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Taxonomy and Phylogeny of Acanthocephala from Japanese Fishes

(日本産魚類に寄生する鉤頭虫類の系統分類学的研究)

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7. Kita Y, Nitta M, & Kajihara H (2024) Systematics of *Pseudocavisoma* (Acanthocephala: Echinorhynchida): assessment of familial affiliation, establishment of a new species, and complementary redescription of the type species based on syntypes. *Systematic Parasitology* 101:73.
8. Kita Y, Nitta M, Abe H, Kaburagi S, Fujita T, Toyota K, Kondo Y, & Kajihara H (2025) A new species of *Pseudoacanthocephalus* (Acanthocephala: Pseudoacanthocephalidae) from Sado Island, Japan, with a report of its accidental occurrence in a marine elasmobranch. *Folia Parasitologica* 72: 028.
9. Kita Y, Sekine H, Nagata W, Doi R, Waki T, & Kajihara H (2025) Morphological and molecular characteristics of *Longicollum alemniscus* (Acanthocephala:

- Echinorhynchida), with a taxonomic revision of the genus *Longicollum*.
Zoological Science 42: 484–491.
10. Kita Y & Kajihara H (2025) First record of *Cavisoma magnum* (Acanthocephala: Echinorhynchida) from Japanese waters, with systematic revision on Cavisomatidae. Species Diversity 30: 241–248.
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CHAPTER I

GENERAL INTRODUCTION

SYSTEMATICS

Taxonomic background

Acanthocephala, commonly known as thorny-headed worms, is a phylum comprising exclusively endoparasitic species (Amin 2013). Approximately 1,300 species are currently recognized worldwide (Amin 2013; Gibson & Wayland 2025a). The earliest recorded acanthocephalan was described by Redi (1684), and the first genus, *Acanthocephalus*, was established by Koelreuther (1771). Subsequently, Rudolphi (1808) recognized Acanthocephala as a phylum-level taxon. Since then, numerous species, genera, families, and orders have been described and systematized according to various criteria. Historical classification schemes can broadly be divided into those emphasizing trunk spines and cement glands as diagnostic features (e.g., Petrochenko 1956; Golvan 1969) and those that do not (e.g., Amin 1985, 1987, 2013; Meyer 1932; Van Cleave 1936; Yamaguti 1963). Petrochenko (1956) divided the phylum into three classes, which remain generally accepted today: Archiacanthocephala, Eoacanthocephala, and Palaeacanthocephala. Archiacanthocephala, an entirely terrestrial lineage parasitizing birds and mammals, is considered the earliest-diverging among extant acanthocephalans and is characterized by eight cement glands, each containing a single giant nucleus (Amin 1998, 2013). Approximately 160–180 species are known within this class (Amin 1985, 2013; Lynggaard et al. 2021). Eoacanthocephala comprises entirely aquatic species parasitizing reptiles and fishes (around 250 species; Amin 2013), typically characterized

by a single syncytial cement gland. Palaeacanthocephala, the most diverse class with more than 800 species (Amin 2013), occurs in marine, freshwater, and terrestrial environments and parasitizes mammals, birds, reptiles, amphibians, and fishes. A fourth class, Polyacanthocephala, was once recognized (Amin 1987, 2013), but molecular phylogenetic studies have shown it to be nested within Eoacanthocephala (e.g., Gazi et al. 2016). The current taxonomy of Acanthocephala largely follows the frameworks of Golvan (1994) and Amin (2013). However, recent molecular phylogenetic analyses have begun to substantially reshape traditional classifications. Chapter III of this thesis provides a detailed overview of these molecular studies.

Relationships to Rotifera

Morphological similarities between Acanthocephala and Rotifera have been recognized since early comparative studies of their epidermal structures (Ahlrichs 1995, 1997). Ahlrichs (1995) proposed the name Syndermata for the clade comprising Acanthocephala and Rotifera, united by their syncytial epidermis. Subsequent molecular studies placed Acanthocephala firmly within Rotifera and identified Seisonidea—ectosymbionts of leptostracan crustaceans (Phyllocarida)—as the sister group of Acanthocephala (e.g., Garey et al. 1996, 1998; Sielaff et al. 2016). Some authors have consequently treated Syndermata as a phylum-level taxon (e.g., Zrzavý et al. 1998). Nevertheless, it remains common practice in current taxonomy to recognize Acanthocephala and Rotifera as separate phyla. For consistency, this thesis follows that convention.

BODY PLAN

Acanthocephalans are bilaterally symmetrical pseudocoelomates. The body wall consists of a syncytial epidermis connected to an extensive lacunar system (Starling 1985). As they absorb nutrients exclusively through this epidermal–lacunar system, acanthocephalans lack a digestive tract (e.g., Bryant & Nicholas 1965). The most distinctive morphological feature of the group is the retractable, protrusible proboscis armed with numerous hooks, which anchors the parasite to the intestinal wall of its vertebrate host (cf. Petrochenko 1956; Kennedy 2006). The arrangement and morphology of the proboscis hooks are key diagnostic traits for species identification. The cerebral ganglion is situated within the proboscis receptacle. Acanthocephalans are gonochoristic, and no parthenogenetic reproduction has been documented (Kennedy 2006). Males typically possess two testes, a copulatory organ (penis), a copulatory bursa, and a set of cement glands, the number and shape of which vary among taxa. The cement glands secrete substances that form a copulatory plug sealing the female's genital pore after mating (Dezfuli et al. 1999) and may also play a role in male–male competition by sealing another male's copulatory organ (Abele & Gilchrist 1977). In females, most of the body cavity is occupied by eggs. The uterus and uterine bell function in oviposition and in sorting and maturing eggs (Whitfield 1970).

ECOLOGY

Life cycle and host usage

Acanthocephalans generally require two hosts to complete their life cycle: an intermediate host and a definitive host. Adults copulate in the intestine of the definitive host and release eggs that are expelled with feces. Each mature egg contains an acanthor larva (Schmidt 1985). When ingested by an intermediate host, the acanthor penetrates

into the hemocoel, where it develops successively into an acanthella and then a cystacanth. Infection of the definitive host occurs when it consumes an infected intermediate host, after which the cystacanth excysts and matures in the intestine (Kennedy 2006). Intermediate hosts are typically small crustaceans or insects, while vertebrates serve as definitive hosts. Some species also employ paratenic hosts to bridge trophic gaps between the intermediate and definitive hosts (Kennedy 2006). Common paratenic hosts include fishes for aquatic species, and amphibians or small mammals for avian-parasitic species (e.g., Ewald et al. 1991; Sasaki et al. 2019; Oliveira et al. 2024). Most vertebrates can act as definitive hosts, whereas lampreys and elasmobranchs are rarely infected, with reported cases being few or likely accidental (e.g., Golvan et al. 1964; Katahira et al. 2014; Kita et al. 2025a). The breadth of host range differs markedly among species, spanning taxa known only from single host species or genera to those documented to infect a wide array of hosts (e.g., Yamaguti 1963). Nevertheless, rigorous assessment of host specificity remains challenging, as ostensibly high specificity may merely reflect inadequate sampling or limited investigative effort (cf. Kennedy 2006). Furthermore, even taxa that appear to possess broad host ranges may display divergent gene-expression profiles when infecting optimal versus suboptimal hosts (Schmidt et al. 2022), thereby complicating the inference of true host specificity from presence–absence data alone.

Host manipulation

Host manipulation is a well-known ecological phenomenon among acanthocephalans. Experimental studies have primarily focused on freshwater species (e.g., Bethel & Holmes 1977), although similar behavioral alterations have been

documented in terrestrial systems (e.g., Moore 1983). Typically, infected intermediate hosts exhibit reversed phototaxis or thigmotaxis and reduced escape responses (e.g., Cézilly et al. 2000; Perrot-Minnot et al. 2007). Such behavioral changes increase the likelihood of predation by the definitive host (Perrot-Minnot et al. 2007). These effects are thought to result from parasite-induced alterations in the secretion and balance of neurotransmitters within the host's nervous system (e.g., Cozzarolo & Perrot-Minnot 2022; Perrot-Minnot & Parrot 2024).

Environmental parasitology

The field of environmental parasitology emerged following discoveries that acanthocephalans accumulate heavy metals at concentrations far exceeding those in their hosts (e.g., Sures et al. 1999; Sures 2003, 2008; Thielen et al. 2004). Consequently, researchers have proposed using endoparasites, particularly acanthocephalans, as bioindicators for monitoring environmental pollution (Marcogliese 2005; Sures 2008). Among parasitic taxa, acanthocephalans are regarded as particularly suitable indicators owing to their exceptional capacity for metal accumulation (Mehana et al. 2020).

ACANTHOCEPHALANS AS PATHOGENS

Acanthocephalans as zoonotic parasites

No acanthocephalan species is known to use humans as a natural definitive host. Nonetheless, accidental human infections occur, suggesting a zoonotic potential. Such infections typically result either from accidental ingestion of intermediate hosts (e.g., Berenji et al. 2007; Mathison et al. 2016) or from consumption of raw fish serving

as paratenic hosts, which may contain viable cystacanths (e.g., Fujita et al. 2016; Kaito et al. 2019).

Acanthocephalans in the veterinary medicine and the fishery sciences

In livestock and zoo settings, severe infections of acanthocephalans are rare but occasionally reported (e.g., Migliore et al. 2021). In contrast, in fisheries and aquaculture, heavy infections by acanthocephalans have been widely documented and can cause significant economic losses (e.g., Wanstall et al. 1986; Hatai et al. 1987; Aguilar et al. 2018; Cheng et al. 2022). Therefore, acanthocephalans are recognized as important parasitic pathogens in fish health management.

OVERVIEW OF THIS THESIS

The overarching aim of this thesis is to reconsider the taxonomy of Acanthocephala parasitizing Japanese fishes through integrative morphological and molecular approaches. To this end, I conducted: *i*) morphological redescrptions of acanthocephalan specimens collected from Japanese fishes, and *ii*) molecular phylogenetic analyses to improve the resolution of systematic and evolutionary relationships within the class Palaecanthocephala.

Chapter II provides detailed morphological descriptions of representative Japanese species, while Chapter III presents molecular phylogenetic analyses based on multiple gene sequences using Japanese acanthocephalan taxa. Specific background information and methodological details are provided in each chapter.

CHAPTER II

SYSTEMATICS AND TAXONOMY OF FISH-PARASITIZING ACANTHOCEPHALA, BASED ON JAPANESE SPECIES

INTRODUCTION

Currently, about 100 nominal species of acanthocephalans are known from fishes in Japanese waters (cf. Araki 2003; Kita & Kajihara 2023; Kita et al. 2024, 2025), of which 60 are valid (Table 1). In Japan, the taxonomic study of Acanthocephala was started by Fujita (1920, 1921). After that, several Japanese acanthocephalan species were described by Japanese researchers (Harada 1928; Fukui 1929; Fukui & Morisita 1936, 1937a, b) or foreign researchers who were given the Japanese specimens (Golvan 1969; Van Cleave 1925, 1931a). The research of Satyu Yamaguti has most remarkably advanced the taxonomy of Japanese acanthocephalans and exerted a significant international influence (Yamaguti 1935, 1939, 1959, 1963). Japanese acanthocephalan taxonomy continued into the 2000s (e.g., Araki & Machida 1987; Machida 1992; Machida & Araki 1982; Nakajima & Egusa 1975b). Around the 2000s–2020s, acanthocephalan studies were mainly conducted by Kazuya Nagasawa, especially focusing on the freshwater species (e.g., Katahira & Nagasawa 2014; Nagasawa & Nitta 2015). Meanwhile, terrestrial species were also studied by some researchers (Nakao 2016; Nagasawa & Yoshida 2017; Kamimura et al. 2018). Despite these situations, taxonomic studies on marine acanthocephalans were quite scarce (e.g., Sasaki et al. 2019), and only a few studies were based on species using marine fishes as definitive hosts (e.g., Nagasawa & Takami 2017). Furthermore, some areas around Japan have not been examined well in previous studies: around Tosa Bay (only Yamaguti 1939); San-in

(no study); and around Okinawa (only Williams et al. 1996). From 2021, I conducted several taxonomic studies of marine-fish-parasitizing acanthocephalans (Kita & Kajihara 2021, 2023, 2025; Kita et al. 2023, 2024a–d, 2025b) from various localities in Japan (Table 2, Fig. 1). In this chapter, I provide the morphological description and taxonomic summary of the acanthocephalan species from Japanese coastal areas, partially based on my previous studies listed above. Also, taxonomic revisions of some taxa in my previous studies are presented in this chapter.

MATERIALS AND METHODS

Sampling

Specimens were collected from marine and brackish water fishes around the coastal areas of Japan (Table 2, Fig. 1). The hosts were obtained by fishing, cage trapping, and purchasing at markets. Acanthocephalans were collected from the intestine, pylorus, and body cavity of each host. The obtained acanthocephalans were either *i*) flattened under slight pressure with a glass slide and coverslip in 70% ethanol for light microscopy, *ii*) fixed with acetoacid formalin (AFA) for scanning electron microscopy (SEM), or *iii*) fixed in 99% ethanol for DNA extraction (see Chapter III). In addition to newly collected material, I examined multiple glass-slide specimens borrowed from the Meguro Parasitological Museum (MPM) (Tokyo), the National Museum of Nature and Science (NMNS) (Tsukuba), and the National Museum of Natural History (NMNH) (USA) to facilitate detailed comparison with the specimens obtained in this study.

Morphological observations

The flattened specimens were stained with Heidenhain's iron hematoxylin or alum-carmin, dehydrated with a series of ethanol, cleared with xylene, and mounted with Entellan New (Merck, Germany) or Canada Balsam diluted with xylene. The AFA-fixed specimens were dehydrated in a series of ethanol, placed in warmed t-butyl-alcohol for three changes, and freeze-dried at -20°C . The prepared samples were mounted on stubs, sputter-coated with gold (Hitachi E101, Tokyo, Japan), and observed with SEM (Hitachi S-2150) at an accelerating voltage of 20 kV. All specimens were observed under a compound light microscope, and digital photomicrographic images were used for the measurement of each body part and also for producing line drawings of the specimens: drawings were conducted with Adobe Illustrator. Measurements are given in micrometers; otherwise, as noted, the range of measured values was indicated as minimum–maximum (average) in each description. The identification of host fishes followed Nakabo (2018).

TAXONOMY

Systematics

Phylum Acanthocephala Koelreuther, 1771

Class Eoacanthocephala Van Cleave, 1936

Order Neoechinorhynchida Ward, 1917

Family Neoechinorhynchidae Ward, 1917

Genus *Neoechinorhynchus* Hamann in Stiles & Hassall, 1905

Subgenus *Hebesoma* Van Cleave, 1928

***Neoechinorhynchus (Hebesoma) yamagutii* Tkach, Sarabeev, & Shvetsova, 2014**

(Fig. 2)

Neoechinorhynchus agilis: *partim sensu* Yamaguti 1935: 275.

Neoechinorhynchus (Hebesoma) yamagutii Tkach et al., 2014: 299, figs. 19–24.

Type locality. Ariake Sea, Seto Inland Sea, off Numazu (Shizuoka, Japan) (Tkach et al. 2014; Yamaguti 1935).

Other localities. Kiyevka Bay (Russia) (Tkach et al. 2014); off Bizen (Okayama, Japan) (Kita unpubl.).

Type host. *Mugil cephalus* (Mugilidae) (Tkach et al. 2014).

Other hosts. *Liza haematochelia* [= *Chelon haematochelius* (Mugilidae)] (Tkach et al. 2014).

Materials examined. Seven males and one female (YK's private collection), off Bizen, 12 September 2023, from the intestine of *Mugil cephalus*.

Description. *General* (n = 8). Trunk cylindrical, elongate. widest at anterior one third of the body. Giant hypodermal nuclei unclear. Proboscis short, cylindrical, wide, armed with hooks in three types: apical hooks stout, long, less curved, one circular row; subapical hooks middle in size, less curved; basal hooks small, short; hooks in each circular row same in size. Neck short, trapezoidal, thick. Proboscis receptacle single-walled. Lemniscus two, almost equal in size, much longer than receptacle.

Male (n = 7). Trunk 7243–12336 (10576) × 798–1511 (1108). Proboscis cylindrical, short, wide, 147–188 (176) × 138–186 (154). Proboscis, 609–809 (716) × 204–260 (240). Lemniscus, 3131–5704 (4503) in length. Anterior testis 937–1947 (1455) × 367–601 (486). Posterior testis 1102–1542 (1367) × 452–726 (555). Cement gland syncytial, with two cement ducts. Copulatory bursa opening terminally, 295–638 (454) in width.

Female (n = 1). Trunk cylindrical, elongate, 20767×1858 . Proboscis cylindrical, short, wide, 163×155 . Proboscis receptacle single-walled, 678×256 . Lemniscus long, 8622 in length. Genital organs unclear. Eggs elliptical, with polar prolongation, 21–26 (24) in length.

Remarks. Amin (2002) stated that the subgenus *Hebesoma* is characterized by having eggs with polar prolongation, which are lacking in the other subgenus, *Neoechinorhynchus*. However, recent molecular phylogeny showed that each of these subgenera was not a monophyletic group (e.g., Huston et al. 2022; Malyarchuk et al. 2014; Sarabeev et al. 2020), while no taxonomic revision on them has been conducted to date. In this study, I provisionally followed Amin (2002) and compared the present specimens with other congeners having eggs with polar prolongation. The morphology of my specimens differed from other *Hebesoma* species in i) trunk shape (not spindle shape), ii) hook size variation in each circular/longitudinal row, and iii) lemniscus size variation (Amin 2002; Amin et al. 2014; Arredondo & Gil de Pertierra 2012; Tkach et al. 2014). Tkach et al. (2014) established *N. (H.) yamagutii* based on the specimens deposited in MPM (Tokyo, Japan), once identified as “*Neoechinorhynchus agilis*” (cf. Yamaguti 1935). However, they designated the type materials only as “Type material. MPM 22471 (SY 7562, SY 7563), 22472 (SY 75–64), 22473 (SY 75–65), 22474 (SY 75–66)” and no specific holotype specimen was designated. Due to this, the type locality has been uncertain. To improve the information on type materials, the designation of the lectotype specimen within the type materials is needed.

Class Palaeacanthocephala Meyer, 1931

Order Echinorhynchida Southwell & Macfie, 1925

Family Arhythmacanthidae Yamaguti, 1935

Genus *Acanthocephaloides* Meyer, 1932

***Acanthocephaloides neobythitis* Yamaguti, 1939**

(Fig. 3)

Acanthocephaloides neobythitis Yamaguti, 1939: 323, fig. 6.

Neoacanthocephaloides neobythitis: Cable & Quick 1954: 396.

Pseudorhadinorhynchus neobythitis: Petrochenko 1956: 360.

Yamagutisentis neobythitis: Golvan 1969: 196.

Type host. *Neobythites macropus* (Ophidiidae) (Yamaguti 1939).

Other hosts. *Sebastiscus marmoratus* (Sebastidae) (Yamaguti 1939);

Scorpaenopsis cirrosa (Scorpaenidae) (Kita unpubl.).

Type locality. Off Obama (Fukui, Japan) (Yamaguti 1939).

Other locality. Off Sakaiminato (Tottori, Japan) (Kita unpubl.).

Material examined. One female (YK's private collection), off Sakaiminato, 18 June 2024, from the intestine of *Scorpaenopsis cirrosa*.

Description. *Female* (immature, n = 1). Trunk cylindrical, elongate, covered with tiny spines anteriorly, 646 in width. Proboscis cylindrical, elongate, 658 × 165, armed with 10 hooks in 17 rows: basal 2–3 hooks per row small. Proboscis receptacle double-walled, 651 × 209. Uterus 968 in length. Vaginal sphincter single.

Remarks. The present species can be distinguished from other congeners by *i*) proboscis hook arrangement, *ii*) proboscis shape, and *iii*) shape of proboscis hooks (Table 3) except *Acanthocephaloides ichiharai* Araki & Machida, 1987. In the description of Yamaguti (1939, p. 323), there is no mention of the reduction of hook size in the basal region of the proboscis, while the line drawing of the hooks showed them (Yamaguti 1939, fig. 6). The most similar species, *A. ichiharai*, also lacked a description

of the remarkable size-reduction of hooks in the posterior proboscis (Araki & Machida 1987), whereas its line drawings seemed to indicate that the basal three hooks are quite smaller than other ones. In Araki & Machida (1987), *A. neobythitis* and *A. ichiharai* were distinguished by the number of hook rows (16–18 in *A. neobythitis* vs 12–16 in *A. ichiharai*). In each of the original descriptions, the specimens having 16 hook rows were mentioned as “rare”. The present material had 17 hook rows, the general number of rows in *A. neobythitis*. Thus, I identified the specimen as *A. neobythitis*. In this study, I did not observe the type materials of *A. neobythitis* or *A. ichiharai*, so I could not determine whether these two species are synonymous or not. Further morphological study and molecular analysis on them are necessary to solve this issue.

Genus *Heterosentis* Van Cleave, 1931

***Heterosentis fusiformis* (Yamaguti, 1935)**

(Fig. 4)

Arhythmacanthus fusiformis Yamaguti, 1935: 272, figs. 25–26.

Heterosentis fusiformis: Tripathi 1956: 78, table 3.

Type locality. Off Wakayama (Japan) (Yamaguti 1935).

Other localities. Off Mie (Japan) (Yamaguti 1935); off Kannonzaki (Kanagawa, Japan) (Kihara 1959c); off Matoba (Hiroshima, Japan) (Kita unpubl.).

Type host. *Sphoeroides* sp. (Tetraodontidae) (Yamaguti 1935).

Other hosts. *Takifugu niphobles* (Tetraodontidae) (Kihara 1959c); *Plotosus japonicus* (Plotosidae) (Kita unpubl.); *Istigobius hoshinonis* (Gobiidae) (Kita unpubl.).

Materials examined. Five males and six females (YK’s private collection), off Matoba, 6 July 2014 and 26 October 2020, from the intestines of *Istigobius hoshinonis* and *Plotosus japonicus*.

Description. *General* (n = 11). Trunk fusiform to elongate, covered with tiny spines entirely: spines on anterior region not covered anterior cone; spines on posterior region sparse. Proboscis oval to fusiform. Proboscis hooks in three types: apical hooks in one circular row, middle in size, less curved; subapical hooks in one circular row, largest in size, less curved; basal hooks in 14 longitudinal rows with 2–3 hooks per row. Proboscis receptacle double-walled. Cerebral ganglion positioned posterior end of receptacle. Lemniscus longer than receptacle.

Male (n = 5). Trunk 2095–2434 (2249) × 406–508 (451). Proboscis 106–166 (137) × 82–113 (92). Proboscis receptacle 263–296 (279) × 87–110 (101). Lemniscus 396–605 (479) in length. Anterior testis 350–561 (419) × 234–311 (274). Posterior testis 365–451 (409) × 257–341 (291). Cement glands six, clustered, claviform. Saefftigen's pouch 181–236 (208) in length. Copulatory bursa opening terminally, 113–194 (151) in diameter.

Female (n = 6). Trunk 2499–3053 (2808) × 497–632 (566). Proboscis 163–202 (184) × 96–138 (118). Proboscis receptacle 194–437 (295) × 74–125 (99). Lemniscus 450–472 (461) in length (n = 2). Uterus 419–707 in length. Vaginal sphincter single. Eggs elliptical, with swelling portion laterally, 27–37 (32) in length (eggs n = 10).

