister lineage of the clade composed of three genera of the family Transvenidae + *Rhadinorhynchus* spp. + *Neorhadinorhynchus nudus* (Cavisomidae), remained as a pending taxonomic issue of this group.

Of the 11 valid species of the genus *Micracanthorhynchina* (see Amin 2013, Smales 2014), genetic data on only one species, *M. dakusuiensis*, have been available (Gao et al. 2022). This species and our new isolates of *M. brevelemniscus* formed a strongly supported cluster, which formed the earliest diverging branch to the rest of rhadinorhynchids and transvenids. Moreover, the morphology of species of the genus *Micracanthorhynchina* does not fully correspond to the diagnosis of the family Rhadiorhynchidae, because a short proboscis with a small number of hooks in the longitudinal row and the presence of four or six short club-shaped cement glands arranged in a bundle distinguish these acanthocephalans from most other representatives of the family. Together with the genetic divergence of two species of *Micracanthorhynchina* from the rest of the family, this might suggest the status of a separate higher taxon. However, an investigation of further species is necessary to clarify the systematic position of this genus.

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