Remarks. The specimens clearly matched the morphological characters of the genus *Heterosentis* by having unique proboscis hooks (anterior hooks: enlarged; basal hooks: small) and a fusiform, spinose trunk (Van Cleave 1931b). Morphologically, the present materials could be distinguished from other congeners by the arrangement of proboscis hooks and trunk spines, other than *H. fusiformis* and *H. holospinus* Amin, Heckmann, & Ha, 2011 (Table 4). *Heterosentis holospinus* has an enlarged anterior cone and a more elongated trunk, while *H. fusiformis* has a smaller cone and trunk (Amin et

al. 2011b; Yamaguti 1935). My specimens were clearly consistent with *H. fusiformis* in the above traits (Fig. 4). Thus, the specimens in this study were identified as *H. fusiformis*.

Family Cavisomatidae Van Cleave, 1931

Cavisomidae [sic] Van Cleave, 1931: 357.

Cavisomatidae: Petrochenko 1956: 329; Kita & Kajihara 2025: 244.

Amended diagnosis. Trunk aspinose; proboscis cylindrical to claviform; proboscis receptacle double-walled; testes oval; cement glands four, tubular (Kita & Kajihara 2025: 244).

Composition. *Caballerorhynchus* Salgado-Maldonado, 1977, *Cavisoma* Van Cleave, 1931, *Femogibbosus* Paruchin, 1973, *Neorhadinorhynchus* Yamaguti, 1939, *Paracavisoma* Kritscher, 1957, and *Rhadinorhynchoides* Fukui & Morisita, 1937.

Remarks. The authorship of Cavisomatidae is often incorrectly attributed to Meyer (1932) (e.g., Amin 2013; Kita et al. 2024c; Ghanei-Motlagh et al. 2025), but the family name first appeared in Van Cleave (1931c), making this the correct authority.

Genus *Cavisoma* Van Cleave, 1931

***Cavisoma magnum* (Southwell, 1927)**

(Fig. 5)

Oligoterorhynchus magnus Southwell, 1927: 165, figs. 1–4 [off Negapatam (= Negappattinam, India)].

Cavisoma magnum: Van Cleave 1931: 356; Kita & Kajihara 2025: 244, fig. 2.

Type locality. Off Negapatam (= Negappattinam, India) (Southwell 1927).

Other localities. Off Al-Faw (Iraq) (Amin et al. 2018a); off New Caledonia (Foata et al. 2012); Red Sea (Paruchin 1976); off Yomitan (Okinawa, Japan) (Kita & Kajihara 2025); off Zamboanga (the Philippines) (Arthur et al. 1995).

Type host. *Serranus* sp. (Serranidae) (Southwell 1927).

Other hosts. *Acanthurus strigosus* [= currently *Ctenochaetus strigosus*] (Acanthuridae) (Southwell 1927); *Acanthurus* sp. (Acanthuridae) (Paruchin 1976); *Chanos chanos* (Chanidae) (Arthur et al. 1995; Amin et al. 2018b); *Mugil cephalus* (Mugilidae) (Amin et al. 2018b); *Pentapodus caninus* (Nemipteridae) (Kita & Kajihara 2025); *Siganus lineatus* (Siganidae) (Foata et al. 2012).

Material examined. One specimen (male), Invertebrate Collection of Hokkaido University Museum (ICHUM) 9053, off Yomitan, 11 May 2025, from the intestine of *Pentapodus caninus* (Kita & Kajihara 2025).

Description (after Kita & Kajihara 2025). *Male* (n = 1). Trunk aspinose, elongate, cylindrical, 745 width. Proboscis cylindrical, 1052×303 , covered with 8 hooks in 12 longitudinal rows: anterior 5 hooks well-curved, gradually larger toward basal proboscis, blade 66–86 (82.2); posterior 3 hooks less-curved, gradually smaller toward basal proboscis, blade 67–72 (65.5). Proboscis receptacle 2047×334 . Lemnisci unclear. Testes two, tandem, oval, attached to each other: anterior testis 521×192 ; posterior testis 423×186 . Cement glands 4, tubular, attached to posterior testis. Saeftigen's pouch well-developed.

Remarks. The single specimen in Kita & Kajihara (2025) agreed morphologically with previous descriptions of *Cavisoma magnum* (Arthur et al. 1995; Amin et al. 2018b), including proboscis shape, hook morphology, and cement gland

structure. This was the first record of the species from Japan and from a nemipterid host.

Family Echinorhynchidae Cobbold, 1879

Genus *Echinorhynchus* Zoega in Müller, 1776

***Echinorhynchus dissimilis* Yamaguti, 1939**

(Figs. 6A–D, 7A, D)

Echinorhynchus dissimilis Yamaguti, 1939: 319, figs. 3–4.

Type locality. Maisaka (Shizuoka, Japan) (Yamaguti 1939).

Other localities. Off Kesennuma (Miyagi, Japan) (Araki & Machida 1987); off Ibaraki (Japan) (this study); off Onahama (Fukushima, Japan) (Araki & Machida 1987); off Otsuchi (Iwate, Japan) (Araki & Machida 1987); off Samani (Hokkaido, Japan) (Araki & Machida, 1987); off Urakawa (Hokkaido, Japan) (Kita unpubl.).

Type host. *Lotella physics* (Moridae) (Yamaguti 1939).

Other hosts. *Gadus macrocephalus* (Gadidae) (Araki & Machida 1987); *Hexagrammos otakii* (Hexagrammidae) (Araki & Machida 1987); *Lophius litulon* (Lophiidae) (Araki & Machida 1987); *Physiculus japonicus* (Moridae) (Araki & Machida 1987; Kita unpubl.); *Sebastes oblongus* (Sebastidae) (Araki & Machida 1987); *Zeus faber* (Zeidae) (Kita unpubl.).

Materials examined. Fifteen specimens from the intestine of *Physiculus japonicus* and *Zeus faber* from off Urakawa and off Ibaraki; and 50 specimens of the deposited specimens from MPM (Tokyo, Japan) and NMNS (Tsukuba, Japan), with catalog numbers MPM 22063-SY 3403–3404; MPM 22424-SY 5233, NSMT-As-130a–

131a; NSMT-As-134; NSMT-As-174; NSMT-As-179a; NSMT-As-208; NSMT-As-1324b; NSMT-As-1540; NSMT-As-1556; NSMT-As-2136; NSMT-As-2145.

Description. *General* (n = 65). Trunk elongate, cylindrical, posterior end slightly sharpened. Proboscis subcylindrical, short, swollen in middle-ventral side, armed with 9–11 hooks in 22–30 rows. Proboscis hooks curved, slightly smaller at basal proboscis. Proboscis receptacle double-walled, elongate. Lemniscus elongate, same or shorter than proboscis receptacle. Cephalic ganglion positioned middle of receptacle.

Male (n = 23). Trunk 3820–10486 (7535) (n = 22) × 558–1281 (903). Proboscis 299–582 (517) (n = 13) × 213–470 (370). Proboscis receptacle 602–1417 (1078) × 164–445 (307). Lemniscus 514–1403 (1020) (n = 8) in length. Testes two, tandem. Anterior testis 543–1814 (1102) × 319–727 (540). Posterior testis 478–1599 (1043) (n = 22) × 296–701 (550) (n = 22). Cement glands six, oval, lined in moniliform or irregularly overlapped. Saeftigen pouch 384–1039 (721) in length. Copulatory bursa 281–519 (428) (n = 6) in diameter.

Female (n = 42). Trunk 8762–32668 (16882) (n = 39) × 595–1644 (1073). Proboscis 423–789 (586) (n = 34) × 241–580 (392). Proboscis receptacle 666–1866 (1133) × 119–492 (296). Lemniscus 839–1480 (1105) (n = 11) in length. Uterus 770–3161 (1709) (n = 32) × 45–202 (101) (n = 32). Eggs elongate, elliptical, 90–104 (96) (eggs n = 10) in length.

Remarks. The specimens of this study have *i*) an aspinose trunk and *ii*) six, oval, and moniliform-lined cement glands; thus, I could determine that they belong to the genus *Echinorhynchus* (cf. Petrochenko 1956). Compared to other congeners, the present specimens have unique characteristics for *E. dissimilis*: *i*) proboscis are subcylindrical, short, and swollen in the middle-ventral side; and *ii*) arrangement of

proboscis hooks is 9–11 hooks in 22–30 rows (Yamaguti 1939; Petrochenko 1956; Golvan 1969; Huffmann & Kliever 1977; Rodjuk 1986; Didenko 1992; Wayland et al. 1997; Wayland et al. 1999; Smales 2012; Sheema et al. 2017; Lei et al. 2020; Kita & Kajihara 2023).

***Echinorhynchus hexagrammi* Baeva, 1965**

(Fig. 8)

Echinorhynchus hexagrammi Baeva, 1965: 28, fig. 2; Kita & Kajihara 2021: 3, fig. 1.

Echinorhynchus salmonis: partim sensu Araki & Machida 1987: 3–4.

Type locality. Terpeniya Bay (Sakhalin, Russia) (Baeva 1965)

Other localities. Akkeshi Bay (Katahira & Nagasawa 2011; Kita & Kajihara 2021); off Samani (Araki & Machida 1987); off Kushiro (Araki & Machida 1987).

Type host. *Hexagrammos octogrammus* (Hexagrammidae) (Baeva 1965).

Other hosts. *Eleginus glacilis* (Gadidae) (Katahira & Nagasawa 2011); *Hemitripterus villosus* (Hemitriptoridae) (Araki & Machida 1987); *Hexagrammos stelleri* (Hexagrammidae) (Araki & Machida 1987); *Liparis* sp. (Kita & Kajihara 2021); *Podothecus sachi* (Agonidae) (Araki & Machida 1987); *Sebastes oblongus* (Sebastidae) (Araki & Machida 1987); *Verasper moseri* (Pleuronectidae) (Araki & Machida 1987).

Material examined. One male, ICHUM 6249, Akkeshi Bay (43°00'22.56"N, 144°48'47.16"E), 28 August 2020, from the intestine of *Liparis* sp.

Description (after Kita & Kajihara 2021). *Male* (n = 1). Trunk elongate, cylindrical, aspinose; maximum width at quarter length from the anterior end, 5310 × 530 (length × width). Proboscis cylindrical, 650 × 150. Proboscis hooks arranged in 15 longitudinal rows, each with 11–12 hooks (mostly 11); blade longer in anterior hooks; hook root more or less consistent in length throughout each row except for basalmost

two hooks; blade longer than root in every hook; basal-most two hooks thinner, less curved, and with smaller roots; Maximum hook blade 50, with root 42. Neck present, trapezoidal, short. Proboscis receptacle double-walled, 470×110 . Cerebral ganglion situated at middle of proboscis receptacle. Lemniscus approximately same length as proboscis receptacle, 450 in length. Testes oval, separated, tandem, situated in middle of trunk; anterior testis 850×270 ; posterior testis 550×260 . Cement glands 6, oval, arranged in tandem, $125\text{--}295 \times 150\text{--}200$. Copulatory bursa opening sub-terminally

Remarks. In the present material, the cement glands were arranged in tandem, the number of the longitudinal rows of the proboscis hooks was 15, the numbers of proboscis hooks in each row were 11–12, and the ratio of the length of the proboscis receptacle against the lemnisci was almost 1:1. Of the 53 known congeners in *Echinorhynchus*, the two species *E. hexagrammi* and *E. laurentianus* Ronald, 1957 conform to these characteristics (Baeva 1965; Ronald 1957). I identified my specimen as *Echinorhynchus hexagrammi* because the lengths of the proboscis hook roots were almost 42 μm (Kita & Kajihara 2021), which falls within the range of 35–45 μm so far reported for this species (Baeva 1965; Katahira & Nagasawa 2011), rather than 24–29 μm in *E. laurentianus*; the latter has so far been known from the Atlantic coast of Canada (Ronald 1957).

***Echinorhynchus lotellae* Yamaguti, 1939**

(Figs. 6E–H, 7B, C)

Echinorhynchus lotellae Yamaguti, 1939: 318, figs. 1–2; Araki & Machida 1987: 3.

Echinorhynchus sebastolobi Kovalenko, 1986: 157, fig. 1.

Type locality. Maisaka (Shizuoka, Japan) (Yamaguti 1939).

Other localities. Off Kesennuma (Miyagi, Japan) (Araki & Machida 1987); off Ibaraki (Japan) (Kita unpubl.); off Onahama (Fukushima, Japan) (Araki & Machida 1987); off Otsuchi (Iwate, Japan) (Araki & Machida 1987).

Type host. *Lotella physics* (Moridae) (Yamaguti 1939).

Other hosts. *Crystallias matsushimae* (Liparidae) (Kita unpubl.); *Liparis tessellatus* (Liparidae) (Araki & Machida 1987); *Lophius litulon* (Lophiidae) (Araki & Machida 1987); *Physiculus japonicus* (Moridae) (Araki & Machida 1987; Kita unpubl.); *Sebastolobus macrochir* (Sebastidae) (Araki & Machida 1987); *Verasper moseri* (Pleuronectidae) (Araki & Machida 1987); *Zeus faber* (Zeidae) (Kita unpubl.).

Materials examined. Two specimens from the intestine of *Zeus faber* from off Ibaraki; and 69 specimens of the deposited specimens from MPM and NMNS, with catalog numbers MPM 22062-SY 3402; MPM 22062-SY 3404; MPM 22426-SY 5235, NSMT-As-136c; NSMT-As-164; NSMT-As-203; NSMT-As-1324c; NSMT-As-1545; NSMT-As-1707.

Description. *General* (n = 71). Trunk elongate, cylindrical. Proboscis cylindrical, elongate, armed with 13–16 hooks in 14–18 rows. Proboscis receptacle double-walled, elongate. Lemniscus almost same or shorter than proboscis receptacle. Cephalic ganglion positioned middle of receptacle.

Male (n = 35). Trunk 5053–18662 (9225) × 565–1187 (835). Proboscis 614–983 (849) (n = 15) × 139–229 (170) (n = 33). Proboscis receptacle 701–1739 (1220) × 177–369 (237). Lemniscus 815–1879 (1172) in length (n = 25). Testes two, tandem. Anterior testis 641–1910 (1061) × 345–712 (503). Posterior testis 670–1845 (984) × 363–786 (491). Cement glands six, oval, lined in moniliform. Saeftigen's pouch 591–1591 (823). Copulatory bursa 372–524 (465) (n = 6) in diameter.

Female (n = 36). Trunk 6857–28445 (13776) (n = 34) × 429–2276 (982). Proboscis 558–1075 (805) (n = 21) × 121–253 (194) (n = 35). Proboscis receptacle 717–1925 (1283) (n = 35) × 158–422 (250) (n = 35). Lemniscus 858–1729 (1326) (n = 16) in length. Uterus 534–1539 (865) (n = 31) × 23–133 (66) (n = 31). Eggs elliptical, 46–57 (53) (eggs n = 10) in length.

Remarks. Unspined trunk and six, oval, and moniliform-lined cement glands in the present specimens indicate its affiliation with *Echinorhynchus* (cf. Petrochenko 1956). *Echinorhynchus lotellae* can be distinguished from species other than *E. sebastolobi* Kovalenko, 1986, which share the same characteristics, by the presence of 13–16 hooks on the proboscis in 14–18 rows and the elongated proboscis (Yamaguti 1939; Petrochenko 1956; Golvan 1969; Huffmann & Kliever 1977; Kovalenko 1986; Rodjuk 1986; Zdzitowiecki & Valtonen 1987; Didenko 1992; Wayland et al. 1997; Wayland et al. 1999; Smales 2012; Sheema et al. 2017; Lei et al. 2020; Kita & Kajihara 2023). Araki & Machida (1987) considered *E. sebastolobi* as a junior synonym of *E. lotellae* due to its morphological differences might not be in the range of the interspecific level (cf. Kovalenko 1986). Although currently *E. sebastolobi* is considered a valid taxon in some research or databases (e.g., Amin 2013; Gibson & Wayland 2025b), in this study, I followed Araki & Machida's (1987) consideration.

***Echinorhynchus sasakiae* Kita & Kajihara, 2023**

(Fig. 9)

Echinorhynchus sasakiae Kita & Kajihara, 2023: 737, fig. 1.

Type locality. Akkeshi Bay (Hokkaido, Japan) (Kita & Kajihara 2023).

Other locality. Off Nemuro (Hokkaido, Japan) (Kita & Kajihara 2023).

Type host. *Hexagrammos lagocephalus* (Hexagrammidae) (Kita & Kajihara 2023).

Materials examined. A total of 15 specimens: ICHUM 8526, holotype, male; ICHUM 8527, allotype, female; ICHUM 8528–8540, paratypes, ten males and six females (ICHUM 8526, 8528, 8529, 8535–8538, one male; ICHUM 8527, 8533, 8534, 8539, 8540, one female; ICHUM 8530 and 8532, one male and one female; ICHUM 8531, two males).

Description (after Kita & Kajihara 2023). *General* (n = 18). Trunk cross-sectionally elliptical, elongate, unspined. Fully everted proboscis subcylindrical, strongly swollen in middle, oval to spherical in lateral view, with 14–15 rows of hooks and 7–10 hooks per row. Anterior 3–5 hooks short, strongly curved, with large root; posterior 4–5 hooks long, weakly curved, with very short root. Neck short. Proboscis receptacle double-walled, wide. Cephalic ganglion at middle of proboscis receptacle. Lemniscus length almost same or slightly longer than proboscis receptacle.

Male (n = 11). Trunk 11.1–32.9 (25.1) (mm) × 511.8–1638.0 (1036.2). Neck short, trapezoidal, 111.1–193.3 (166.4). Proboscis subcylindrical, strongly swollen in middle, oval to spherical in lateral view, 1189.7–1889.3 (1425.0) × 794.3–1095.8 (961.1). Proboscis hooks different in shape between anterior and posterior side; anterior 3–5 hooks short, strongly curved, hook blade 35.3–51.1 (42.3) in length, with large root; posterior 4–5 hooks long, weakly curved, hook blade 57.1–84.0 (64.8), with very short root. Proboscis receptacle double-walled, 2341.4–3489.4 (2935.1) × 746.6–1239.4 (957.3). Lemniscus length almost same or slightly longer than proboscis receptacle, 2395.2–3735.2 (3106.4). Testes two, oval, tandem, apart from each other, positioned at middle of trunk, not attached to proboscis receptacle or cement glands. Anterior testis

2390.6–3776.1 (3086.6) × 1100.5–1614.2 (1368.7). Posterior testis 2319.4–3360.4 (2886.3) × 1117.3–1591.6 (1299.8). Cement glands six, oval, moniliform, 731.36–1139.72 (923.3) × 381.99 × 624.99 (502.9). Saefftigen's pouch 1967.4–2824.6 (2273.0) in length (n = 5). Genital pore opening terminally. Copulatory bursa 1342.7–2199.0 (1658.5) in width.

Female (n = 7). Trunk 18.9–73.44 (31.2) (mm) × 443.6–1214.1 (1041.3). Neck short, trapezoidal, 137.7–289.6 (215.1). Proboscis subcylindrical, strongly swollen in middle, oval to spherical in lateral view, 1371.9–2036.2 (1615.0) × 1016.2–1360.8 (1137.0). Proboscis hooks different in shape between anterior and posterior ones: anterior 3–5 hooks short, strongly curved, hook blade 32.3–72.5 (53.0) in length, with large root; posterior 4–5 hooks long, weakly curved, hook blade 57.1–122.4 (93.9), with very short root. Proboscis receptacle double-walled, 3442.1–4292.7 (3769.9) × 1135.5–1567.1 (1280.6) (n = 3). Uterine bell 690.8 in length (n = 1). Uterus 2872.7 long (n = 1). Eggs elliptical, elongate, 125.2–158.5 (141.7) (eggs n = 10). Genital pore opening terminally.

Remarks. The present acanthocephalans show the following three morphological characteristics: *i*) cement glands six in number and moniliform in shape; *ii*) trunk spines absent; and *iii*) proboscis hooks dorsoventrally symmetrical. These characteristics undoubtedly fit the diagnosis for *Echinorhynchus* (Petrochenko 1956; Golvan 1969; Amin 1987). One of the most striking features of *E. sasakiae* is the shape of the proboscis. Among the 53 species currently recognized as valid in *Echinorhynchus*, the proboscis is similarly shaped only in *E. dissimilis* and *E. veli* George & Nadakal 1978, whereas it is cylindrical and elongated in all the other congeners (Fujita 1921; Yamaguti 1939; Petrochenko 1956; Golvan 1969; Huffmann &

Kliever 1977; Kovalenko 1986; Rodjuk 1986; Didenko 1992; Wayland et al. 1997; Wayland et al. 1999; Smales 2012; Sheema et al. 2017; Lei et al. 2020). From these two species, however, *E. sasakiae* can be distinguished by the arrangement of proboscis hooks (14–15 rows of hooks and 7–10 hooks per row in *E. sasakiae*; 27 rows of hooks and 10–11 hooks per row in *E. dissimilis*; 12–15 rows of hooks and 10–14 hooks per row in *E. veli*) and the shape of the hook (anteriorly short and curved, posteriorly long and weakly curved in *E. sasakiae*; each hook being the same in shape, curved in all hooks in *E. dissimilis* and *E. veli*) (Yamaguti 1939, 1963; Petrochenko 1956; Golvan 1969; Araki & Machida 1987; Sheema et al. 2017) (Table 5). *Echinorhynchus sasakiae* can also be distinguished from all eight species previously known from Japanese waters by the proboscis shape, the number of hook rows, the number of hooks per row, and the shape of the hooks (Table 5).

Family Filisomatidae Van Cleave, 1928

Filisomatidae [sic] Van Cleave, 1928: 148.

Filisomatidae: Kita & Kajihara 2025: 245.

Amended diagnosis. Trunk aspinose, elongate, slender; proboscis elongate, cylindrical; proboscis receptacle double-walled, long; lemniscus broad; testes elliptical, separated; cement glands four, filiform, very long (Kita & Kajihara 2025: 245).

Composition. *Filisoma* Van Cleave, 1928.

Remarks. Originally erected by Van Cleave (1928) for *Filisoma*, this family was effectively synonymized with Rhadinorhynchidae Lühe, 1912 by Meyer (1932), who included *Filisoma* in Rhadinorhynchidae. *Filisoma* was subsequently moved to Gorgorhynchidae Van Cleave & Lincicome, 1940 by Van Cleave & Lincicome (1940), while this family-group taxon should have been referred to as Filisomatidae according

to the Principle of Priority. *Filisoma* was later placed in Cavisomatidae (Petrochenko 1956; Yamaguti 1963; Amin 2013); again, based on the Principle of Priority, the name Filisomatidae should have been applied to this family-group taxon. Due to *Filisoma*'s distinct morphology and phylogenetic position (Kita & Kajihara 2025; see Chapter III), I consider it justifiable to reinstate Filisomatidae as a separate family. Whether the original spelling Filisomidae is correct or incorrect seems to be undecided under the current 4th edition of the International Code of Zoological Nomenclature (hereafter “the Code”) [International Commission on Zoological Nomenclature (ICZN) 1999].

Filisomidae would appear to be an incorrect original spelling because it violates Article 29.3 of the Code: the ending of its type genus *Filisoma* derives from the New Latin, itself from Ancient Greek σῶμα (*sōma*, “body”), whose genitive singular is σώματος (*sōmatos*, Ancient Greek) or somatis in New Latin. In either case, the stem should be Filisomat-, in accordance with the provisions of this Article. However, Filisomidae must simultaneously be regarded as a correct original spelling because it does not fall under any provision of Article 32.5.3 of the Code. In the 3rd edition of the Code (ICZN 1985), Article 32(c)—the equivalent of Article 32.5 of the 4th edition— included a provision declaring a name to be an incorrect original spelling if “(i) it contravenes a provision of Articles 27 to 31”. No such provision was carried over into the 4th edition, likely due to a simple oversight (L. Raty, personal communication). In the upcoming 5th edition, a subordinate Article will be added—provisionally worded as “32.5.3.5. is based on an incorrectly determined stem of the generic name [Art. 29.3]”—as an addition to the current Article 32.5.3 (“A family-group name is an incorrect original spelling and must be corrected if it...”) (F. Welter-Schultes, personal communication). In this thesis, I adopt Filisomatidae as an “emendation” attributed to the original author of Filisomidae,

although this emendation must be regarded as “unjustified” under Article 33.2.3 of the Code. I strongly recommend that subsequent authors refer to this family group name as Filisomatidae, attributed to Van Cleave, 1928, so that this emendation may be treated as “justified” in the future under Article 33.2.3.1 of the Code, until the 5th edition of the Code is published.

Family Leptorhynchoididae Witenberg, 1932

Leptorhynchoididae Witenberg, 1932: 262; Kita et al. 2023: 4.

Illiosentidae Golvan, 1960: 141.

Rhadinorhynchidae: *partim sensu* Amin 1985: 49.

Echinorhynchidae: *partim sensu* Yamaguti 1959: 319.

Amended diagnosis. Palaeacanthocephala, Echinorhynchida; Trunk cylindrical, elongate; proboscis cylindrical; neck short; proboscis receptacle double-walled; testes two, tandem; cement glands eight, elongate, claviform to pyriform (Kita et al. 2023).

Composition. *Brentisentis* Leotta, Schmidt & Kuntz, 1982; *Dentitruncus* Sinzar, 1955; *Dollfusentis* Golvan, 1969; *Goacanthus* Gupta & Jain, 1980; *Illiosentis* Van Cleave & Lincicome, 1939; *Indorhynchus* Golvan, 1969; *Koronacantha* Monks & Pérez-Ponce de León, 1996; *Leptorhynchoides* Kostylev, 1924 (type genus); *Metacanthocephalus* Yamaguti, 1959; *Neotegorhynchus* Lisitsyna, Xi, Orosová, Barčák, & Oros, 2022; *Paradentitruncus* Moravec & Sey, 1989; *Pseudoleptorhynchoides* Salgado-Maldonado, 1976; *Pseudorhadinorhynchus* Achmerov & Dombrovskaja-Achmerova, 1941; *Tegorhynchus* Van Cleave, 1921; *Telosentis* Van Cleave, 1923.

Remarks. Kita et al. (2023) showed that *Metacanthocephalus ovicephalus* (Zhukov, 1960) was more closely related to nine species in eight genera (*Brentisentis*

yangtzensis Yu & Wu, 1989, *Dentitruncus truttae* Sinzar, 1955, *Dollfusentis bravoae* Salgado-Maldonado, 1976, *Koronacantha mexicana* Monks & Pérez-Ponce de León, 1996, *Koronacantha pectinaria* (Van Cleave, 1940), *Leptorhynchoides thecatus* (Linton, 1891), *Neotegorhynchus cyprini* (Yin in Zhang, 1961), *Pseudoleptorhynchoides lamothei* Salgado-Maldonado, 1976, and *Illiosentis* sp.) than to any other species included in the phylogenetic analysis. Of these nine, five (*K. mexicana*, *K. pectinaria*, *L. thecatus*, *P. lamothei*, and *Illiosentis* sp.) exclusively formed a clade and were called Illiosentidae in García-Varela & González-Oliver (2008); the remaining four (*B. yangtzensis*, *De. truttae*, *Do. bravoae*, *N. cyprini*), as well as *M. ovicephalus*, were not employed in García-Varela & González-Oliver (2008). Citing Monks & Pulido-Flores's (2002) taxonomic redescription of *Illiosentis heteracanthus* Cable & Linderorth, 1963, García-Varela & González-Oliver (2008) stated that the four genera *Koronacantha*, *Leptorhynchoides*, *Pseudoleptorhynchoides*, and *Illiosentis* would share certain morphological features such as a cylindrical and elongated proboscis; numerous longitudinal rows of hooks; a double-walled proboscis receptacle, having hypodermic nuclei and longer or shorter tubular lemnisci than proboscis receptacle; and, in males, eight cement glands. Although neither Monks & Pulido-Flores (2002) nor García-Varela & González-Oliver (2008) explicitly diagnosed Illiosentidae by these characters, the latter are essentially the same as what Kita et al. (2023) utilized to circumscribe Leptorhynchoididae. In addition to the nine genera included in Kita et al.'s (2023) analysis (*Brentisentis*, *Dentitruncus*, *Dollfusentis*, *Koronacantha*, *Leptorhynchoides*, *Metacanthocephalus*, *Neotegorhynchus*, *Pseudoleptorhynchoides*, and *Illiosentis*), another five (*Goacanthus*, *Indorhynchus*, *Paradentitruncus*, *Pseudorhadinorhynchus*, and *Telosentis*) have been reported to match this diagnosis (Yamaguti 1959; Golvan

1969; Monks & Pulido-Flores 2002; Achmerov & Dombrovskaja-Achmerova 1941; Gupta & Jain 1980; Moravec & Sey 1989; Van Cleave 1923; Van Cleave & Lincicome 1939). The Leptorhynchoididae in the sense of Kita et al. (2023) would be equivalent to not only Illiosentidae sensu García-Varela & González-Oliver (2008) but also a union of the two families Illiosentidae Golvan, 1960, and Leptorhynchoididae Witenberg, 1932, both in the sense of Golvan (1969). Golvan (1969) differentiated the two families by the presence (in Illiosentidae) or absence (in Leptorhynchoididae) of trunk spines, while regarding these two as sharing the same characters that are used to circumscribe Leptorhynchoididae in the sense of Kita et al. (2023). It means that, so far as this clade is regarded as a family-level taxon, the presence/absence of trunk spines should be utilized as taxonomic characters at the ranks below family.

Genus *Indorhynchus* Golvan, 1969

Rhadinorhynchus: *partim sensu* Tripathi (1956).

Indorhynchus Golvan, 1969: 40; Kita et al. 2024b: 8.

Amended diagnosis. Leptorhynchoididae; proboscis claviform or cylindrical; number of proboscis hook rows greater than that of hooks per row; proboscis receptacle double-walled, with ganglion not precise in position; trunk long, cylindrical with 9–12 circular rows of spines; lemnisci longer than receptacle extending up to anterior testis; testes located about midtrunk; cement glands eight, pyriform or cylindrical; Saeftigen's pouch large; eggs with three membranes, with or without polar prolongations of middle shell (Kita et al. 2024b).

Remarks. The two species having eight cement glands and formerly belonging to *Metarhadinorhynchus* Yamaguti, 1959—*M. echeneisi* Gupta & Sinha, 1991 and *M. thapari* Gupta & Gupta, 1975—can no longer be placed in that genus after my finding

that *M. lateolabracis* has six cement glands (Kita et al. 2024b; see below). These two Indian species show at least six morphological characteristics that are consistent with those in the type species of *Indorhynchus*, viz. *I. indicus* (Tripathi, 1956): *i*) the proboscis is cylindrical, not narrowed; *ii*) the number of proboscis hook rows is greater than that of hooks per row; *iii*) a cylindrical and elongate trunk covered anteriorly by spines; *iv*) a bulbous swelling behind the spinose region of the trunk is absent; *v*) eight claviform cement glands; and *vi*) marine fishes as definitive host (Golvan 1969; Gupta & Gupta 1975; Gupta & Sinha 1991). In terms of the number and arrangement of the proboscis hooks, *Indorhynchus* was diagnosed to have 12–14 hooks in 18–20 longitudinal rows by Naidu (2012). I modified this feature in a way that species in which the number of proboscis hook rows is greater than that of hooks per row can be placed in this genus, no matter how many hooks and rows are present, so that the two Indian species can be placed in *Indorhynchus*. Of the two, *I. thapari* parasitizes ariid fish (Table 6), showing the same host range as that of *I. indicus*. I consider the nominal species *Rhadinorhynchus arii* Wang, 1966 as belonging to *Indorhynchus* in the sense of this thesis and distinct from all other species (Table 6). My view is thus different from that of Amin (2013), who regarded it as synonymous with *Rhadinorhynchus cyprini* and belonging to the genus *Metarhadinorhynchus*. When establishing *Neotegorhynchus*, Lisitsyna et al. (2022) accepted Amin's (2013) concept of *Metarhadinorhynchus cyprini* and transferred the latter to the new genus, distinguishing it from *Indorhynchus* by the proboscis length and armature. In terms of the number of proboscis hook rows, Lisitsyna et al. (2022) regarded it as 12–14 in *Neotegorhynchus* versus 18–22 in *Indorhynchus*. In *R. arii*, on the other hand, the proboscis has 21–22 hooks in 24 rows (Wang 1966) (Table 6). The species thus does not match *Neotegorhynchus* in the sense

of Lisitsyna et al. (2022), but now can be placed in *Indorhynchus* (as modified above). To make the distinction between the two genera, *Indorhynchus* and *Neotegorhynchus*, more explicit, I also modify the diagnosis of the latter (see below). *Indorhynchus arii* shows a similar host range (ariid fishes) to those in other *Indorhynchus* species, an ecological feature that may support the generic affiliation of the species.

Genus *Metacanthocephalus* Yamaguti, 1959

***Metacanthocephalus ovicephalus* (Zhukov, 1960)**

(Figs. 10, 11)

Leptorhynchoides ovicephalus Zhukov, 1960: 90, fig. 67.

Metacanthocephalus ovicephalus: Golvan 1969: 55, fig. 33; Kita et al. 2023: 4, figs. 2, 3.

Type locality. Off Shikotan Island (Hokkaido, Japan) (Zhukov 1960).

Other localities. Iwanai Port (Hokkaido, Japan) (Kita et al. 2023); off Rausu (Hokkaido, Japan) (Kita et al. 2023).

Type host. *Pseudopleuronectes obscurus* (Pleuronectidae) (Zhukov 1960; Kita et al. 2023).

Other hosts. *Pseudopleuronectes schrenki* (Pleuronectidae) (Kita et al. 2023);
Pseudopleuronectes herzensteini (Pleuronectidae) (Araki & Machida 1987);
Pseudopleuronectes yokohamae (Pleuronectidae) (Araki & Machida 1987);
Acantholumpenus mackayi (Lumpenidae) (Araki & Machida 1987).

Materials examined. Seven specimens: ICHUM 8408, female, from the intestine of *Pseudopleuronectes schrenki*, whole mount on a glass slide, stained with Heidenhain's iron hematoxylin, collected by Y. Kita, April 10, 2021, Iwanai, Hokkaido, Japan; ICHUM 8409, 8410, male, other information same as ICHUM 8408; ICHUM 8411, female, from the intestine of *Pseudopleuronectes obscurus*, whole mount on a

glass slide, stained with alum-carmin, collected by M. Sasaki, June 7, 2018, Rausu, Hokkaido, Japan; ICHUM 8412, the same information as ICHUM 8411; ICHUM 8413, male, other information same as ICHUM 8411; ICHUM 8414, the same information as ICHUM 8413.

Description (after Kita et al. 2023). *General* (n = 7). Trunk cylindrical, anterior one-fifth widest. Proboscis cylindrical, slightly oval, covered with heavy cuticular layer, armed with 18–19 longitudinal rows of hooks and 8–9 hooks per row. Hooks gradually smaller toward posterior end of proboscis. Hook armature similar in both sexes. Neck short, smooth. Trunk spine absent. Hypodermal nuclei not confirmed. Proboscis receptacle elongate, double-walled.

Male (n = 4, otherwise noted). Trunk cylindrical, elongate, anterior one-fifth widest, $8464.7\text{--}10,891.5 \times 1284.7\text{--}1529.4$. Proboscis cylindrical, slightly oval, armed with hooks, $520.1\text{--}551.8 \times 241.7\text{--}319.7$ (n = 3). Proboscis receptacle elongate, double-walled, $770.7\text{--}999.9 \times 192.2\text{--}236.3$. Testes oval, tandem. Anterior testis $704.0\text{--}946.3 \times 481.3\text{--}720.3$. Posterior testis $615.4\text{--}788.7 \times 458.5\text{--}658.7$. Cement glands elongate, claviform, eight. Seminal vesicle width $260.4\text{--}438.9$ (n = 2). Saeftigen's pouch length $570.5\text{--}790.9$. Copulatory bursa width $744.4\text{--}963.3$ (n = 3).

Female (n = 3, otherwise noted). Trunk cylindrical, elongate, anterior one-fifth widest, $11,387.9\text{--}15,119.2 \times 1546.0\text{--}2111.6$. Proboscis cylindrical, slightly oval, armed with hooks $556.8\text{--}568.1 \times 289.5\text{--}332.6$ (n = 2). Proboscis receptacle elongate, double-walled, $1050.1\text{--}1462.0 \times 146.3\text{--}286.2$ (n = 2). Uterine bell length 207.2 (n = 1). Uterus 551.7×65.1 (n = 1). Vagina with single sphincter. Eggs elongate, elliptical, length $40.2\text{--}52.6$ (eggs n = 10).

Remarks. My specimens were morphologically identifiable as *Metacanthocephalus* Yamaguti, 1959 by having a trunk and proboscis that are both cylindrical in shape; eight, elongate and claviform cement glands in males; and no trunk spines; these characteristics conform to the generic diagnosis provided by Yamaguti (1959). Furthermore, based on the number of longitudinal hook rows (18–19) and hooks per row (8–9) in my material, it was identified as *M. ovicephalus* (cf. Zhukov 1960), in comparison with the other five congeners (numerals in parentheses indicating the number of longitudinal hook rows and hooks per row, respectively): *M. campbelli* (13–15, 8–10) (Leiper & Atkinson 1914); *M. dalmori* (14, 5) (Zdzitowiecki 1983); *M. johnstoni* (14–16, 6–7) (Zdzitowiecki 1983); *M. rennicki* (12, 5–7) (Leiper & Atkinson 1914); and *M. pleuronichthydis* (21–26, 7–10) (Yamaguti 1959). Zhukov (1960, p. 91, fig. 67b) described and illustrated branched hypodermal nuclei, which were not confirmed in my material; this would probably be due to my staining technique. My morphological examination revealed a single vaginal sphincter in *M. ovicephalus*, a character that was not mentioned in any previous literature (Zhukov 1960). By this character, as well as geographical distribution and host fish, the six congeners in *Metacanthocephalus* can be divided into two groups: i) *M. pleuronichthydis* and *M. ovicephalus*, possessing a single vaginal sphincter, distributed in and around Japanese waters, and mostly parasitizing flounders, and ii) *M. campbelli*, *M. dalmori*, *M. johnstoni*, and *M. rennicki*, possessing double vaginal sphincters, distributed in the Southern Ocean, and parasitizing icefish (Leiper & Atkinson 1914; Zdzitowiecki 1983). This suggests a potential division of *Metacanthocephalus* into two subgenera, or discrimination of the latter four Antarctic species into a new genus, which, however, is beyond the scope of the present study.

Genus *Neotegorhynchus* Lisitsyna, Xi, Orosová, Barčák, & Oros, 2022

Rhadinorhynchus: *partim sensu* Yin 1961, Wang 1966, Yin & Wu 1984.

Brentisentis: *partim sensu* Yu & Wu 1989.

Metarhadinorhynchus: *partim sensu* Wang 1986.

Neotegorhynchus Lisitsyna et al., 2022: 86.

Amended diagnosis. Proboscis long, narrowed, cylindrical, often curved ventrally; number of proboscis hook rows smaller than that of hooks per row; otherwise as in Lisitsyna et al. (2022).

Remarks. In terms of the proboscis armature, *Neotegorhynchus* was diagnosed by Lisitsyna et al. (2022) as having 19–23 hooks in 12–14 longitudinal rows. To make the distinction between this genus and *Indorhynchus* clearer, I propose a partial amendment of the diagnosis so that the number of proboscis hook rows must always be smaller than that of hooks per row, no matter how many hooks and rows exist (see also under *Indorhynchus* above). The nominal species *Rhadinorhynchus arii* and *Rhadinorhynchus cyprini* were placed in *Metarhadinorhynchus* by Wang (1986). After that, they were synonymized as *M. cyprini* by Amin (2013) before Lisitsyna et al. (2022) established *Neotegorhynchus* and transferred the species to it as *N. cyprini*. In this thesis, I dismiss this synonymization (see above under *Indorhynchus*) and retain *R. cyprini* alone in *Neotegorhynchus*. Lisitsyna et al. (2022: 86) ascribed the author of the type species *Rhadinorhynchus cyprini* as *Neotegorhynchus cyprini* to “Yin et Wu, 1984” when establishing *Neotegorhynchus*, while the species had been published in 1961 with Yin as the sole author for the name. The latter, appearing as “*Rhadinorhynchus cyprini* Yin”, was contained in a book titled ‘Zhong guo dan shui yu lei yang shi xue’ [Chinese Freshwater Fish Culture], edited by ‘Zhong guo dan shui yang yu jing yan zong jie wei

yuan hui' [Chinese Freshwater Fish Farming Experience Summary Committee] (Yin 1961). The book consists of 14 chapters; the original description and illustrations of *R. cyprini* Yin appear on pages 517–519 and are contained in chapter 12, titled 'Yu bing fang zhi' [Fish Disease Prevention and Control], authored by Da-Shu Ni, Wen-Ying Yin, De-Ming Wang, Qi-Liu Chen, and Hui-Sheng Wu. The editorial committee of the book consisted of 14 members and was headed by Yu-Fan Zhang (Yin 1961). Meanwhile, Yin & Wu (1984) described *Rhadinorhynchus cyprini* as a new species, with the indication "n. sp.", but without citing the 1961 book. From a morphological perspective, the two publications in 1961 and 1984 appear to be dealing with the same taxon (Table 7). As Article 50.1 of the International Code of Zoological Nomenclature (ICZN 1999) stipulates, the author of a name "is the person who first publishes it" [emphasis added] and if "a work is by more than one person [i.e., Zhang and the other 13 editorial members] but it is clear from the contents that only one of these [i.e., Yin] is responsible for the name or act, then that person is the author". In the case of *Rhadinorhynchus cyprini*, it is clearly Yin alone in 1961, instead of Yin & Wu in 1984. According to Recommendation 51E of the Code, it should be expressed as something like 'Yin in Zhang, 1961', 'Yin in Zhang, [and the other 13 editorial member names], 1961', or 'Yin in Zhong guo dan shui yang yu jing yan zong jie wei yuan hui, 1961'; for brevity, I prefer the first expression. Gibson in Gibson & Wayland (2024) regarded 'Rhadinorhynchus cyprini Yin & Wu, 1984' as being preoccupied by *R. cyprini* Yin, 1961 while noting that "I have not traced its original publication" [of the latter species]. My opinion is that there is no such nominal species as 'Rhadinorhynchus cyprini Yin & Wu, 1984' and there is thus no primary homonymy.

Genus *Pseudorhadinorhynchus* Achmerov & Dombrovskaja-Achmerova, 1941

***Pseudorhadinorhynchus leuciscus* (Krotov & Petrochenko in Petrochenko, 1956)**

(Fig. 12)

Hemirhadinorhynchus leuciscus Krotov & Petrochenko in Petrochenko, 1956: 367, figs. 164–167.

Pseudorhadinorhynchus leuciscus: Golvan 1969: 46.

Type locality. Southern Sakhalin (Krotov & Petrochenko in Petrochenko 1956).

Other localities. Off Esashi (Hokkaido, Japan) (Nagasawa & Takami 2017), off Hama-Atsuma (Hokkaido, Japan) (Nagasawa & Takami 2017), off Moheji (Hokkaido Japan) (Nagasawa & Takami 2017), off Otsuchi (Iwate, Japan) (Araki & Machida 1987), off Samani (Hokkaido, Japan) (Araki & Machida 1987), off Tomihama (Hokkaido, Japan) (Nagasawa & Takami, 2017), off Urakawa (Hokkaido, Japan) (this study), Hei River (Iwate, Japan) (Hashimoto 2000).

Type host. *Leuciscus waleckii* (Cyprinidae) (Krotov & Petrochenko in Petrochenko, 1956).

Other hosts. *Tribolodon hakonensis* (Cyprinidae) (Machida & Araki 1982; Araki & Machida 1987; Hashimoto 2000; Nagasawa & Takami, 2017); *Tribolodon brandtii* (Cyprinidae) (this study); *Spirincus lanceolatus* (Osmeridae) (Araki & Machida, 1987).

Material examined. ICHUM 8338, one immature female, off Urakawa, 1 August 2021, from the intestine of *Tribolodon brandtii*.

Description. *Female* (n = 1). Trunk cylindrical, elongate, 3916 × 879. Anterior side of trunk armed with spines. Proboscis cylindrical, elongate, 574 × 204. Proboscis hooks in 14 longitudinal rows of 10 each. Maximum hook blade 58 long and minimum hook blade 17 long. Proboscis receptacle elongate, 1071 × 104. Lemnisci very long and

narrow, unequal in length, 2863–3707. Uterine bell unclear. Uterus 524×104 . Vaginal sphincter 119 in diameter. Eggs absent.

Remarks. The shape of the proboscis and the armature of trunk spines determined this specimen to be a species of the genus *Pseudorhadinorhynchus*. Based on the number of hook rows and hooks per row, this species can be distinguished from other congeners of *Pseudorhadinorhynchus* except *P. samegaiensis* (Achmerov & Dombrovskaja-Achmerova 1941; Gupta & Gupta 1972; Nakajima & Egusa, 1975b; Machida & Araki 1982; Gupta & Fatma 1985; Gupta & Naqvi 1983; Moravec & Sey 1989; Kumar 1992; Popovic et al. 1999; Saxena 2003). *Pseudorhadinorhynchus samegaiensis* is a small species that matures with a body size of less than 4 mm. In contrast, *P. leuciscus* does not mature with a body size of less than 4 mm (Nakajima & Egusa 1975). In addition, *P. samegaiensis* exhibits a fusiform body, whereas *P. leuciscus* is cylindrical in body shape. Being about 4 mm in length, not matured, and cylindrical, my specimen does not fit the diagnosis of *P. samegaiensis* but rather can be identified as *P. leuciscus*.

Family Micracanthorhynchinidae Yamaguti, 1963

Micracanthorhynchinidae Yamaguti, 1963: 65.

Rhadinorhynchidae: *partim sensu* Amin 1985: 49.

Amended diagnosis. Body size small. Trunk cylindrical, fusiform to claviform. Trunk spines present, distributed evenly or only anteriorly. Proboscis claviform or fusiform, cylindrical. Proboscis hooks larger in anterior portion. Cephalic ganglion positioned middle to basal of receptacle. Cement glands four to six (occasionally), fusiform to claviform (Kita et al. 2024c: 3).

Composition. *Miracanthorhynchina* Strand, 1936 (type genus);

Pseudocavisoma Golvan & Houin, 1964.

Remarks. Based on the molecular phylogenetic analysis, Kita et al. (2024c) modified Yamaguti's (1963) original diagnosis for Miracanthorhynchinae so that *Pseudocavisoma* could be placed in it.

Genus *Miracanthorhynchina* Strand, 1936

***Miracanthorhynchina segmentata* (Yamaguti, 1959)**

(Fig. 13)

Allorhadinorhynchus segmentatum [sic] Yamaguti, 1959: 32, figs. 11–13.

Miracanthorhynchina segmentata: Araki & Machida 1987: 8, figs. 8–10.

Type host. *Hyporhamphus sajori* (Hemirhamphidae) (Araki & Machida 1987; Yamaguti 1959; Kita unpubl.).

Type locality. Seto Inland Sea (Yamaguti 1959).

Other localities. Off Otsuchi (Iwate, Japan) (Araki & Machida 1987); off Hama-Saroma (Hokkaido, Japan) (Kita unpubl.).

Materials examined. Eleven males and six females (YK's private collection), 21 June 2025, from the intestine of *Hyporhamphus sajori*.

Description. *General* (n = 17). Trunk cylindrical, fusiform. Body wall with pseudosegmentation, covered with aligned tiny spines anteriorly. Proboscis claviform, armed with 10–12 hooks in 12 rows: anterior 4–5 hooks long, curved; basal 5–7 hooks short, curved. Proboscis receptacle double-walled. Cerebral ganglion positioned middle of receptacle. Lemniscus longer than receptacle.

Male (n = 11). Trunk cylindrical, fusiform, 3798–5782 (4786) × 812–1078 (947). Proboscis claviform, 410–609 (522) × 134–211 (166). Largest proboscis hook

blade 58–67 (62) in length (hooks $n = 10$). Proboscis receptacle double-walled, 603–1014 (848) $\times$ 207–293 (258). Lemniscus longer than receptacle, 610–1423 (962) in length. Anterior testis 918–1343 (1093) $\times$ 528–758 (616). Posterior testis 677–1051 (916) $\times$ 511–756 (662). Cement glands four, claviform, clustered. Saeftigen's pouch 769–955 (849) in length. Copulatory bursa opening subterminally, 369–769 (556) in diameter. Muscular bursal cap present posterior end.

Female ($n = 6$). Trunk cylindrical, elongate, 5795–7945 (6714) $\times$ 1095–1498 (1277). Proboscis claviform, 485–782 (598) $\times$ 193–232 (215). Proboscis receptacle double-walled, 843–1014 (927) $\times$ 156–372 (272). Lemniscus longer than receptacle, 1153–1355 in length. Uterus 446–484 (465) in length ($n = 3$). Eggs elliptical, with polar prolongation, 44–57 (50) in length.

Remarks. Yamaguti (1959) originally described this species as *Allorhadinorhynchus segmentatum*, with the establishment of the genus *Allorhadinorhynchus*. In the literature, the number of cement glands is stated as two. However, in Araki & Machida (1987), the authors re-examined the type materials of this species, and they found that the true number of cement glands was four, not two (Table 8). Due to this and other morphological similarities, they suggested the new combination with the genus *Micracanthorhynchina*. In this study, I did not observe the type materials and the specimens used in Araki & Machida (1987), but the obtained specimens also showed four cement glands. Thus, I obeyed the taxonomic revision provided by Araki & Machida (1987) in this study. From the other congeners, *M. segmentata* can be distinguished by *i*) the arrangement of proboscis hooks and *ii*) the number of cement glands, other than *M. hemirhamphi* (Table 8). *M. segmentata* and *M. hemirhamphi* can be distinguished by the length of the largest hook blade (cf. Araki &

Machida 1987). In this study, I could not observe the hook blade length of females due to their condition, whereas the range of hook blade length of males resembled that of *M. segmentata* (58–79), not of *M. hemirhamphi* (90) (cf. Araki & Machida 1987; Baylis 1944).

Genus *Pseudocavisoma* Golvan & Houin, 1964

***Pseudocavisoma setoense* Kita, Nitta, & Kajihara, 2024**

(Figs. 14, 15, 16C)

Pseudocavisoma setoense Kita et al., 2024c: 73, figs. 1–2.

Type locality. Off Ihota (Yamaguchi, Japan) (Kita et al. 2024c).

Type host. *Chromis notata* (Pomacentridae) (Kita et al. 2024c).

Materials examined. In total, 29 females and 30 females on 23 glass slides; and two specimens (sex unknown) for SEM observation. Holotype, one of five males mounted on a glass slide, together registered as ICHUM 8909, 9 August 2016.

Paratypes, 58 specimens on 23 glass slides: ICHUM 8901, two males, one female; ICHUM 8903, one male; ICHUM 8904, one male, one female; ICHUM 8905, two males; ICHUM 8906, two males; ICHUM 8907, one male, one female; ICHUM 8908, one male, two females; ICHUM 8909, four males; ICHUM 8910, two males, three females; ICHUM 8911, one male, one female; ICHUM 8912, one male; ICHUM 8913, two males; ICHUM 8914, four females; ICHUM 8915 two females; ICHUM 8916, eight females; ICHUM 8917, one female; ICHUM 8918, two females; ICHUM 8919, one male; ICHUM 8920, three males; ICHUM 8921, two males; ICHUM 8922, one male, one female; ICHUM 8923, one male, one female. ICHUM 8901–8913, 9 August 2016; ICHUM 8914–8923, 25 August 2017.

Description (after Kita et al. 2024c). *General* (n = 20). Body size small.

Trunk elongate, cylindrical, covered with tiny spines anteriorly. Trunk spines 2–3 (2) in length (spines n = 10). Proboscis cylindrical, fusiform, narrower than trunk width. Proboscis hooks 6–7 in 14–15 longitudinal rows. Anterior 3 hooks large, strongly curved. Posterior 3–4 hooks small, less curved. Hook size reduced toward posterior, not gradually. Neck significant, trapezoidal. Proboscis receptacle elongate, double-walled. Cephalic ganglion positioned mid-posterior region of receptacle. Lemnisci elongate. Genital pore opening subterminally.

Male (n = 10, otherwise noted). Trunk elongate, cylindrical, covered with tiny spines anteriorly, 2678–7303 (5500) × 319–739 (586). Proboscis cylindrical, fusiform, 183–275 (220) × 110–143 (128). Proboscis receptacle elongate, double-walled, 339–797 (606) × 101–214 (169). Lemnisci elongate, 1224–1660 (1471) (n = 9) in length. Testes two, tandem, oval, attached to each other. Anterior testis 290–1325 (873) × 184–526 (425). Posterior testis 301–1286 (864) × 182–531 (403). Cement glands four, claviform, clustered. Saeffigen's pouch elongate, 373–1349 (914). Copulatory bursa opening subterminally, 384–525 (473) (n = 6) in width.

Female (n = 10). Trunk elongate, cylindrical, covered with tiny spines anteriorly, 4039–9869 (7372) × 415–865 (632). Proboscis cylindrical, fusiform, 180–256 (227) × 105–152 (136). Proboscis receptacle elongate, double-walled, 458–865 (666) × 109–183 (150). Lemnisci elongate, 859–1734 (1255) (n = 6) in length. Uterus 639–1413 (960) in length (n = 8). Eggs elliptical, 49–58 (53) in length (eggs n = 10).

Remarks. This species can be distinguished from *Pseudocavisoma chromitidis* (Cable & Quick, 1954), the only member of this genus other than *P. setoense* (Cable & Quick 1954), by the trunk spines in its arrangement (present only anteriorly in *P.*

setoense vs. evenly distributed in *P. chromitidis*) and size (2–3 in *P. setoense* vs. 8–10 μm in *P. chromitidis*).

***Pseudocavisoma chromitidis* (Cable & Quick, 1954)**

(Fig. 16A, B)

Cavisoma chromitidis Cable & Quick, 1954: 399.

Rhadinorhynchoides chromitidis: Yamaguti 1963: 54.

Pseudocavisoma chromitidis: Golvan & Houin 1964: 573; Kita et al. 2024c: 7, fig. 3A, B.

?*Rhadinorhynchoides chromitidis*: Gupta & Lata 1967: 338; Bhattacharya 2007: 146.

?*Pseudocavisoma chromatidis* [sic]: Naidu 2012: 109.

Type locality. Off Puerto Rico (Cable & Quick 1954).

Type host. *Chromis marginata* [currently *Azurina multilineata*]

(Pomacentridae) (Cable & Quick, 1954).

Materials examined. USNM 1348243 (deposited in the United States National Museum of Natural History, USA), syntypes of *Cavisoma chromitidis*, five female individuals on a single slide.

Description (after Kita et al. 2024c). *Female* (n = 5). Body size small. Trunk elongate, cylindrical, entirely and evenly covered with tiny spines. Trunk spines 8–10 in length (spines n = 5), 4911–6281 (5656) $\times$ 790–984 (862). Proboscis cylindrical, fusiform, narrower than trunk width, 250–355 (285) $\times$ 105–152 (136). Proboscis hooks 8 in 14 longitudinal rows. Hook size gradually reduced posteriorly. Neck significant, trapezoidal. Proboscis receptacle elongate, double-walled, 458–865 (666) $\times$ 103–136 (117). Cephalic ganglion positioned in middle of receptacle. Lemnisci elongate, 718–1019 (888) in length. Uterus 1252–1863 (1433) in length. Eggs elliptical, 38–41 (39) in length (eggs n = 5). Genital pore opening subterminally.

Remarks. Records from India (Gupta & Lata 1967; Bhattacharya 2007; Naidu 2012) require scrutiny with fine morphology and nucleotide sequence data. The Indian specimens were described as “aspinose” (Gupta & Lata 1967: 338), but the trunk spines might have been overlooked, as were in the original description of *Cavisoma chromitidis*. Golvan (1969) doubted Gupta & Lata’s (1967) species identification because the cement glands were described as “syncytial” (op. cit., 338), which is abnormal among palaeacanthocephalans. On the other hand, the relevant line drawing by Gupta & Lata (1967, fig. 22) clearly shows the outlines of four cement glands, indicating that the glands would be ‘clustered’, instead of ‘syncytial’. The host fish of the Indian records may be *Teuthis oramin*, currently *Siganus canaliculatus* (Siganidae), although it was indicated as “*Teuthis (Teuthis) bamin*” (Naidu 2012: 111) and “*Tenthis bamin*” (Gupta & Lata 1967: 338; Bhattacharya 2007: 146). The specific name could be a transcription error, as there is no fish with that name.

Family Pomphorhynchidae Yamaguti, 1939

Spirorhynchidae Harada, 1935: 20, type genus *Spirorhynchus* Harada, 1935, invalid under Art. 39 of the Code.

Spiracanthorhynchinae Harada, 1938: 426, type genus *Spiracanthorhynchus* Harada, 1938.

Pomphorhynchidae Yamaguti, 1939: 328, type genus *Pomphorhynchus* Monticelli, 1905.

Spirorhynchodidae Strand, 1942: 388, type genus *Spirorhynchodes* Strand, 1942.

Composition. *Paralongicollum* Amin, Bauer, & Sidorov, 1991;
Pomphorhynchus Monticelli, 1905; and *Tenuiproboscis* Yamaguti, 1935.

Diagnosis. Given by Yamaguti (1939).

Remarks. According to Art. 23 of the Code (Principle of Priority), the name *Spiracanthorhynchinae* should be considered valid for this family. However, the name *Pomphorhynchidae* has been in prevailing usage. As of 19 February 2025, a Google

Scholar search for this family name yielded over 530 records, while *Spiracanthorhynchinae* returned only one (Harada, 1938). In this study, I maintain the prevailing usage of *Pomphorhynchidae* despite the Principle of Priority. Following a recommendation from one of the reviewers of Kita et al. (2025b), an application has been submitted to the ICZN requesting a ruling to conserve *Pomphorhynchidae* by giving it precedence over *Spiracanthorhynchinae* are considered synonymous whenever the two are treated as such.

Genus *Pomphorhynchus* Monticelli, 1905

Pomphorhynchus Monticelli, 1905: 11; type species, *Echinorhynchus laevis* Zoega in Müller, 1776, fixed by subsequent monotypy (Porta 1908: 413) under Art. 67.2.2 and 69.3.

Longicollum Yamaguti, 1935: 260; type species, *Longicollum pagrosomi* Yamaguti, 1935, fixed by monotypy; not *Longicollum* Jepson, Khramov, & Ohl, 2018a: 565 (Neuroptera; substituted with *Longipronotum* Jepson, Khramov, & Ohl, 2018b).

Spirorhynchus Harada, 1935: 20; type species, *Spirorhynchus alemniscus* Harada, 1935, fixed by monotypy.

Spiracanthorhynchus Harada, 1938: 424; type species, *Spirorhynchus alemniscus* Harada, 1935, under Art. 67.8 of the Code.

Spirorhynchodes Starnd, 1942: 388; type species, *Spirorhynchus alemniscus* Harada, 1935, under Art. 67.8 of the Code.

Remarks. Generally, two pomphorhynchid genera, *Pomphorhynchus* and *Longicollum*, could be distinguished by the presence of a neck bulb (e.g., Yamaguti 1963; Golvan 1969). However, the molecular analysis of Zhao et al. (2025) revealed that two species, *Pomphorhynchus zhoshanensis* Li, Chen, Amin, & Yang, 2017 and *Longicollum pagrosomi* Yamaguti, 1935, were completely identical in their mitochondrial protein coding genes and nuclear ribosomal genes, despite there being a clear difference in the morphology of their neck. Thus, the authors considered *Longicollum* as a junior synonym of *Pomphorhynchus*. In this thesis, I followed the

taxonomic decision by Zhao et al. (2025), but the morphological comparison was conducted among former *Longicollum* species.

***Pomphorhynchus alemniscus* (Harada, 1935)**

(Fig. 17)

Spirorhynchus alemniscus Harada, 1935: 21, figs. 8, 9a–e.

Longicollum minor Fukui & Morisita, 1936: 41.

Spiracanthorhynchus alemniscus: Harada 1938: 424, figs. 4a, b.

Longicollum alemniscus: Fukui & Morisita 1937a: 36; Kita et al. 2025b: 487–489, fig. 1.

Spirorhynchodes alemniscus: Strand 1942: 388.

Pomphorhynchus alepniscus [sic]: Zhao et al. 2025: 941.

Type locality. Taiwan (Harada, 1935).

Other localities. Fukue (Tahara, Aichi, Japan) (Fukui & Morisita, 1936); Kita-Jukken River (Tokyo, Japan) (Kita et al. 2025b); off Aichi (Fukui and Morisita, 1938).

Type host. *Scatophagus argus* (Scatophagidae) (Harada 1935).

Other hosts. *Acanthogobius flavimanus* (Gobiidae) (Kita et al. 2025b); *Anguilla japonica* (Anguillidae) (Fukui & Morisita 1938); *Lutianus russelli* [= currently *Lutjanus russellii*] (Lutjanidae) (Harada 1935); *Paralichthys olivaceus* (Paralichthyidae) (Fukui & Morisita, 1937); *Parasilurus asotus* [= currently *Silurus asotus*] (Siluridae) (Fukui & Morisita, 1938); *Plotosus anguillaris* [= currently *Plotosus japonicus*] (Plotosidae) (Fukui & Morisita, 1938); *Sparus macurocephalus* [= currently *Acanthopagrus schlegelii*] (Sparidae) (Fukui & Morisita, 1938); *Tridentiger* cf. *obscurus* (Gobiidae) (Kita et al. 2025b).

Materials examined. Six males and four females (ICHUM 8999–9004), 12 November 2024, from the intestine of *Acanthogobius flavimanus* and *Tridentiger* cf. *obscurus*.

Description (after Kita et al. 2025b). *General* (n = 10). Trunk cylindrical, elongate, swollen in anterior portion (Fig. 1A). Proboscis “Kolben-like”, armed with 11–12 longitudinal rows of nine–10 hooks. Neck long, uniformly cylindrical, strongly twisted. Proboscis receptacle double-walled, elongate. Cerebral ganglion positioned at middle to posterior region of proboscis receptacle. Lemnisci broad, very short. Genital pore opening subterminally.

Male (n = 6, otherwise noted). Trunk 2890–3872 (3346) × 622–1027 (804). Proboscis 446–656 (535) (n = 5) × 203–293 (240) (n = 5). Neck 1876–3466 (2571) × 185–371 (283). Proboscis receptacle 2386–3959 (3167) × 96–140 (119). Lemnisci 102–221 (152) in length. Testes two, oval, tandem, touching each other. Anterior testis 282–475 (360) × 184–317 (237). Posterior testis 306–524 (369) × 170–325 (249). Cement glands six, pyriform to claviform. Saeffigen’s pouch 215–349 (271) in length. Copulatory bursa 334 in width (n = 1).

Female (n = 4, non-gravid). Trunk 2741–3403 (3172) × 657–921 (794). Proboscis 610–703 (648) × 260–296 (282). Neck 1828–2810 (2196) × 220–328 (292). Proboscis receptacle 2837–3744 (3162) × 97–151 (129). Lemnisci 111–205 (153) in length. Uterus 626–921 (769) in length. Vaginal sphincter single.

Remarks. This species could be distinguished from other “*Longicollum*” by *i*) having a strongly twisted neck, *ii*) the shape of the proboscis, *iii*) the arrangement of proboscis hooks, and *iv*) uniform neck width (Tables 9, 10) (Harada 1935; Yamaguti 1935; Fukui & Morisita 1938; Dollfus & Golvan 1963; Golvan 1969; Gupta & Gupta 1970, 1980; Jain & Gupta 1980; Gupta & Naqvi 1984; Gupta & Fatma 1985; Saxena et al. 2008).

***Pomphorhynchus pagrosomi* (Yamaguti, 1935)**

(Fig. 18)

Longicollum pagrosomi Yamaguti, 1935: 257, figs. 11–14.

Pomphorhynchus zhoushanensis Li et al., 2017a: 694, figs. 1–2.

Pomphorhynchus pagrosomi: Zhao et al. 2025: 941.

Type locality. Seto Inland Sea (Yamaguti 1935).

Other localities. Off Kita-Matsuura (Nagasaki, Japan) (Hatai et al. 1987); off Namhae (Korea) (Kim et al. 2011); off Naru (Nagasaki, Japan) (Ogawa & Inouye 1997); off Zhoushan Islands (East China Sea) (Li et al. 2017a); Pingtung (Taiwan) (Cheng et al. 2022); off Aomori (Ichihara 1964c); Sagami Bay (Ichihara 1965); Toyama Bay (Yamaguti 1935); off Tamano (Okayama, Japan) (Kita unpubl.); off Bizen (Okayama, Japan) (Kita unpubl.); off Ijika (Mie, Japan) (this study); off Ushitsu (Ishikawa, Japan) (Kita unpubl.); off Takojima (Ishikawa, Japan) (Kita unpubl.).

Type host. *Pagrosomus unicolor* [= currently *Pagrus auratus* (Sparidae)] (Yamaguti 1935).

Other hosts. *Branchiostegus japonicus* (Maracanthidae) (Kita unpubl.); *Callionymus* sp. (Callionymidae) (Kita unpubl.); *Gymnocranius griseus* (Lethrinidae) (Yamaguti 1935); *Lutjanus erythropterus* (Lutjanidae) (Cheng et al. 2022); *Oplegnathus fasciatus* (Oplegnathidae) (Yamaguti 1935; Li et al. 2017a); *Pagrus major* (Sparidae) (Hatai 1983, 1987; Ichihara 1964c); *Leptojulis poecilepterus* (Labridae) (Yamaguti 1935); *Parapristipoma trilineatum* (Haemulidae) (Yamaguti 1935; Ichihara et al. 1965); *Pleuronichthys cornutus* (Pleuronectidae) (Kita unpubl.); *Siganus fuscescens* (Siganidae) (Yamaguti 1935); *Sillago sihama* (Sillagonidae) (Yamaguti 1935); *Stephalolepis cirrhifer* (Monacanthidae) (Kita unpubl.); *Takifugu rubripes*

(Tetraodontidae) (Ogawa & Inouye 1997); *Trachurus japonicus* (Carangidae) (Yamaguti 1935); *Zebrias zebrinus* (Soleidae) (Yamaguti 1963; Kita unpubl.).

Materials examined. Eleven males and six females (YK's private collection), off Ijika, off Takojima, off Ushitsu, off Bizen, and off Tamano, 29 July 2022, 17 September 2022, 6 September 2023, and 13–15 September 2023, from the intestines of *Branchiostegus japoniscus*, *Callionymus* sp., *Pleuronichthys cornutus*, *Stephanolepis cirrhifer*, and *Zebrias zebrinus*.

Description. *General* (n = 17). Trunk cylindrical, elongate, swollen in anterior end. Proboscis claviform, cylindrical, armed with 9–10 hooks in 14 rows. Neck long, swollen in middle, slightly twisted. Proboscis receptacle elongate, double-walled. Cerebral ganglion positioned posterior region of receptacle. Lemniscus quite short.

Male. (n = 11). Trunk 3794–15843 (8574) × 602–1900 (1262). Proboscis 610–963 (766) × 278–519 (407). Neck 1712–3376 (2374) × 403–1218 (764). Proboscis receptacle 2728–5461 (3606) × 204–493 (319). Lemniscus 110–263 (176) in length. Anterior testis 224–1996 (768) × 138–931 (462). Posterior testis 223–925 (670) × 98–698 (423). Cement glands six, clustered, oval to elongate. Saeftigen's pouch 488–1676 (874) in length. Copulatory bursa 315–618 (498) in diameter (n = 2).

Female (n = 6). Trunk 8245–11750 (9958) × 973–1790 (1510). Proboscis 651–941 (805) × 329–576 (448). Neck long 2046–3435 (2779) × 333–1061 (833). Proboscis receptacle 2967–4739 (4137) × 207–363 (277). Lemniscus 169–207 (187) in length. Uterus elongate, 1539–1838 (1703). Eggs elliptical, elongate, 54–82 (66) (eggs n = 10).

Remarks. In this study, I reported several new host records of *Pomphorhynchus pagrosomi*. The host range of this species is quite wide (15 families of fish after this study), while the distribution of this species is limited to the water of

eastern Asia (see above). The record from Türkiye (Oğuz & Kvach 2006) might be caused by the misidentification. In Zhao et al. (2025), the authors synonymized the two genera, *Pomphorhynchus* and *Longicollum*, based on the mitophylogenomic study on the two species *Pomphorhynchus zhoushanensis* and *Longicollum pagrosomi* obtained from the same locality and host species. In Japan, one species, *Pomphorhynchus sebastichthydis* Yamaguti, 1939, was found in the marine fish of Nagasaki (Yamaguti 1939): the proboscis hook arrangement (11–12 hooks in 12 rows) was similar to that of *P. pagrosomi* (Yamaguti 1935, 1939; Table 9). Although the original description of *P. zhoushanensis* distinguished the species from *P. sebastichthydis* by the hook armature, the current molecular-based study showed that such differences in hooks (and also the presence of a neck bulb) could not divide the species. I could not examine the specimens identical to *P. sebastichthydis* in the present study, so further surveys and molecular phylogenetic studies are needed on this species to determine whether *P. sebastichthydis* is synonymous with *P. pagrosomi* or not.

Family Rhadinorhynchidae Lühe, 1912

Genus *Rhadinorhynchus* Lühe, 1911

***Rhadinorhynchus laterospinosus* Amin, Heckmann, & Ha, 2011**

(Fig. 19)

Rhadinorhynchus laterospinosus Amin et al., 2011a: 72, 73, figs. 21–26; Kita et al. 2024a: 174–175, fig. 2.

Type locality. Off Cat Ba Island (Halong Bay, Vietnam) (Amin et al. 2011a).

Other localities. Budai Harbor (Taiwan) (Lisitsyna et al. 2023); off Binh Thuan (Vietnam) (Amin et al. 2019a); off Hai Phong (Vietnam) (Amin et al. 2019a); off Nah Trang (Khanh Hoa, Vietnam) (Amin et al. 2019a); off Quang Binh (Vietnam)

(Amin et al. 2019a); off Shanwei (Guangdong, China) (Xie et al. 2025b); off Taipei (Taiwan) (Lisitsyna et al. 2023); off Tosa-Shimizu (Kochi, Japan) (Kita et al. 2024a); off Yilan (Taiwan) (Lisitsyna et al. 2023).

Type host. *Balistes* sp. (Balistidae) (Amin et al. 2011a).

Other hosts. *Alectis ciliaris* (Carangidae) (Amin et al. 2019a); *Auxis rochei* (Scombridae) (Amin et al. 2019a); *Auxis thazard* (Scombridae) (Amin et al. 2019a; Kita et al. 2024a; Xie et al. 2025b); *Katsuwonus pelamis* (Scombridae) (Lisitsyna et al. 2023); *Leiognathus equulus* (Leiognathidae) (Amin et al. 2019a); *Lutjanus bitaeniatus* (Lutjanidae) (Amin et al. 2019a); *Megalaspis cordyla* (Carangidae) (Amin et al. 2019a); *Nuchequula flavaxilla* (Leiognathidae) (Amin et al. 2019a); *Scomber australasicus* (Scombridae) (Lisitsyna et al. 2023); *Trichiurus lepturus* (Trichiuridae) (Lisitsyna et al. 2023); and *Tylosurus* sp. (Belonidae) (Amin et al. 2019a).

Material examined. Ten specimens, ICHUM 8572–8581, off Tosa-Shimizu, 8 and 10 October 2022, from the intestine of *Auxis thazard*.

Description (after Kita et al. 2024a). *General* (n = 10). Trunk cylindrical, elongate. Proboscis cylindrical, elongate, with 15–16 hook rows and 22–24 hooks per row. Basal hooks distinctly large. Trunk spines distributed in separated area of anterior end of trunk, connected with a few lateral spines. Proboscis receptacle elongate, double-walled. Lemnisci unclear. Genital pore opening subterminally.

Male (n = 3). Trunk 8.31–9.32 (mm) × 617–806. Proboscis cylindrical, 1509–2240 × 149–296. Proboscis receptacle 1970–3201 × 286–434. Testes tandem, oval. Anterior testis 1049–1147 × 373–586. Posterior testis 906–1305 × 402–590. Cement glands four, tubular, tandem in two rows. Saefftigen's pouch fusiform, 1391 in length (n = 1). Copulatory bursa 678–860 in width.

Female (n = 7; one of them was damaged). Trunk 11.70–20.55 (mm) × 543–872. Proboscis 1190–1971 × 147–311. Proboscis receptacle 2767–4621 × 176–330. Uterus elongate, 2652–4750 × 64–314.

Remarks. The generic placement of this material in *Rhadinorhynchus* is obvious, due to its cylindrical trunk anteriorly with spines as well as the four tubular cement glands (Amin et al. 2019a). It can be identified as *R. laterospinosus* because i) the trunk spines are distributed in two regions, and they are connected to each other with several spines; and ii) the number of proboscis hook rows is 15–16 and 22–24 per row (Amin et al. 2011a, 2019a). *Rhadinorhynchus laterospinosus* was originally described by Amin et al. (2011a) based on a single female specimen, obtained from a trigger fish, *Balistes* sp., in Vietnam. Later, Amin et al. (2019a) redescribed the morphological characteristics based on male and female specimens obtained from various fishes in Vietnam, including the frigate tuna *A. thazard*, and Lisitsyna et al. (2023) added the record of this species from Taiwan. The specimens from Tosa-Shimizu (Kochi) represent the first record of *R. laterospinosus* from Japan, expanding the known distribution range of the species northeastward for about 1400 km.

***Rhadinorhynchus nudus* Harada, 1938**

(Fig. 20)

Rhadinorhynchus nudus Harada, 1938: 420, figs. 2a, b.

Rhadinorhynchus (*Neorhadinorhynchus*) *nudus*: Yamaguti 1939: 345.

Nipporhynchus nudus: Van Cleave & Lincicome 1940: 79.

Echinorhynchoides nudus: Petrochenko 1956: 291.

Neogorgorhynchus nudus: Golvan 1960: 151.

Neorhadinorhynchus nudus: Yamaguti 1963: 53.

Diplosetis nudus: Pichelin & Cribb 2001: 293.

Gymnorhadinorhynchus mariserpentis Steinauer et al., 2019: 126, figs. 3–5.

Rhadinorhynchus mariserpentis: Huston et al. 2020: 15.

Type locality. Off Keelung (Taiwan) (Harada 1938).

Other localities. Laucala Bay (Fiji) (Amin & Nahhas 1994); off Aftab (Iran) (Ghanei-Motlagh et al. 2025); off Nha Trang (Vietnam) (Amin et al. 2018d); off Shalm El-Sheikh (Egypt) (Hassanine 2006); off Shanwei (Guangdong, China) (Li et al. 2018); off Wakamatsu (Fukuoka, Japan) (Steinauer et al. 2019); off Hondo (Kumamoto, Japan) (Kita unpubl.).

Type host. *Trachurus japonicus* (Carangidae) (Harada 1938).

Other hosts. *Auxis thazard* (Scombridae) (Amin et al. 2018d; Li et al. 2018); *Euthynnus affinis* (Scombridae) (Amin & Nahhas 1994; Kita unpubl.); *Rastrelliger kanagurta* (Scombridae) (Hassanine 2006); *Regalecus russellii* (Regalecidae) (Steinauer et al. 2019).

Materials examined. Five males and five females (YK's private collection), off Hondo, 8 June 2023, from the intestine and pyloric organ of *Euthynnus affinis*.

Description. *General* (n = 10). Trunk cylindrical, elongate, aspinose, slightly swollen in middle. Proboscis cylindrical, elongate, armed with 25 hooks in 13–15 longitudinal rows. Proboscis receptacle double-walled, elongate. Lemniscus elongate, generally longer than receptacle. Genital pore opening subterminally.

Male (n = 5). Trunk 7949–10640 (9341) × 1233–1364 (1322). Proboscis 1109–1310 (1179) × 102–167 (137). Proboscis receptacle 2082–2749 (2387) × 270–327 (307). Lemniscus 1902–2761 (2428) in length. Anterior testis 951–1356 (1158) × 571–734 (663). Posterior testis 842–1145 (965) × 630–766 (714). Cement glands four, tubular. Saeftigen's pouch 1146–1961 (1586) in length. Copulatory bursa opening subterminally, 1032–1154 (1093) in diameter.

Female (n = 5). Trunk 9868–11734 (10597) × 1297–1694 (1515). Proboscis 1246–1618 (1419) × 104–173 (143). Proboscis receptacle elongate, 2665–3007 (2816) × 295–461 (358). Uterus elongate, 3476–4193 (3724) in length. Eggs elliptical, 57–72 (65) in length.

Remarks. Yamaguti (1939) established the subgenus *Neorhadinorhynchus* and assigned two species, *R. aspinosus* Fukui & Morisita, 1937, and *R. nudus*, as members of this subgenus. Later, Yamaguti (1963) elevated this subgenus to genus under Cavisomatinae, and the acanthocephalan systematics based on morphology followed this taxonomic revision (e.g., Amin 1985, 2013). However, recent molecular phylogenetic studies revealed that this species should be classified into the genus *Rhadinorhynchus*, as an original description of this species (Harada 1938; Ghanei-Motlagh et al. 2025). In this study, I followed this suggestion and considered this species as a member of *Rhadinorhynchus*. To assess the validation of the genus *Neorhadinorhynchus*, examination of the specimens and DNA information of *N. aspinosus*, the type species of this genus, is needed.

***Rhadinorhynchus seriolae* (Yamaguti, 1963)**

(Fig. 21)

Rhadinorhynchus pristis (not of Rudolphi 1802): Fukui & Morisita 1937b: 1844.

Nipporhynchus seriolae Yamaguti, 1963: 104.

Rhadinorhynchus seriolae: Golvan 1969: 81; Kita et al. 2024a: 172–174, fig. 1.

Type locality. Off Momotori (Toshi Island, Mie, Japan) (Yamaguti 1963).

Other localities. Off Killarney (Victoria, Australia) (Smales 2014b); off Minami-Ise (Mie, Japan) (Kita et al. 2024a); off Sir John Young Banks (New South

Wales, Australia) (Smales 2014c); Tokyo (market, collected site unknown) (Yamaguti 1963).

Type host. *Seriola quinqueradiata* (Carangidae) (Yamaguti 1963).

Other hosts. *Scomber japonicus* (Scombridae) (Yamaguti 1963); *Seriola lalandi* (Carangidae) (Smales 2014c); *Thunnus orientalis* (Scombridae) (this study).

Material examined. Three specimens (on one slide), ICHUM 8571, off Minami-Ise, 22 August 2022, from the intestine of *Thunnus orientalis*.

Description (after Kita et al. 2024a). *Male* (n = 3). Trunk cylindrical, elongate, 5.77–7.66 (mm) × 428–673. Proboscis cylindrical, elongate, 1595–1617 × 175–192, covered with 23–25 hooks in 12–13 rows. Basal hooks distinctly large. Trunk spines short, thick. Regions covered with spines divided into two, distributed within length of proboscis receptacle. Proboscis receptacle thick, double-walled, elongate, 1389–2199 × 203–216. Lemnisci shorter than proboscis receptacle, 1159–1396 (n = 2). Testes two, oval, tandem in line. Anterior testis 508–1469 × 275–504. Posterior testis 541–669 × 335–440. Cement glands four, tubular. Saefftigen's pouch 833–984 in length (n = 2). Copulatory bursa not everted.

Remarks. The cylindrical trunk, anterior trunk spines, elongate proboscis, enlarged basal proboscis hooks, and four tubular cement glands in the present material indicate its affiliation in *Rhadinorhynchus* (Amin et al. 2019d). *Rhadinorhynchus seriola* can be distinguished from other congeners by i) trunk spines distributed in two fields, ii) about 24 proboscis hooks in about 12 rows, and iii) lemnisci shorter than the proboscis receptacle (Amin et al. 2011; Smales 2014c). Records of specimens identified as *R. seriola* exist in addition to those listed in the synonym list. Ichihara et al. (1968) identified acanthocephalans from mackerel in Sagami Bay as *Nipporhynchus seriola* (=

R. seriolae). They further claimed that the specimen identified as *R. japonicus* in Kanda (1958) was a synonym of *N. seriolae*. The identification of Ichihara et al. (1968) was questioned by Amin & Heckmann (2017). As a basis for their doubt, they cited the fact that the hook arrangement differs from the original description of *R. seriolae*. Amin et al. (2011) have also determined that *R. japonicus* is a valid name. Furthermore, in the original description of *R. japonicus* (Fujita 1920), the arrangement of proboscis hooks was written as 10 rows $\times$ 17–18 hooks per row, while *R. japonicus* in Kanda (1958) and *N. seriolae* in Ichihara et al. (1968) were 16–18 rows $\times$ 20–25 hooks per row. The acanthocephalans in Kanda (1958) and Ichihara (1968) resemble *R. ditrematis* (15–16 $\times$ 24) (Yamaguti 1939) rather than *R. seriolae* or *R. japonicus*, but I have not seen the actual specimens, so I cannot be certain. Based on the above situation, I agree with Amin & Heckmann (2017) and speculate that *N. seriolae* in Ichihara et al. (1968) is a misidentification. Therefore, I do not include Ichihara et al. (1968) and Kanda (1958) in the synonym list for *R. seriolae* in this thesis.

Family Transvenidae Pichelin & Cribb, 2001

Genus *Sclerocollum* Schmidt & Paperna, 1978

***Sclerocollum neorubrimaris* Amin, Heckmann, & Ha, 2018**

(Figs. 22, 23)

Sclerocollum neorubrimaris Amin et al., 2018c: 118, figs. 1–13.

Type locality. Off Nha Trang (Vietnam) (Amin et al. 2018c).

Other locality. Off Miyakojima Island (Okinawa, Japan) (Kita unpubl.).

Type host. *Siganus guttatus* (Siganidae) (Amin et al. 2018c)

Other host. *Siganus argenteus* (Siganidae) (Kita unpubl.).

Materials examined. Seven specimens, ICHUM 8519–8525, off Miyakojima Island, 25 April 2022, from the intestine of *Siganus argenteus*.

Description. *General* (n = 7). Trunk cylindrical, elongate, unspined, anterior one-fourth widest. Anterior end of trunk covered with sclerotized plaques. Proboscis short, cylindrical, armed with 13–14 longitudinal rows of hooks and 9–10 hooks per row. Proboscis hooks curved, all equal in size. Hook arrangement same in both sexes. Basal proboscis hooks not forming a ring. Neck short. Proboscis receptacle double-walled. Cephalic ganglion positioned at posterior receptacle. Lemniscus length less than twice of receptacle length.

Male (n = 4). Trunk cylindrical, elongate, 10.5–23.4 (mm) × 1132.6–2543.0. Proboscis short, cylindrical, not narrowed posteriorly, 410.0–556.0 × 125.5–168.1. Proboscis receptacle double-walled, 963.2–1338.1 × 187.8–264.6. Lemniscus 1327.5–2205.8 length. Testes oval, tandem. Anterior testis 807.8–1700.8 × 445.3–1210.7. Posterior testis 793.4–1726.7 × 475.8–985.2. Cement glands tubular, elongate, 4 in 2 pairs: anterior pair 937.5–2239.1 length; posterior pair 887.9–1917.6 length. Saeftigen's pouch 786.4–1386.9 length. Copulatory bursa almost as wide as trunk, 756.0–1437.6 width.

Female (n = 3). Trunk cylindrical, elongate, 14.4–20.6 (mm) × 1516.6–2822.3. Proboscis short, cylindrical, not narrowed posteriorly, 370.1–452.0 (n = 2) × 122.3–166.2. Proboscis receptacle, lemniscus, and uterine bell of specimens unclear. Uterus 1659.1 × 220.7 (n = 1). Vaginal sphincter well defined, single. Gonopore opening terminal. Eggs fusiform, elongate, 21.1–30.9 length (eggs n = 10).

Remarks. The two main reasons for identifying the specimens obtained in this study as a member of *Sclerocollum* were *i*) the presence of sclerotized plaques and *ii*)

the fact that the basal proboscis hooks were not forming a ring. Compared to other *Sclerocollum* species (Table 11), *Sc. neorubrimaris* differs from *Sc. australe* in the position of testes is different in the trunk (middle in *Sc. neorubrimaris* vs. posterior in *Sc. australe*) (Pichelin et al. 2016), and from *Sc. australe*, *Sc. rubrimaris* and *Sc. saudii* in the position of the cephalic ganglion in relation to the proboscis receptacle (posterior in *Sc. neorubrimaris* vs middle in these three) (Schmidt & Paperna 1978; Al-Jahdali 2010; Pichelin et al. 2016). Also, the length of the lemniscus is 1–2 times as proboscis receptacle in *Sc. neorubrimaris*, while in *Sc. rubrimaris* it is almost equal to the receptacle (Schmidt & Paperna 1978; Amin et al. 1984, 2018c). In addition, the number of proboscis hooks per row in *Sc. neorubrimaris* is different from that in *Sc. robustum* (9–10 vs. 12–13) (Schmidt & Paperna 1978; Amin et al. 2018c).

Genus *Trajectura* Pichelin & Cribb, 2001

***Trajectura ikedai* (Machida, 1992)**

(Fig. 24)

Diplosentis ikedai Machida, 1992: 37, figs. 1–5.

Trajectura ikedai: Pichelin & Cribb 2001: 297.

Type locality. Off Amami-Oshima Island (Kagoshima, Japan) (Machida 1992)

Other locality. Off Miyakojima Island (Okinawa, Japan) (Kita unpubl.)

Type host. *Cirrhilabrus cyanopleura* (Labridae) (Machida 1992).

Other host. *Pterocaesio digramma* (Caesionidae) (Kita unpubl.).

Material examined. One male (YK's private collection), off Miyakojima Island, 23 April 2022, from the intestine of *Pterocaesio digramma*.

Description. *Male* (n = 1). Trunk cylindrical, elongate, aspinose, 883 in width. Proboscis cylindrical, 405 × 138, armed with 7–9 hooks in 12 rows: hook size reduced

toward base. Proboscis receptacle double-walled, 879×236 . Lemniscus long, 1615 in length. Anterior testis 1596×758 . Posterior testis 1665×758 . Cement glands two, claviform. Copulatory bursa opening terminally, 668 in diameter.

Remarks. The present material showed a larger number of hooks per row than the original description [7–9 hooks in this study vs. 7–8 in Machida (1992)]. In this study, I could not obtain female individuals who have a structure called “conical process” on their trunk.

Order Polymorphida Petrochenko, 1956

Family Istmosacanthidae Smales, 2012

Genus *Metarhadinorhynchus* Yamaguti, 1959

Metarhadinorhynchus Yamaguti, 1959: 322; Kita et al. 2024b: 5.

Gorgorhynchoides Cable & Linderth, 1963: 715.

Amended diagnosis. Istmosacanthidae; trunk cylindrical, elongate, with narrowed anterior portion armed with numerous spines, arranged irregularly, bulbous swelling present behind spinose region; proboscis cylindrical, claviform, with numerous hooks; proboscis hooks gradually smaller toward basal. Longitudinal rows of hooks at least 17 or more at posterior proboscis; neck developed, aspinose; proboscis receptacle double-walled; lemniscus elongate, tubular; testes tandem, at middle-level of trunk; cement glands six, filiform, quite elongate, very close to each other, forming bundle; uterus elongate; vagina divided into two bulbous portions (Kita et al. 2024b).

Remarks. The nominal species at least once included in *Metarhadinorhynchus* are the following six: i) *Rhadinorhynchus arii* Wang, 1966; ii) *Rhadinorhynchus cyprini* Yin in Zhang, 1961; iii) *Metarhadinorhynchus echeneisi* Gupta & Sinha, 1991; iv) *Metarhadinorhynchus lateolabracis* Yamaguti, 1959; v) *Metarhadinorhynchus thapari*

Gupta & Gupta, 1975; and vi) *Metarhadinorhynchus valiyathurae* Nadakal, John, & Jacob, 1990 (Wang 1966, 1986; Gupta & Gupta 1975; Nadakal et al. 1990; Gupta & Sinha 1991; Amin 2013; Lisitsyna et al. 2022). Of these, *R. arii* and *R. cyprini* (both with eight cement glands) had been synonymized with each other (Amin 2013, p. 287) before being transferred to *Neotegorhynchus* Lisitsyna et al., 2022 by Lisitsyna et al. (2022), whereas Kita et al. (2024b) reinstated *R. arii* as *Indorhynchus arii* and retained *R. cyprini* in *Neotegorhynchus*. *Metarhadinorhynchus valiyathurae*, possessing six cement glands, had been moved to *Gorgorhynchoides* by Bhattacharya (2007) before Kita et al. (2024b). Therefore, apart from the type species *M. lateolabracis*, the genus also included two more species at the start of Kita et al.'s (2024b) study, *M. echeneisi* and *M. thapari*, both with eight cement glands; Kita et al. (2024b) transferred these two to *Indorhynchus* by modifying the generic diagnosis of the latter, yielding *I. echeneisi* and *I. thapari*. Before Kita et al. (2024b), *Metarhadinorhynchus* and *Gorgorhynchoides* had been distinguished from each other essentially only by the number of cement glands, which was supposedly eight and six, respectively (Yamaguti 1959; Cable & Linderorth 1963). After Kita et al.'s (2024b) finding that the type species *M. lateolabracis* has six instead of eight cement glands, the two genera could not be separated any longer; *Gorgorhynchoides* was considered a junior synonym of *Metarhadinorhynchus* by Kita et al. (2024b). The 12 species that used to belong to *Gorgorhynchoides* were automatically assigned to *Metarhadinorhynchus*. In terms of the number of longitudinal rows of proboscis hooks, *Gorgorhynchoides* was originally diagnosed to have more than 20 (Cable & Linderorth 1963). This value was modified to be at least 17 in the amended diagnosis by Kita et al. (2024b), with *Gorgorhynchoides* having been synonymized with *Metarhadinorhynchus*. This was chiefly because in *M.*

golvani it could be estimated—by counting the minimum number of hooks in the spiral rows—that there would be at least 17 rows on the posterior portion of the proboscis (Table 12; Chandra et al. 1984), although the exact number is unclear due to the uncommon manner of counting hook rows employed in the original description (Chandra et al. 1984). In *M. valiyathuræ*, it is stated to be minimally 18 in the original description (Nadakal et al. 1990). *Gorgorhynchus lateolabris* Yin & Wu, 1984, originally described as a parasite of *Lateolabrax japonicus* from China (Yin & Wu 1984), perfectly fits the diagnosis of *Metarhadinorhynchus* proposed by Kita et al. (2024b) by having, for instance, *i*) a claviform proboscis with 16–17 hooks arranged in 24–26 longitudinal rows, *ii*) well developed aspinose neck, and *iii*) six cement glands, among other characters. Therefore, this species was moved to *Metarhadinorhynchus* (Kita et al. 2024b). *Metarhadinorhynchus lateolabris* (Yin & Wu, 1984) may be a junior synonym of *M. orientalis* (Wang, 1966), as the latter has 16–18 hooks arranged in 26 longitudinal rows, utilizing the same host (Wang 1966; Yin & Wu 1984). At the moment, however, such important characteristics as the number of trunk spines and the presence/absence of a bulbous portion in the anterior trunk are not known in *M. orientalis* because these are not mentioned in the original description (Wang 1966). Examination of the type material in future studies will show whether or not the two are actually synonymous.

***Metarhadinorhynchus lateolabracis* Yamaguti, 1959**

(Figs. 25, 26)

Metarhadinorhynchus lateolabracis Yamaguti, 1959: 322, figs. 4–7; Kita et al. 2024b: 6–8, figs. 1, 2.

Type locality. Shibukawa (Okayama, Japan) (Yamaguti 1959).

Other localities. Off Oku (Okayama, Japan) (Kita et al. 2024b); Kamo River (Hiroshima, Japan) (Kita et al. 2024b).

Type host. *Lateolabrax japonicus* (Cuvier, 1828) (Lateolabracidae) (Kita et al. 2024b; Yamaguti 1959).

Materials examined. MPM Coll.-No. 22601-SY6970–6971: deposited in Meguro Parasitological Museum (Tokyo, Japan); ICHUM 8794–8803: 24 June 2019, 21 July 2019, and 12 September 2023, from the intestine of *Lateolabrax japonicus*.

Description (after Kita et al. 2024b). *Male* (n = 8). Trunk cylindrical, elongate, 23.67–46.14 (35.89) (mm) (n = 5) × 780–1355 (1043), with narrowed anterior portion armed with numerous spines arranged irregularly. Spinose region not divided into two. Trunk spines 7–9 in each spine row. Bulbous swelling present behind spinose region. Proboscis cylindrical, claviform, 595–942 (737) × 326–498 (390), with numerous hooks, 18–20 hooks in 23–25 rows. Neck developed, aspinose. Proboscis receptacle double-walled, 1226–1828 (1465) × 283–476 (358). Lemnisci elongate, tubular, 4110–5189 (4643) in length. Testes elliptical, tandem, at middle-level of trunk. Anterior testis 1126–1875 (1519) × 372–588 (508). Posterior testis 1219–1932 (1556) × 394–620 (507). Cement glands six, filiform, quite elongate, very close to each other around body axis. Saeftigen's pouch 818–1244 (946) in length (n = 5). Copulatory bursa 606–1851 (1135) in diameter (n = 3).

Female (n = 6, including two immature individuals). Trunk cylindrical, elongate, 8.69–65.43 (34.92) (mm) × 759–1269 (990), with narrowed anterior portion armed with numerous spines arranged irregularly. Trunk spine arrangement same as male. Bulbous swelling present behind spinose region. Proboscis cylindrical, claviform, 572–894 (694) × 269–488 (350), with numerous hooks. Proboscis hook arrangement

same as male. Proboscis hooks gradually smaller toward basal. Neck developed, aspinose. Proboscis receptacle double-walled, 1022–1792 (1308) × 235–405 (297). Lemniscus elongate, tubular, 2784–5421 (4119) (n = 4) in length. Uterus elongate, 825–3414 (2066) in length. Vagina divided into two bulbous portions. Genital pore opened subterminally. Eggs elongate, fusiform to elliptical, 70–83 (77) in length.

Remarks. *Metarhadinorhynchus lateolabracis* can be distinguished from other congeners by *i*) undivided spinose region and *ii*) 18–20 proboscis hooks in 23–25 longitudinal hook rows (Yamaguti 1959; Cable & Linderorth 1963; Wang 1966, 1986; Cable & Mafarachisi 1970; Chandra et al. 1984; Yin & Wu 1984; Gupta & Fatma 1987; Nadakal et al. 1990; Bhattacharya & Banerjee 2003; Smales 2014b; Huston & Smales 2021) (Table 12). Kita et al. (2024b) expanded the known range of proboscis hook arrangement (number of hooks per row and hook rows) of this species compared to that of the original description (20 hooks in 23 rows versus 18–20 hooks in 23–25 rows) (Yamaguti 1959). As to the number of proboscis hooks, Yamaguti (1959, p. 28) explained with a footnote, “The exact number of the hooks in each row is unable to make out owing to the proboscis being invaginated at the apex.” This condition was confirmed in my re-examination of the type material, so it was not surprising that my newly collected specimens showed more variation in the arrangement of hooks than in the original description.

Family Polymorphidae Meyer, 1931

Genus *Bolbosoma* Porta, 1908

***Bolbosoma vasculosum* (Rudolphi, 1819)**

(Fig. 27)

Echinorhynchus vasculosus Rudolphi, 1819: 334.
Echinorhynchus aurantiacus Risso, 1826: 261.
Echinorhynchus pellucidus Leuckart, 1828: 23.
Echinorhynchus annulatus Molin, 1858: 143.
Echinorhynchus capitatus von Linstow, 1880: 49.
Echinorhynchus serrani Linton, 1888: 534.
Echinorhynchus bifasciatus Lühe, 1905: 338.
Bolborhynchus pellucidus: Porta, 1906: 269.
Bolborhynchus capitatus: Porta, 1906: 269.
Echinosoma vasculosus [sic]: Porta 1908a: 413.
Bolbosoma vasculosum: Porta 1908b: 273.
Bolbosoma capitatum: Porta 1908b: 275.
Bolbosoma aurantiacum: Porta 1908b: 273.
Bolbosoma thunni Harada, 1935: 15.
Bolbosoma physeteris Gubanov in Delyamure, 1955: 335.
Bolbosoma sp.: Kita et al. 2024d: 319, fig. 1.

Type locality. Off Napoli (Italy) (Rudolphi 1819).

Other localities. Atlantic (Costa et al. 2000; Yamaguti 1963); Pacific (Yamaguti 1963)

Other localities around Japan. Off Katsuura (Wakayama) (Kikuchi & Nakajima 1993) [definitive host]; off Naha (Okinawa) (Kita et al. 2024d); off Awase (Okinawa) (Kita et al. 2024d); off Nagasaki (Kita et al. 2024d); off Minami-Chita (Aichi) (Kita et al. 2024d); Mikawa Bay (Kita et al. 2024d).

Type host. *Brama brama* (Bramidae) (Rudolphi 1819). [paratenic]

Other paratenic hosts. *Aphanopus carbo* (Trichiuridae) (Costa et al. 2000); *Trachurus picturatus* (Carangidae) (Costa et al. 2000); *Thunnus thynnus* (Scombridae) (Harada 1935); *Thunnus obesus* (Scombridae) (Lisitsyna et al. 2023).

Other paratenic hosts around Japan. *Beryx splendens* (Berycidae) (Kita et al. 2024d); *Etelis radiosus* (Lutjanidae) (Kita et al. 2024d); *Malakichthys* sp.

(Acropomatidae) (Kita et al. 2024d); *Pristipomoides argyrogrammicus* (Lutjanidae) (Kita et al. 2024d); *Pristipomoides sieboldii* (Lutjanidae) (Kita et al. 2024d); *Trichiurus lepturus* (Trichiuridae) (Kita et al. 2024d).

Materials examined. Eight specimens, ICHUM 8618–8624 (cystacanth larvae).

Description (after Kita et al. 2024d). Cystacanth larva (n = 8). Trunk cylindrical, elongate, 6979–11992 (8443) × 721–874 (834), with bulbous portion anteriorly: covered with two spiny regions. Proboscis cylindrical, fusiform, 695–854 (748) × 384–470 (422), armed with 8–10 hooks in 18–19 rows. Proboscis receptacle 1326–2057 (1600) × 269–480 (399). Lemniscus 963–1292 (1082) in length.

Remarks. The congeners of *Bolbosoma* (11 valid species), including *B. vasculosum*, are generally known as parasites of cetaceans, and thus, their distribution spreads worldwide (cf. Amin & Margolice 1998; Costa et al. 2000; Ru et al. 2022). Also, marine fish species can serve as paratenic hosts of *Bolbosoma* (see Chapter I). In Japan, the record of *Bolbosoma vasculosum* obtained from its definitive host is only one (as *B. capitatum*: Kikuchi & Nakajima 1993), from *Pseudorca crassidens* caught off Katsuura (Wakayama, Japan). In contrast, the *Bolbosoma* larvae with their morphology could be consistent with *B. vasculosum*, which was recorded from Sagami Bay (Ichihara 1964a, 1964b) (Table 13). Kita et al. (2024d) obtained several *Bolbosoma* larvae from marine fishes around Japan. But at that time, there were no sufficient molecular data of *Bolbosoma* generated from adult individuals. To make sense of the identity of acanthocephalan larvae, in general, DNA barcoding with the gene marker sequences of adult specimens should be conducted. Therefore, the authors did not identify the specimens at the species level. However, García-Gallego et al. (2023, 2025) provided

further molecular data from adult individuals of *B. vasculosum*. In this study, I confirmed that the gene marker (cytochrome *c* oxidase subunit I) sequence obtained in Kita et al. (2024d) was almost identical (*p*-distance: 0–0.026) to that of adult *B. vasculosum*. Thus, I concluded that the specimens of this study should be identified as *B. vasculosum*.

CHAPTER III

INTERFAMILIAL RELATIONSHIPS WITHIN THE CLASS PALAEACANTHOCEPHALA INFERRED FROM MOLECULAR EVIDENCE

INTRODUCTION

The family-level classification system within the class Palaeacanthocephala (with 20 families in two orders) has long been debated, with conflicting hypotheses based on morphological and molecular evidence. Morphological studies have traditionally relied on characters such as the presence or absence of trunk spines, the arrangement of proboscis hooks, the condition of hypodermal nuclei, and variation in cement-gland morphology (e.g., Petrochenko 1956; Yamaguti 1963; Golvan 1969; Amin 1985, 1987, 2013). However, despite the extensive use of these characters in taxonomic diagnoses, the correspondence between these traits and the actual phylogenetic relationships among families has remained unclear. A major morphology-based attempt to infer higher-level relationships by Monks (2001) provided an important starting point, but it included only a subset of palaeacanthocephalan families and predated the accumulation of molecular data. Two decades after Monks (2001), molecular-based attempts employing cytochrome *c* oxidase I (*cox1*), 18S rRNA (18S), and 28S rRNA (28S) have clarified the approximate framework of many palaeacanthocephalan families (e.g., Huston et al. 2020; García-Varela & Andrade-Gómez 2021; Kita et al. 2023, 2024a, b). These markers have generally been sufficient to confirm the monophyly of most families, but they have proven inadequate for resolving inter-familial relationships and deeper branching order. Several regions of the tree persistently show low support or

conflicting topologies. For example, relationships among Rhadinorhynchidae, Transvenidae, and Micracanthorhynchinidae remain unstable across studies (Gao et al. 2022; Amin et al. 2023; Kita et al. 2024b). Likewise, within Polymorphida, the relative positions of Polymorphidae, Centrorhynchidae, Plagiorhynchidae, and Isthmosacanthidae differ among analyses and often receive little statistical support (García-Varela & Nadler 2005; Verweyen et al. 2011; Kita et al. 2024a). These long-standing ambiguities indicate that deeper nodes in the palaeacanthocephalan tree cannot be reliably resolved with the traditional three-gene approach.

To resolve deeper nodes within Palaeacanthocephala, recent studies have increasingly turned to mitochondrial genomes, most of which have relied almost exclusively on amino acid sequences of the 12 protein-coding genes (PCGs) (Steinauer et al. 2005; Gazi et al. 2012, 2015, 2016; Pan & Nie 2013; Weber et al. 2013; Song et al. 2016, 2019; Pan & Jiang 2018; Muhammad et al. 2019a, b, 2020a, b, c, 2023; Sarwar et al. 2021; Dai et al. 2022; Gao et al. 2022, 2023; T-Y Zhao et al. 2023; Li et al. 2024; C-H Zhao et al. 2024; Xie et al. 2024, 2025a, 2025b; F Chen et al. 2025; Ren et al. 2025; García-Gallego et al. 2025). These studies have expanded taxon sampling and have improved our understanding of some problematic lineages; however, methodological diversity has remained minimal. In particular, nucleotide-based datasets, as well as mitochondrial and nuclear ribosomal genes combined with mitochondrial PCGs, have been rarely explored (Gao et al. 2022). Moreover, several key families—most notably Transvenidae and Isthmosacanthidae—have lacked any mitochondrial genome data, preventing robust evaluation of their phylogenetic placement and of deeper relationships among palaeacanthocephalan families. This underlines the need not only for broader

taxon sampling but also for systematic comparison of alternative data usage, which has not yet been undertaken in previous mitogenomic studies.

In this study, I address the following four objectives: *i*) confirmation of the current resolution—which is expected to be low, though—of inter-family phylogenetic relationships in traditional three-gene-based phylogenetic analyses; *ii*) comparison of tree robustness between different combinations of datasets based on mitochondrial protein-coding genes (either amino-acid sequences or nucleotide sequences) and with/without mitochondrial/nuclear ribosomal sequences; *iii*) to infer the phylogenetic position of Transvenidae within Echinorhynchida; and *iv*) to infer the phylogenetic position of Isthmosacanthidae within Polymorphida. For the first objective, I employed 159 OTUs of Acanthocephala, including 25 OTUs derived from the specimens used in Chapter II. For the second objective, I sequenced the complete mitochondrial genomes of eight palaeacanthocephalan species, including the first mitogenomic representatives of Transvenidae and Isthmosacanthidae. The last two objectives will be based on the outcome of the second objective. My primary goal was to clarify the branching order and inter-familial relationships within Palaeacanthocephala. Through these efforts, this study aims to establish a more robust phylogenetic framework for Palaeacanthocephala, thereby providing a foundation for future research on the taxonomy and evolutionary history of the group.

MATERIALS AND METHODS

Materials and DNA extraction

For the molecular work, I used the specimens of the acanthocephalan species listed in Table 14. Total DNA was extracted from the parts of the specimens fixed in

99% ethanol. The DNA extraction followed these methods. *i)* using a silica-based method (Boom et al. 1990) after the specimen was incubated overnight at 55°C in 180 µl of ATL Buffer (Qiagen) and 20 µl of Proteinase K (> 700 U/ml; Kanto Chemical). *ii)* suspending part of the body in 50 µl lysis solution containing 10% (*w/v*) Chelex 100 (Bio-rad) and 200 µg/ml proteinase K (New England Biolabs), and incubated at 56°C for 3 hrs with brief shaking. The proteinase K was subsequently inactivated by incubation at 95°C for 15 min. *iii)* performed using NucleoSpin (TaKaRa).

Amplification and direct sequencing of gene sequences

For *cox1*, the sequences were amplified by polymerase chain reactions (PCRs) in 10 µl reaction volumes: each solution contained 1 µl of total DNA template, 1 µl of 10 × Ex *Taq* Buffer (Takara Bio), 0.8 µl dNTP mix (2.5 mM; Takara Bio), each 0.3 µl of primer (10 pmol/ µl; forward: 5'-GGTCAACAAATCATAAAGATATTGG-3'; reverse: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3'; see Folmer et al. 1994), and 0.05 µl of Takara Ex *Taq* DNA polymerase (5 U/µl; Takara Bio) in deionized water. The PCR condition for COI was 95°C for 5 min; 35 cycles of 95°C for 50 s, 45°C for 50 s, and 72°C for 80 s; and 72°C for 7 min.

For 18S and 28S, PCR was conducted in 10 µl reaction volumes: each solution contained 1 µl of total DNA template, 1 µl of 10 × Ex *Taq* Buffer, 0.8 µl dNTP mix (2.5 mM), 0.3 µl of primer (10 pmol/ µl), and 0.05 µl of Takara Ex *Taq* DNA polymerase (5 U/µl) in deionized water. PCR cycling parameters included denaturation at 94°C for 3 min, followed by 35 cycles of 94°C for 1 min, annealing at 58 to 50°C (touch down) for 1 min, and extension at 72°C for 1 min, followed by a post-amplification incubation at 72°C for 7 min. Primers for 18S consisted of two amplicons: amplicon 1 was forward

5'-AGATTAAGCCATGCATGCGT-3' and reverse 5'-AACTTTTCGTTCTTGATTAATG-3'; amplicon 2 was forward 5'-GCAGCGCGGTAATTCCAGCTC-3' and reverse 5'-GCAGGTTACCTACGGAAA-3' (Kita & Kajihara 2023, 2025; Kita et al. 2024a–2024d, 2025a, 2025b). Primers for 28S consisted of three amplicons: amplicon 1 was forward 5'-CAAGTACCGTGAGGGAAAGTTGC-3' and reverse 5'-CAGCTATCCTGAGGGAAAC-3'; amplicon 2 was forward 5'-ACCCGAAAGATGGTGAACCTATG-3' and reverse 5'-CTTCTCCAACGTCAGTCTTCAA-3'; amplicon 3, forward 5'-CTAAGGAGTGTGTAACAACCTCACC-3' and reverse 5'-AATGACGAGGCATTTGGCTACCTT-3' (Kita & Kajihara 2023, 2025; Kita et al. 2024b, 2024c). Direct sequencing was performed with a BigDye Terminator Kit ver. 3.1 (Applied Biosystems, USA) or QuantumDye Terminator Kit v3 (Tomy Digital Biology, Japan), and ABI genetic analyzer 3500 (Applied Biosystems, USA) or SeqStudio Genetic Analyzer (Applied Biosystems, USA).

Next-generation sequencing, *de novo* assembly, and annotation of mitogenomes

The buffer of the DNA solution was exchanged with buffer EB (Qiagen) to avoid inhibiting the subsequent enzymatic reaction by EDTA. The total DNAs were quantified by Qubit 4 (Thermo Fisher Scientific) with a dsDNA HS Assay kit (Thermo Fisher Scientific, USA). A Colibri ES DNA library Prep kit for Illumina systems with UD indexes (Thermo Fisher Scientific, USA) was used to make the shotgun library. The amount of input DNA was ca. 10 ng, and the library target was 300–800 bp. The fragmentation step was set to 37°C for 10 min. The library amplification was conducted

for 16 cycles. The other procedures were followed by the manufacturer's method. The shotgun library was quantified by Qubit 4 and qualified by TapeStation 4200 (Agilent, USA) with a D1000 DNA assay kit (Agilent, USA). The indexed library was pooled with other libraries, and paired-end sequencing was conducted with the reagent kit V2 (500 cycles) by the MiSeq system (Illumina).

The resulting R1 and R2 fastq files were filtered by fastp ver. 0.23.2 (S Chen et al. 2018), and sequential processes were conducted by CLC Genomics Workbench ver. 24 (Qiagen). The de novo assembly was conducted with default settings, and contigs including target regions were selected by nucleotide BLAST search (McGinnis & Madden 2004; Camacho et al. 2009), both implemented in CLC Genomics Workbench. The genome annotation was conducted with MitoS2 (Donath et al. 2019) and GeSeq (Tillich et al. 2017) automatically. Some PCGs that could not be determined by the tools above were discovered by using ORF finder (<https://www.ncbi.nlm.nih.gov/orffinder/>). Some tRNA genes could not be detected in this study. To make the circular figures of each mitochondrial genome, I used the online version of Proksee (Grant et al. 2023) (<https://proksee.ca/>).

Molecular phylogenetic analyses

In the phylogenetic analyses of the traditional DNA dataset in this study, I used traditional three gene markers (cox1, 18S, and 28S), while mitophylogenomic analyses employed four different datasets for molecular phylogenetic analysis: *i*) amino acid sequences translated from the PCGs only (AA dataset); *ii*) DNA sequences of the PCGs only (DNA dataset); *iii*) DNA sequences of the PCGs combined with two mitochondrial ribosomal RNA genes (12S rRNA [12S] and 16S rRNA [16S]) (DNA + R dataset); and

iv) DNA sequences of the PCGs combined with two mitochondrial RNA genes (12S and 16S) and two nuclear RNA genes (18S and 28S) (DNA + RR dataset).

Additional sequence data were retrieved from The International Nucleotide Sequence Database Collaboration (INSDC) (Table 14): for the traditional dataset, taxa of Archiacanthocephala and Eoacanthocephala used for the mitophylogenomics were employed as the outgroup; for mitophylogenomic analyses, adding to the taxa of Archiacanthocephala and Eoacanthocephala, three rotiferan species, *Philodina citrina*, *Rotaria rotatoria*, and *Seison* sp., were employed as the outgroup; Sequences of each gene were aligned with MAFFT ver. 7 (Kato & Standley 2013) and trimmed by Clipkit ver. 2.7.0 (Steenwyk et al. 2020) and BMGE ver. 1.12 (Criscuolo & Gribaldo 2010). For each dataset, editing and concatenating sequences were done with MEGA ver. 7 (Kumar et al. 2016). Reconstruction of the molecular phylogenetic tree was performed with the maximum-likelihood method (ML) by IQ-TREE3 ver. 3.0.1 (Wong et al. 2025), and Bayesian inference (BI) by MrBayes ver. 3.2.7 (Ronquist et al. 2012): ML analyses were performed under a partition model. The optimal substitution models and schemes for the ML analysis were determined by using ModelFinder (Kalyaanamoorthy et al. 2017): the determined models were listed in Table 15. Branching support within the ML tree was assessed by analyses of 10,000 bootstrap pseudoreplicates with ultrafast bootstrap approximation (Hoang et al. 2018). For BI, the optimal substitution models were selected using PartitionFinder ver. 2.1.1. (Lanfear et al. 2017) under the Akaike criterion (Akaike 1974) with the greedy algorithm (Lanfear et al. 2012): the determined models were also listed in Table 15. Markov chain Monte Carlo process used random starting trees and involved four chains each in two parallel runs for 1,000,000 generations, with the first 25% of trees discarded as burn-in. Run convergence was

evaluated by the average standard deviation of split frequencies being < 0.009 , and the potential scale reduction factor of tree lengths being 1.000. For evaluation of the resulting trees, an ultrafast bootstrap value (UF) higher than 90% and a Bayesian posterior probability (BPP) higher than 0.95 were considered as highly supporting.

RESULTS

Phylogeny based on the traditional dataset

In the resulting trees, Eoacanthocephala was nested within Palaeacanthocephala clade (Fig. 28). The order Polymorphida (Polymorphidae + Plagiorhynchidae + Centrorhynchidae + Isthmosacanthidae + Pyriproboscidae). *Metacanthocephalus ovicephalus* and *Pseudorhadinorhynchus leuciscus* were grouped within Leptorhynchoididae. Echinorhynchidae was shown to be polyphyletic; however, all species newly added in this study (*Echinorhynchus dissimilis*, *E. gadi* [type species], *E. hexagrammi*, *E. lotellae*, and *E. sasakiae*) formed a well-supported monophyletic clade. Within Pomphorhynchidae, *Pomphorhynchus alemniscus* and *P. pagrosomi* formed a sister-group relationship. Cavisomatidae was split into two distinct lineages, with *Cavisoma magnum* branching within the genus *Rhadinorhynchus*. Transvenidae was recovered as a monophyletic group except for *Pararhadinorhynchus magnus*. The two additional species included in this study, *Sclerocollum neorubrimaris* and *Trajectura ikedai*, were clearly nested within the transvenid clade. Micracanthorhynchinidae, represented by *M. segmentata*, *Pseudocavisoma setoense*, and three other species of *Micranthorhynchina*, formed a single, distinct lineage relative to other families. Isthmosacanthidae, including *Metarhadinorhynchus latolabracis*, were closely related to Pyriproboscidae and *Sharpilosentis peruviansis*.

Branch support values for deeper relationships among families were generally low. Only the clade comprising Arhythmacanthidae, Filisomatidae, Paracanthocephalidae, and Pseudoacanthocephalidae received full support from both ML and BI analyses (UF = 100, BPP = 1.00).

Phylogeny based on the mitochondrial PCGs, 18S, and 28S

PCGs and ribosomal genes. The mitochondrial genomes obtained in this study exhibited the same gene order in both protein-coding and ribosomal genes as previously reported for other acanthocephalans (Fig. 29). As in earlier studies, all genomes lacked *atp8*, and gene order was completely conserved across species (Figs. 29–31; Tables 16–23). Several tRNA genes, however, could not be detected with any of the annotation programs employed.

AA dataset. The amino-acid dataset recovered a topology broadly consistent with previous mitophylogenomic studies (Fig. 32), and all eight newly sequenced species occupied phylogenetic positions expected from earlier molecular evidence. Palaeacanthocephala was clearly shown as a monophyletic group. *Sclerocollum neorubrimaris* (Transvenidae) formed a sister relationship with the clade composed of Cavisomatidae + Rhadinorhynchidae, whereas *Metarhadinorhynchus lateolabracis* (Isthmosacanthidae) was placed as sister to the remaining polymorphidan taxa. Echinorhynchida was strongly supported as paraphyletic with respect to the monophyletic Polymorphida. Within Echinorhynchida, most branches showed high support (UF > 90; BPP > 0.95), although one deep node remained weakly supported (UF < 90). *Echinorhynchus gymnocyprii* was recovered in a lineage distinct from other *Echinorhynchus* species. Within Polymorphida, the branching order among

Centrorhynchidae and Polymorphidae remained ambiguous, and several internal branches within Polymorphidae received low support.

DNA dataset. The topology inferred from the nucleotide dataset was overall similar to that obtained from the AA dataset (Fig. 33), but support values were generally lower. Within Echinorhynchida, the support for relationships among eight families forming the sister group to Polymorphida was reduced, with the weakest node showing UF = 56. The branch placements of the newly sequenced *S. neorubrimaris* and *M. lateolabracis* remained the same as in the AA tree. A notable change was observed in Polymorphida: *Southwellina hispida* and *Polymorphus minutus*, recovered as sister species in the AA dataset, were no longer placed together in the DNA dataset, although support for both placements was low (UF < 80). As in the AA dataset, *E. gymnocyprii* was separated from other *Echinorhynchus* species.

DNA + R dataset. Incorporating ribosomal regions improved the overall resolution within Palaeacanthocephala (Fig. 34). Most branches within Echinorhynchida reached high support, with only one node remaining low (UF < 90). The positions of *S. neorubrimaris* and *M. lateolabracis* were consistent with those in the AA and DNA analyses. In contrast, support values within Polymorphida showed little improvement, and several internal branches—particularly within Polymorphidae—remained poorly resolved. The placement of *E. gymnocyprii* again differed from that of other *Echinorhynchus* species.

DNA + RR dataset. The DNA + RR dataset yielded the highest overall support within Echinorhynchida, with all nodes receiving UF > 95 (Fig. 35). The phylogenetic relationships among families in this order were recovered with strong confidence, and branch lengths were generally shorter than in the AA and DNA analyses. The positions

of the newly added *S. neorubrimaris* and *M. lateolabracis* were identical to those recovered in the other datasets. However, resolution within Polymorphida remained low, and support values for several internal nodes—including those defining relationships within Polymorphidae—did not improve even under this dataset. As in all other analyses, *E. gymnocyprii* was consistently placed outside the main *Echinorhynchus* clade.

DISCUSSION

Traditional dataset

My analysis (Fig. 28) reaffirmed that the use of only three loci (cox1, 18S, and 28S) is useful for confirming monophyly of some families, but extremely limited for resolving relationships among families within the class. This limitation has been noted previously. Huston et al. (2020), for instance, analyzed 18S and 28S and proposed several taxonomic revisions (e.g., the establishment of Pyriproboscidae and the transfer of Isthmosacanthidae to Polymorphida). However, although they were able to recover the monophyly of major lineages, the branching order among families remained poorly resolved. Similar molecular phylogenetic studies covering the entire class remain scarce (e.g., García-Varela & Nadler 2005, 2006), and most datasets available to date are biased toward either Echinorhynchida (e.g., Kita et al. 2024c; Aguilar-Aguilar et al. 2025; Ghanei-Motlagh et al. 2025) or Polymorphida (e.g., García-Varela et al. 2013). My analysis suggests that severe long-branch attraction may occur within Leptorhynchoiidae, which likely results in artificially drawing that taxon toward Archiacanthocephala and producing an apparent polyphyly of Palaeacanthocephala. Such a pattern has not been recovered in studies that excluded most polymorphidan taxa

(e.g., Kita et al. 2024c; Aguilar-Aguilar et al. 2025; Ghanei-Motlagh et al. 2025). These comparisons strongly indicate that the three-gene dataset alone cannot reliably resolve family-level phylogeny. While this approach remains useful for species- and genus-level comparisons among closely related taxa, a more information-rich dataset is essential for analyses that target higher-level relationships.

My analyses also reveal that several taxa appear polyphyletic, including Cavisomatidae, Plagiorhynchidae, *Echinorhynchus*, *Filisoma*, *Pararhadinorhynchus*, and several genera within Polymorphidae. Cavisomatidae is currently considered to consist of six genera (Amin 2013; Kita & Kajihara 2025), yet Kita & Kajihara (2025) demonstrated that *Cavisoma magnum*, the type species of the type genus of the family, clusters fully within the clade of *Rhadinorhynchus*. In addition, Aguilar-Aguilar et al. (2025) showed that *Caballerorhynchus lamothei* represents a distinct lineage from *Cavisoma*. My results are consistent with these findings, indicating that the validity of Cavisomatidae needs to be re-evaluated carefully. Similarly, the polyphyly of Plagiorhynchidae, *Filisoma*, and *Pararhadinorhynchus* has been noted in several previous studies (García-Varela et al. 2020a; Aguilar-Aguilar et al. 2025). For Plagiorhynchidae and *Filisoma*, the absence of *cox1* data for *Lueheia azteca* and the absence of 18S and 28S data for *Filisoma argusum* limit my ability to make definitive taxonomic conclusions. Analyses incorporating the missing loci are required before these taxa can be assessed with confidence. In the case of *Pararhadinorhynchus*, I cannot exclude the possibility that one of two OTUs included in my dataset was misidentified; therefore, re-examination of voucher specimens will be necessary. A more detailed discussion of *Echinorhynchus* is provided below.

Dataset performance comparison and overall phylogenetic patterns

Among the four datasets examined (Figs. 32–35), the DNA + RR dataset produced the strongest and most stable phylogenetic signals, particularly within Echinorhynchida, where all deeper nodes showed high support. Previous studies have demonstrated that several families in this order—most notably Rhadinorhynchidae, Transvenidae, and Micracanthorhynchinidae—tend to exhibit long branches in the traditional dataset, which often depress support values and introduce long-branch attraction artifacts (Gao et al. 2022; Amin et al. 2023; Kita et al. 2024b; Ghanei-Motlagh et al. 2025). By integrating mitochondrial protein-coding genes with ribosomal regions from both mitochondrial and nuclear genomes, my analyses effectively mitigated these issues and improved branch stability: the approximate phylogenetic relationships among families are similar to those reported by Kita et al. (2024c), and other studies have also yielded similar trees (e.g., Gao et al. 2022; Ghanei-Motlagh et al. 2025), while relationships among Leptorhynchoididae, Rhadinorhynchidae, and Polymorphida were clearly different from Amin et al. (2023). In contrast, internal relationships within Polymorphida did not improve across any dataset. Although the addition of *Metarhadinorhynchus lateolabracis* (Isthmosacanthidae) represents the first mitogenomic sampling for the family, and its position within this order was consistently recovered, most relationships among Polymorphidae, Centrorhynchidae, and Plagiorhynchidae remained poorly resolved. These results indicate that Polymorphida may require fundamentally different types of genomic data—such as transcriptomes or nuclear genomes—to resolve its deeper radiations. With the exception of the pioneering work of Wey-Fabrizius et al. (2014), such datasets remain scarce in Acanthocephala.

Transvenidae and the major Echinorhynchida assemblage

This study provides the first mitogenomic sampling of Transvenidae, represented by *Sclerocollum neorubrimaris*, and the resulting trees offer the most robust assessment to date of the evolutionary relationships among several major families within Echinorhynchida. Across all datasets, but especially under DNA + RR, Transvenidae was consistently recovered as sister to a clade including Rhadinorhynchidae, and Cavisomatidae, while Micracanthorhynchinidae was shown as sister to Transvenidae + Rhadinorhynchidae + Cavisomatidae. These four families have repeatedly exhibited long branches and unstable placements in the previous molecular phylogenies, yet they formed a single clade in the present analyses. This assemblage also exhibits several morphological features that may reflect shared ancestry. Rhadinorhynchidae and Cavisomatidae share a characteristic arrangement of four tubular cement glands (cf. Kita & Kajihara 2025), whereas Transvenidae have two to four tubular cement glands and Micracanthorhynchinidae have four to six claviform cement glands (cf. Pichelin & Cribb 2001; Lisitsyna et al. 2023), suggesting a directional trend in cement-gland evolution within this clade. Proboscis morphology and trunk spination patterns likewise show degrees of overlap among these families, though homoplasy remains likely. By bringing Transvenidae into a mitochondrial phylogenomic context for the first time, my results provide critical molecular evidence that helps stabilize the relationships among these previously problematic families. Despite this progress, several families traditionally assigned to Echinorhynchida—including Diplosentidae, Fessisentidae, Filisomatidae, Paracanthocephalidae, and Spinulacorpidae—remain unsampled in mitogenome-based studies. Incorporating these missing taxa will be essential for further evaluating the internal structure of this order

and for determining whether additional lineages belong within the Transvenidae–Rhadinorhynchidae–Cavisomatidae–Micracanthorhynchidae assemblage. An additional point of interest within this assemblage concerns *Echinorhynchus gymnocyprii*, which was consistently placed outside the main *Echinorhynchus* clade and instead positioned closer to Pomphorhynchidae in all datasets. This placement contradicts traditional classifications treating Echinorhynchidae as a coherent family and highlights unresolved taxonomic issues within the group. Because the published mitochondrial and nuclear ribosomal sequences of *E. gymnocyprii* lack accompanying morphological documentation, misidentification cannot be ruled out. However, as suggested by Kita & Kajihara (2023), it is also possible that the taxa (*E. salmonis* and *E. veli*) represent genuinely divergent lineages more closely allied with Pomphorhynchidae than with other *Echinorhynchus* species. Clarifying this case will require integrative analyses combining rigorous morphological reassessment with fresh DNA-confirmed material.

All datasets consistently recovered Echinorhynchida as paraphyletic with respect to Polymorphida. This pattern has been observed in several previous analyses (e.g., Huston et al. 2020; Kita et al. 2023) and conflicts with traditional morphology-based classifications, which treated Echinorhynchida as a natural, monophyletic group. Many of the diagnostic traits used historically to define Echinorhynchida—such as the presence or absence of trunk spines, cement gland number and arrangement, and various proboscis characters—(cf. Petrochenko 1956; Yamaguti 1963; Amin 1987) are now known to exhibit substantial homoplasy. My findings strongly support the conclusion that Echinorhynchida, as currently circumscribed, does not represent a natural group and warrants taxonomic reevaluation. While formal revision is beyond the scope of the

present study, the phylogenetic framework developed here provides a robust basis for future reassessment.

Isthmosacanthidae and family-level relationships within Polymorphida

The inclusion of *Metarhadinorhynchus lateolabracis* (Isthmosacanthidae) constitutes the first mitogenomic sampling for this family, and its placement within Polymorphida was consistently and strongly supported across all datasets. This finding corroborated earlier studies using nuclear ribosomal DNA and multi-marker analyses (e.g., Huston et al. 2020; Kita et al. 2024a) and firmly established Isthmosacanthidae as a distinct early-diverging lineage. This strongly suggests an evolutionary scenario in which the common ancestor of Polymorphida parasitized fish (freshwater to marine), subsequently diverging to parasitize a wide variety of hosts (avians or mammals) with differing habitats (terrestrial or aquatic). In contrast, relationships among the remaining families of Polymorphida—Centrorhynchidae, Plagiorhynchidae, and Polymorphidae—remained unstable. Several internal branches received low support even in the most information-rich dataset (DNA + RR). This persistent lack of resolution suggests either rapid radiation within the order or insufficient phylogenetic signal in mitochondrial genomes. Past mitophylogenomic studies have relied primarily on amino acid datasets, and although my study explored multiple data-processing strategies, none yielded a stable topology for internal relationships. Resolving the deeper phylogenetic structure of Polymorphida will require broader taxon sampling and the integration of nuclear genomic or transcriptomic data, which remain scarce for this group.

Conclusions

Overall, the present mitophylogenomic analyses, together with the traditional three-gene dataset, provide a substantially improved framework for understanding family-level relationships within Palaeacanthocephala. The DNA + RR dataset in particular yields a well-supported backbone for Echinorhynchida and clarifies the placement of previously problematic families such as Transvenidae and Isthmosacanthidae. At the same time, the persistence of poorly resolved nodes—especially within Polymorphida except Isthmosacanthidae—and the repeated recovery of non-monophyletic assemblages underscore that palaeacanthocephalan systematics is still far from settled. Future progress will require expanded taxon sampling across underrepresented families, the incorporation of genomic-scale nuclear data, and integrative analyses that explicitly combine molecular evidence with carefully re-evaluated morphological characters. The phylogenetic backbone presented here offers a necessary starting point for such efforts and provides a stable context within which to reconsider higher-level classification in Palaeacanthocephala.

CHAPTER IV

SUMMARY

This thesis provides a comprehensive, systematic, and phylogenetic reassessment of acanthocephalans parasitic in marine and brackish-water fishes of Japan, with a particular focus on higher-level relationships within the class Palaeacanthocephala. Although Japan has a long history of acanthocephalan research, the taxonomy of many species has remained unstable due to incomplete original descriptions, limited modern redescrptions, and substantial gaps in molecular sampling across families. To address these issues, I conducted extensive field collections, detailed morphological analyses, and multi-locus and mitogenomic phylogenetic studies integrating newly obtained data from previously unsampled lineages.

During my PhD, I published 10 papers on 11 species of palaeacanthocephalans, each presented by both morphological descriptions (based on light and scanning electron microscopy) and molecular data (Kita & Kajihara 2021, 2023, 2025; Kita et al. 2023, 2024a–d; 2025a, b). Of these 11 species, three were new to science (Kita & Kajihara, 2023; Kita et al. 2024c, 2025a), one of which parasitizes frogs (Kita et al. 2025a) and is therefore not included in Chapter II of this thesis. In it, I provided morphological accounts for the remaining 10 fish-parasitizing species, along with another 12 species based on my unpublished results. These 22 species represent 15 genera, 11 families, three orders, and two classes within the phylum Acanthocephala. Among these higher taxa, I amended the diagnoses of three families—Cavisomatidae (Kita & Kajihara 2025), Leptorhynchoididae (Kita et al. 2023), and Micracanthorhynchinidae (Kita et al. 2024c). I also proposed amended diagnoses for the

family Filisomatidae (Kita & Kajihara 2025) and for two genera, *Indorhynchus* Golvan, 1969, and *Neotegorhynchus* Lisitsyna et al., 2022 (Kita et al. 2024b), although no specimens from these taxa were examined. The unpublished 12 species include such poorly known species as *Neoechinorhynchus* (*Hebesoma*) *yamagutii*, *Heterosentis fusiformis*, *Acanthocephaloides neobythitis*, *Echinorhynchus dissimilis*, and *E. lotellae*. In addition, *Cavisoma magnum*, *Rhadinorhynchus laterospinosus*, and *Sclerocollum neorubrimaris* were recorded from Japan for the first time, considerably expanding their known distributions. My comparative evaluation of morphological traits—including proboscis armature, trunk spination, cement gland number and structure, and egg wall morphology—indicated that some characters traditionally used at higher taxonomic levels exhibited greater phylogenetic utility than previously appreciated, whereas others showed clear evidence of homoplasy. In particular, trunk spination and cement gland organization appeared to contain signals relevant to deep-level systematics, although certain states were also prone to convergence. Overall, Chapter II established an updated taxonomic foundation for marine acanthocephalans in Japan and underscored the necessity of integrating morphology with molecular evidence.

Built on this groundwork, Chapter III addressed long-standing uncertainty in the interfamilial relationships within Palaeacanthocephala. Traditional higher-level classifications based on morphology varied widely, with different authors emphasizing distinct characteristics, often leading to conflicting hypotheses. Likewise, molecular studies based solely on *cox1*, 18S, and 28S have succeeded in clarifying the placement of many families but have consistently failed to provide stable internal relationships, partly due to limited phylogenetic signal and the prevalence of long-branch attraction in several lineages. To overcome these limitations, I generated partial sequences of the

three traditional loci from multiple species across Japanese waters and obtained complete mitochondrial genomes from eight palaeacanthocephalan species, including the first mitogenomic representatives of Isthmosacanthidae and Transvenidae. Using them and other public data, I constructed five phylogenetic datasets (including the traditional gene combination dataset) that incorporated amino acid sequences, nucleotide alignments of protein-coding genes, and combined mitochondrial and nuclear rRNA genes. Comparative analyses revealed that datasets incorporating ribosomal regions—particularly the DNA + RR dataset (nucleotide sequences of mitochondrial 12 protein-coding genes + mitochondrial two ribosomal genes + nuclear two ribosomal genes)—produced the most stable and well-supported topologies, especially within Echinorhynchida. These analyses elucidated relationships among several historically problematic families, recovering a robust clade comprising Rhadinorhynchidae, Cavisomatidae, Transvenidae, and Micracanthorhynchinidae. The newly added *Sclerocollum neorubrimaris* (Transvenidae) consistently occupied a position that clarified the placement of the family for the first time. Likewise, *Metarhadinorhynchus lateolabraxis* (Isthmosacanthidae) was stably recovered as an early-diverging lineage of Polymorphida, providing the first confirmation of its phylogenetic position. In contrast, deeper relationships within Polymorphida remained poorly resolved across all datasets, suggesting either rapid radiation or insufficient phylogenetic signal in the present datasets alone. These results implied that resolving internal relationships within Polymorphida would require expanded taxonomic sampling and, crucially, the incorporation of nuclear genomic data such as transcriptomes—an area in which acanthocephalan research remains limited. Importantly, all analyses consistently recovered Echinorhynchida as paraphyletic with

respect to Polymorphida, contradicting long-held morphological classifications. This finding indicated that several classical diagnostic characters—such as trunk spines, cement gland configuration, and specific aspects of proboscis architecture—would be prone to convergence and do not reliably reflect evolutionary history. Although this thesis did not attempt a formal taxonomic revision of these orders, the phylogenetic framework established here lays the essential foundation for re-evaluating morphological characteristics and identifying true synapomorphies.

Together, the two chapters of this thesis provide an integrative reassessment of the systematics and higher-level relationships of marine fish-parasitizing acanthocephalans. Chapter II delivers an updated morphological and taxonomic baseline for the Japanese fauna, while Chapter III establishes one of the most robust phylogenomic frameworks to date for Palaeacanthocephala. By combining detailed morphological analyses with multi-locus and mitogenomic datasets, this work advances the understanding of acanthocephalan diversity, evolution, and taxonomy, and offers a stable platform for future morphological, genomic, and ecological studies across the phylum.

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TABLES

Table 1. A checklist of 60 species (in 13 families, four orders, and two classes) of fish-parasitizing acanthocephalans recorded from Japan. Only those identified to the species level are listed.

Taxon	Host	Locality	Reference
1. Class Eoacanthocephala			
1. Order Neoechinorhynchida			
1. Family Neoechinorhynchidae			
1. <i>Neoechinorhynchus</i> (<i>Hebesoma</i>) <i>yamagutii</i>	<i>Mugil cephalus</i> (Mugilidae)	Ariake Sea, Seto Inland Sea, Suruga Bay	Yamaguti (1935, 1939); Tkach et al. (2014); Kita (unpubl.)
	<i>Chelon haematocheli</i> (Mugilidae)		
2. <i>Neoechinorhynchus</i> (<i>Neoechinorhynchus</i>) <i>coiliae</i>	<i>Coilia nasus</i> (Engraulidae)	Ariake Sea	Yamaguti (1939)
3. <i>Neoechinorhynchus</i> (<i>Neoechinorhynchus</i>) <i>johnii</i>	<i>Protonibea diacanthus</i> (Sciaenidae)	East China Sea	Yamaguti (1939)
4. <i>Neoechinorhynchus zacconis</i> l	<i>Zacco platypus</i> (Cyprinidae)	Lake Kobata (Kyoto)	Yamaguti (1935)
2. Order Gyraacanthocephala			
2. Family Quadrigyridae			
5. <i>Acanthogyrus</i> (<i>Acanthosentis</i>) <i>alternatospinus</i>	<i>Rhodeus ocellatus</i> (Cyprinidae)	Lake Biwa (Shiga)	Amin (2005)
6. <i>Acanthogyrus</i> (<i>Acanthosentis</i>) <i>parareceptaculis</i>	<i>Cobitis biwae</i> (Cobitidae)	Lake Biwa (Shiga)	Amin (2005)
7. <i>Acanthogyrus</i> (<i>Acanthosentis</i>) <i>tylosuri</i>	<i>Ablennes hians</i> (Belonidae)	Lake Hamana (Shizuoka), off Kochi	Yamaguti (1939)
2. Class Palaeacanthocephala			
3. Order Echinorhynchida			
3. Family Arhythmacanthidae			
8. <i>Acanthocephaloides claviformis</i>	<i>Physiculus japonicus</i> (Moridae)	off Otsuchi (Iwate)	Araki & Machida (1987)
9. <i>Acanthocephaloides ichiharai</i>	<i>Physiculus japonicus</i> (Moridae)	off Otsuchi (Iwate), off Kesenuma (Miyagi)	Araki & Machida (1987)
	<i>Paralichthys olivaceus</i> (Paralichthyidae)		
10. <i>Acanthocephaloides neobythitis</i>	<i>Neobythites macrops</i> (Ophidiidae)	off Obama (Fukui)	Yamaguti (1939); Kita (unpubl.)
	<i>Sebastiscus marmoratus</i> (Sebastidae)		
11. <i>Acanthocephaloides rhinoplagusiae</i>	<i>Paraplusia japonica</i> (Cynoglossidae)	Seto Inland Sea, Toyama Bay, Sagami Bay	Ichihara (1965); Yamaguti (1935)
12. <i>Heterosentis fusiformis</i>	<i>Sphoeroides</i> sp. (Tetraodontidae)	off Wakayama, off Mie, off Kannonzaki (Kanagawa)	Yamaguti (1935); Kihara (1959c); Kita (unpubl.)
	<i>Takifugu niphobles</i> (Tetraodontidae)		
13. <i>Heterosentis plotosi</i>	<i>Plotosus lineatus</i> (Siluridae)	off Misaki (Kanagawa), off Wakayama, off Momotori (Mie)	Fukui & Morisita (1936); Yamaguti (1935)
14. <i>Hypoechinorhynchus alaeopis</i>	<i>Poecilopsetta plinthus</i> (Pleuronectidae)	off Maisaka (Shizuoka)	Yamaguti (1939)
4. Family Cavisomatidae			

15. <i>Cavisoma magnum</i>	<i>Pentapodus caninus</i> (Nemipteridae)	off Yomitan (Okinawa)	Kita & Kajihara (2025)
16. <i>Neorhadinorhynchus aspinosus</i>	<i>Siganus fuscescens</i> (Siganidae)	off Momotori (Mie), off Numazu (Shizuoka), Tokyo (market)	Fukui & Morisita (1937a); Kamegai (1963); Yamaguti (1939)
	<i>Prionurus scalprum</i> (Acanthuridae)		
	<i>Conger myriaster</i> (Congridae)		
17. <i>Rhadinorhynchoides miyagawai</i>	<i>Salvelinus malma</i> (Salmonidae)	Taguchi River (Niigata)	Fukui & Morisita (1937b)
5. Family Echinorhynchidae			
18. <i>Echinorhynchus cotti</i>	<i>Oncorhynchus masou</i> (Salmonidae)	Kanita River (Aomori), Lake Biwa (Shiga)	Amin et al. (2007); Fukui & Morisita (1937b); Nagasawa & Egusa (1981); Shimazu (1999); Yamaguti (1935, 1939)
	<i>Oncorhynchus mykiss</i> (Salmonidae)		
	<i>Salvelinus leucomaensis</i> (Salmonidae)		
	<i>Pseudobagrus nudiceps</i> (Bagridae)		
	<i>Anguilla japonica</i> (Anguillidae)		
	<i>Cottus reinii</i> (Cottidae)		
	<i>Gnathopogon caeruleus</i> (Cyprinidae)		
	<i>Gymnogobius isaza</i> (Gobiidae)		
	<i>Hemibarbus barbus</i> (Cyprinidae)		
	<i>Plecoglossus altivelis</i> (Plecoglossidae)		
	<i>Sarcocheilichthys variegatus</i> (Cyprinidae)		
	<i>Silurus biwaensis</i> (Siluridae)		
	<i>Tridentiger brevispinis</i> (Gobiidae)		
	<i>Channa argus</i> (Channidae)		
	<i>Cyprinus carpio</i> (Cyprinidae)		
	<i>Opsariichthys uncirostris</i> (Cyprinidae)		
	<i>Tanakia limbata</i> (Cyprinidae)		
	<i>Rhinogobius</i> sp. (Gobiidae)		
	<i>Hypomesus nipponensis</i> (Osmeridae)		
19. <i>Echinorhynchus dissimilis</i>	<i>Lotella phycis</i> (Moridae)	off Maisaka (Shizuoka), off Otsuchi (Iwate), off Kesenuma (Miyagi),	Araki & Machida (1987); Yamaguti (1939); Kita (unpubl.)
	<i>Sebastes oblongus</i> (Sebastidae)	off Onahama (Fukushima), off Samani (Hokkaido)	
	<i>Hexagrammos otakii</i> (Hexagrammidae)		
	<i>Paralichthys olivaceus</i> (Paralichthyidae)		
	<i>Verasper moseri</i> (Pleuronectidae)		
	<i>Physiculus japonicus</i> (Moridae)		
	<i>Lophius litulon</i> (Lophiidae)		
	<i>Zeus faber</i> (Zeidae)		
	<i>Pennahia argentata</i> (Sciaenidae)		

20. *Echinorhynchus gadi*

Oncorhynchus keta (Salmonidae)
Oncorhynchus masou (Salmonidae)
Chlorophthalmus albatrossis (Chlorophthalmidae)
Stereolepis doederleini (Stereolepidae)
Arctoscopus japonicus (Trichodontidae)
Pennahia argentata (Sciaenidae)
Stichaeus nozawae (Stichaeidae)
Stichaeus grigorjewi (Stichaeidae)
Bothrocara zestum (Zoarcidae)
Sebastes owstoni (Sebastidae)
Sebastes vulpes (Sebastidae)
Sebastes oblongus (Sebastidae)
Pleurogrammus azonus (Hexagrammidae)
Hexagrammos stelleri (Hexagrammidae)
Hexagrammos otakii (Hexagrammidae)
Myoxocephalus jaok (Cottidae)
Myoxocephalus polyacanthocephalus (Cottidae)
Dasycottus setiger (Psychrolutidae)
Gymnocanthus herzensteini (Cottidae)
Hemitripterus villosus (Hemitriptoridae)
Aptocyclus ventricosus (Cyclopteridae)
Liparis tanakae (Liparidae)
Liparis owstoni (Liparidae)
Liparidae sp.
Careproctus sp. (Liparidae)
Careproctus trachysoma (Liparidae)
Atheresthes evermanni (Pleuronectidae)
Hippoglossoides dubius (Pleuronectidae)
Cleisthenes pinetorum (Pleuronectidae)
Verasper moseri (Pleuronectidae)
Lepidopsetta mochigarei (Pleuronectidae)
Myzopsetta punctatissima (Pleuronectidae)
Pseudopleuronectes herzensteini (Pleuronectidae)
Glyptocephalus stelleri (Pleuronectidae)

Miomote River (Niigata), off Iwanai (Hokkaido), Tokyo, off Onahama (Fukushima), off Otsuchi (Iwate), off Samani (Hokkaido), off Kamo (Yamagata), off Kesenuma (Miyagi), off Kushiro (Hokkaido), off Fukaura (Aomori), off Usujiri (Hokkaido), Sea of Japan, Hokkaido

Araki & Machida (1987); Fujita (1920); Kamegai (1962c); Van Cleave (1931); Yamaguti (1935)

	<i>Microstomus achne</i> (Pleuronectidae)		
	<i>Reinhardtius hippoglossoides</i> (Pleuronectidae)		
	<i>Physiculus japonicus</i> (Moridae)		
	<i>Lotella phycis</i> (Moridae)		
	<i>Gadus macrocephalus</i> (Gadidae)		
	<i>Gadus chalcogrammus</i> (Gadidae)		
	<i>Lophius litulon</i> (Lophiidae)		
21. <i>Echinorhynchus hexagrammi</i>	<i>Sebastes oblongus</i> (Sebastidae)	off Samani (Hokkaido), off Kushiro, Akkeshi Bay	Araki & Machida (1987); Katahira & Nagasawa (2011); Kita & Kajihara (2021)
	<i>Hexagrammos stelleri</i> (Hexagrammidae)		
	<i>Hemitripterus villosus</i> (Hemitriptoridae)		
	<i>Podothecus sachi</i> (Agonidae)		
	<i>Verasper moseri</i> (Pleuronectidae)		
	<i>Eleginus gracilis</i> (Gadidae)		
	<i>Liparis</i> sp. (Liparidae)		
22. <i>Echinorhynchus kushirosensis</i>	<i>Verasper moseri</i> (Pleuronectidae)	off Kushiro (Hokkaido)	Fujita (1921)
23. <i>Echinorhynchus lotellae</i>	<i>Sebastolobus macrochir</i> (Sebastidae)	off Otsuchi (Iwate), off Onahama (Fukushima), off Maisaka (Shizuoka)	Yamaguti (1939); Araki & Machida (1987); Kita (unpubl.)
	<i>Physiculus japonicus</i> (Moridae)		
	<i>Lophius litulon</i> (Lophiidae)		
	<i>Liparis tessellatus</i> (Liparidae)		
	<i>Verasper moseri</i> (Pleuronectidae)		
	<i>Lotella phycis</i> (Moridae)		
	<i>Zeus faber</i> (Zeidae)		
24. <i>Echinorhynchus parasiluri</i>	<i>Silurus asotus</i> (Siluridae)	Lake Biwa (Shiga)	Fukui (1929)
25. <i>Echinorhynchus sasakiæ</i>	<i>Hexagrammos lagocephalus</i> (Hexagrammidae)	Akkeshi Bay, off Nemuro (Hokkaido)	Kita & Kajihara (2023)
26. <i>Echinorhynchus truttae</i>	<i>Salvelinus leucomaensis</i> (Salmonidae)	Shikotan Island (Hokkaido)	Zhukov (1960)
27. <i>Echinorhynchus yamagutii</i>	<i>Conger myriaster</i> (Congridae)	off Fukui	Golvan (1969)
	<i>Bothrocara zestum</i> (Zoarcidae)		
6. Family Leptorhynchoididae			
28. <i>Metacanthocephalus ovicephalus</i>	<i>Pseudopleuronectes obscurus</i> (Pleuronectidae)	off Fukaura (Aomori), off Otsuchi (Iwate), off Kushiro (Hokkaido) off Iwanai (Hokkaido), off Rausu (Hokkaido), Shikotan Island (Hokkaido)	Araki & Machida (1987); Kita et al. (2023); Zhukov (1960)
	<i>Pseudopleuronectes schrenki</i> (Pleuronectidae)		
	<i>Pseudopleuronectes herzensteini</i> (Pleuronectidae)		
	<i>Pseudopleuronectes yokohamae</i> (Pleuronectidae)		
	<i>Acantholumpenus mackayi</i> (Lumpenidae)		
29. <i>Metacanthocephalus pleuronichthydis</i>	<i>Pleuronichthys cornutus</i> (Pleuronectidae)	off Shibukawa (Okayama)	Yamaguti (1959)

30. <i>Pseudorhadinorhynchus leuciscus</i>	<i>Spirinchus lanceolatus</i> (Osmeridae) <i>Tribolodon hakonensis</i> (Cyprinidae)	off Samani (Hokkaido), off Otsuchi (Iwate), off Esashi (Hokkaido), off Moheji (Hokkaido), off Tomihama (Hokkaido), off Hama-Atsuma (Hokkaido), Hei River (Iwate)	Machida & Araki (1982); Araki & Machida (1987); Nagasawa & Takami (2017); Hashimoto (2000); Kita (unpubl.)
31. <i>Pseudorhadinorhynchus samegaiensis</i>	<i>Oncorhynchus mykiss</i> (Salmonidae) <i>Oncorhynchus masou</i> (Salmonidae) <i>Anguilla japonica</i> (Anguillidae) <i>Hemibarbus barbus</i> (Cyprinidae) <i>Opsariichthys uncistrostris</i> (Cyprinidae) <i>Tribolodon hakonensis</i> (Cyprinidae) <i>Gasterosteus microcephalus</i> (Gasterosteidae) <i>Gymnogobius isaza</i> (Gobiidae)	Lake Biwa (Shiga), Samegai Trout Experimental Station (Shiga)	Nakajima & Egusa (1975b); Amin et al. (2007)
7. Family Micracanthorhynchinidae			
32. <i>Pseudocavisoma setoense</i>	<i>Chromis notata</i> (Pomacentridae)	off Ihota (Yamaguchi)	Kita et al. (2024c)
8. Family Paracanthocephalidae			
33. <i>Acanthocephalus echigoensis</i>	<i>Oncorhynchus mykiss</i> (Salmonidae) <i>Oncorhynchus nerka</i> (Salmonidae) <i>Oncorhynchus keta</i> (Salmonidae) <i>Oncorhynchus masou</i> (Salmonidae) <i>Plecoglossus altivelis</i> (Plecoglossidae)	Kizaki Fish Cultural Station (Nagano), Lake Aoki (Nagano), Lake Biwa, Sapporo (Hokkaido), Hokkaido, Miomote River (Niigata), Sano River (Yamanashi)	Fujita (1920, 2021); Harada (1935); Kataoka & Momma (1934); Van Cleave (1931)
34. <i>Acanthocephalus gotoi</i>	<i>Anguilla japonica</i> (Anguillidae) <i>Anguilla marmorata</i> (Anguillidae) <i>Silurus asotus</i> (Siluridae) <i>Odontobutis obscurus</i> (Odontobutidae) <i>Gymnogobius urotaenia</i> (Gobiidae) <i>Rhinogobius similis</i> (Gobiidae) <i>Rhinogobius</i> sp. (Gobiidae)	Tokyo, Aichi, Lake Ogura (Kyoto), Lake Biwa (Shiga), Lake Suwa (Nagano), Kamo River (Hiroshima), Renjoji River, Soja River (Ehime), Hiwatashi River (Kochi), various localities**	Van Cleave (1925); Fukui & Morisita (1936); Katahira & Nagasawa (2014); Shimizu & Nagasawa (2018); Yamaguti (1935); Yamaguti (1939)
35. <i>Acanthocephalus japonicus</i>	<i>Hexagrammos otakii</i> (Hexagrammidae) <i>Hexagrammos agrammus</i> (Hexagrammidae) <i>Siganus fuscescens</i> (Siganidae) <i>Inimicus japonicus</i> (Synanceiidae)	Atsumi Peninsula (Aichi), off Momotori (Mie), off Kesenuma (Miyagi); Kawasaki (Kanagawa: market); Sagami Bay	Fukui & Morisita (1936, 1937a); Araki & Machida (1987); Kihara (1959b); Kamegai (1962b)
36. <i>Acanthocephalus longiacanthus</i>	<i>Anguilla marmorata</i> (Anguillidae) <i>Rhinogobius nagoyae</i> (Gobiidae) <i>Rhinogobius fluviatilis</i> (Gobiidae) <i>Rhinogobius</i> sp. (Gobiidae)	Renjoji River (Ehime), Tenchi River (Hiroshima), Kamo River (Hiroshima), Soja River (Ehime), Hiwatashi River (Kochi)	Katahira & Nagasawa (2014); Shimizu & Nagasawa (2018)

37. <i>Acanthocephalus minor</i>	<i>Silurus asotus</i> (Siluridae)	Toyama, Lake Biwa (Shiga), Obama (Fukui), A trout culture experimental station (Hokkaido), Ryukei River (Hokkaido)	Awakura (1972); Fukui & Morisita (1936); Nagasawa et al. (1982); Nagasawa & Nitta (2015); Yamaguti (1935, 1939)
	<i>Odontobutis obscura</i> (Odontobutidae)		
	<i>Carassius</i> sp. (Cyprinidae)		
	<i>Oncorhynchus masou</i> (Salmonidae)		
	<i>Oncorhynchus mykiss</i> (Salmonidae)		
	<i>Salvelinus malma</i> (Salmonidae)		
	<i>Gasterosteus aculeatus</i> (Gasterosteidae)		
	<i>Gymnogobius urotaenia</i> (Gobiidae)		
	<i>Gymnogobius operiens</i> (Gobiidae)		
	<i>Opsariichthys uncirostris</i> (Cyprinidae)		
38. <i>Acanthocephalus opsariichthydis</i>	<i>Zacco platypus</i> (Cyprinidae)	Yodo River (Osaka), Lake Ogura (Kyoto), Lake Biwa (Shiga), Koumi (Nagano), Samegai Trout Experimental Station (Shiga), Lake Suwa (Nagano), Akigawa Valley (Tokyo), Lake Yunoko (Tochigi)	Amin et al. (2007); Ichihara (1964d); Nagasawa et al. (1983, 1987), Nakajima & Egusa (1975a); Yamaguti (1935, 1939)
	<i>Cyprinus carpio</i> (Cyprinidae)		
	<i>Hemibarbus barbus</i> (Cyprinidae)		
	<i>Hemibarbus labeo</i> (Cyprinidae)		
	<i>Hemibarbus longirostris</i> (Cyprinidae)		
	<i>Pseudorasbora parva</i> (Cyprinidae)		
	<i>Gnatopogon elongatus</i> (Cyprinidae)		
	<i>Tribolodon hakonensis</i> (Cyprinidae)		
	<i>Rhynchocypris lagowskii</i> (Cyprinidae)		
	<i>Rhynchocypris oxycephala</i> (Cyprinidae)		
	<i>Pseudogobio esocinus</i> (Cyprinidae)		
	<i>Pungtungia herzi</i> (Cyprinidae)		
	<i>Parabotia curtus</i> (Cobitidae)		
	<i>Cobitis biwae</i> (Cobitidae)		
	<i>Misgurnus anguillicaudatus</i> (Cobitidae)		
	<i>Silurus asotus</i> (Siluridae)		
	<i>Oncorhynchus mykiss</i> (Salmonidae)		
	<i>Oncorhynchus nerka</i> (Salmonidae)		
	<i>Oncorhynchus rhadurus</i> (Salmonidae)		
	<i>Oncorhynchus masou</i> (Salmonidae)		
	<i>Salvelinus fontinalis</i> (Salmonidae)		
	<i>Gymnogobius urotaenia</i> (Gobiidae)		
	<i>Plecoglossus altivelis</i> (Plecoglossidae)		
	<i>Gasterosteus microcephalus</i> (Gasterosteidae)		

9. Family Pomphorhynchidae

39. <i>Pomphorhynchus alemniscus</i>	<i>Paralichthys olivaceus</i> (Paralichthyidae) <i>Acanthopagrus schlegeli</i> (Sparidae) <i>Anguilla japonica</i> (Anguillidae) <i>Silurus asotus</i> (Siluridae) <i>Plotosus lineatus</i> (Siluridae) <i>Tridentiger</i> cf. <i>obscurus</i> (Gobiidae) <i>Acanthogobius flavimanus</i> (Gobiidae)	off Aichi, Kita Jukken River (Tokyo)	Fukui and Morisita (1937a); Kita et al. (2025b)
40. <i>Pomphorhynchus pagrosomi</i>	<i>Pagrus auratus</i> (Sparidae) <i>Pagrus major</i> (Sparidae) <i>Trachurus trachurus</i> (Carangidae) <i>Oplengnathus fasciatus</i> (Oplengnathidae) <i>Sillago sihama</i> (Sillagonidae) <i>Parapristipoma trilineatum</i> (Haemulidae) <i>Acanthopagrus datnia</i> (Sparidae) <i>Gymnocranius griseus</i> (Lethrinidae) <i>Leptojulius poecilepterus</i> (Labridae) <i>Siganus fuscescence</i> (Siganidae) <i>Takifugu rubriceps</i> (Tetraodontidae)	Seto Inland Sea, Toyama Bay, Sagami Bay, Kita-Matsuura (Nagasaki), Naru (Nagasaki); off Aomori	Hatai et al. (1983, 1987); Ichihara (1964c); Ichihara et al. (1965); Ogawa & Inouye (1997); Yamaguti (1935)
41. <i>Pomphorhynchus sebastichthydis</i>	<i>Sebastes oblongus</i> (Sebastidae)	off Nagasaki	Yamaguti (1939)
42. <i>Tenuiproboscis misgurni</i>	<i>Misgurnus fossilis</i> (Cobitidae)	Unknown	Yamaguti (1935)
10. Family Rhadinorhynchidae			
43. <i>Metacanthocephaloides zebrini</i>	<i>Zebrias zebrinus</i> (Soleidae) <i>Suggrundus meerdervoortii</i> (Platycephalidae) <i>Pleuronichthys cornutus</i> (Pleuronectidae) <i>Paralichthys olivaceus</i> (Paralichthyidae)	Seto Inland Sea	Yamaguti (1959)
44. <i>Pseudauchen epinepheli</i>	<i>Epinephelus akaara</i> (Epinephelidae)	Seto Inland Sea	Yamaguti (1939)
45. <i>Rhadinorhynchus carangis</i>	<i>Selaroides leptolepis</i> (Carangidae) <i>Pseudocaranx dentex</i> (Carangidae)	Seto Inland Sea, Sagami Bay	Kamegai (1963); Yamaguti (1939)
46. <i>Rhadinorhynchus ditrematis</i>	<i>Ditrema temminckii</i> (Embiotocidae)	Seto Inland Sea	Yamaguti (1939)
47. <i>Rhadinorhynchus japonicus</i>	<i>Scomber japonicus</i> (Scombridae)	Sapporo (market)	Fujita (1920)
48. <i>Rhadinorhynchus laterospinosus</i>	<i>Auxis thazard</i> (Scombridae)	Tosa-Shimizu (Kochi)	Kita et al. (2024a)

49. <i>Rhadinorhynchus ornatus</i>	<i>Katsuwonus pelamis</i> (Scombridae) <i>Ablennes hians</i> (Belonidae) <i>Coryphaena hippurus</i> (Coryphaenidae)	Hachijojima Island (Tokyo), Tosa Bay, off Chiba, off Mito (Ibaraki), off Misaki (Kanagawa), off Izu (Shizuoka), off Choshi (Chiba), Tokyo (market)	Harada (1928); Kihara (1959a, 1959b); Kamegai (1963); Yamaguti (1935, 1939)
50. <i>Rhadinorhynchus selkirki</i>	<i>Cololabis saira</i> (Scomberesocidae)	Unknown; Tokyo (market)	Kagei (1976); Kihara (1959c)
51. <i>Rhadinorhynchus seriolae</i>	<i>Seriola quinqueradiata</i> (Carangidae) <i>Thunnus orientalis</i> (Scombridae)	off Momotori (Mie), off Minami-Ise (Mie)	Fukui & Morisita (1937); Kita et al. (2024a)
52. <i>Rhadinorhynchus trachuri</i>	<i>Trachurus japonicus</i> (Carangidae)	Tokyo (market)	Harada (1935)
11. Family Transvenidae			
53. <i>Trajectura ikedai</i>	<i>Cirrhitabrax cyanopleura</i> (Labridae)	Amami-Oshima Island (Kagoshima)	Machida (1992)
4. Order Polymorphida			
12. Family Istmosacanthidae			
54. <i>Metarhadinorhynchus lateolabracis</i>	<i>Lateolabrax japonicus</i> (Lateorabracidae)	Seto Inland Sea, off Oku (Okayama), Kamo River (Hiroshima)	Yamaguti (1959); Kita et al. (2024b)
13. Family Polymorphidae			
55. <i>Andracantha phalacrocoracis</i>	<i>Osmerus dentex</i> (Osmeridae)*	off Abashiri (Hokkaido), off Akkeshi (Hokkaido), off Nemuro (Hokkaido)	Sasaki et al. (2019)
56. <i>Bolbosoma nipponicum</i>	<i>Hemitripterus villosus</i> (Hemitriptoridae)*	off Samani (Hokkaido)	Araki & Machida (1987)
57. <i>Corynosoma strumosum</i>	<i>Osmerus dentex</i> (Osmeridae)* <i>Hypomesus japonicus</i> (Osmeridae)* <i>Spirinchus lanceolatus</i> (Osmeridae)* <i>Clupea pallasii</i> (Clupeidae)* <i>Pleurogrammus azonus</i> (Hexagrammidae)* <i>Pseudopleuronectes herzensteini</i> (Pleuronectidae)* <i>Pseudopleuronectes obscurus</i> (Pleuronectidae)* <i>Lepidopsetta mochigarei</i> (Pleuronectidae)* <i>Verasper moseri</i> (Pleuronectidae)* <i>Sebastes trivittatus</i> (Sebastidae)* <i>Myoxocephalus stelleri</i> (Cottidae)* <i>Myoxocephalus polyacanthocephalus</i> (Cottidae)* <i>Gymnocanthus herzensteini</i> (Cottidae)*	off Abashiri (Hokkaido), off Akkeshi (Hokkaido), off Nemuro (Hokkaido), off Esashi (Hokkaido), off Yubetsu (Hokkaido), off Saroma (Hokkaido), off Shakotan (Hokkaido), off Rausu (Hokkaido), off Rumoi (Hokkaido), off Samani (Hokkaido), off Mukawa (Hokkaido)	Araki & Machida (1987); Fujita (1921); Sasaki et al. (2019)
58. <i>Corynosoma semerme</i>	<i>Osmerus dentex</i> (Osmeridae)*	off Abashiri (Hokkaido), off Akkeshi (Hokkaido), off Nemuro (Hokkaido)	Sasaki et al. (2019)
59. <i>Corynosoma villosum</i>	<i>Osmerus dentex</i> (Osmeridae)* <i>Clupea pallasii</i> (Clupeidae)* <i>Pleurogrammus azonus</i> (Hexagrammidae)*	off Abashiri (Hokkaido), off Akkeshi (Hokkaido), off Nemuro (Hokkaido), off Esashi (Hokkaido), off Yubetsu (Hokkaido), off Saroma (Hokkaido), off Shakotan (Hokkaido), off Hama-Tombetsu	Araki & Machida (1987); Sasaki et al. (2019)

	<i>Gadus macrocephalus</i> (Gadidae)*	(Hokkaido), off Rausu (Hokkaido), off Rumoi (Hokkaido), off	
	<i>Paralichthys olivaceus</i> (Paralichthyidae)*	Tomamae (Hokkaido), off Samani (Hokkaido)	
	<i>Platyichthys stellatus</i> (Pleuronectidae)*		
	<i>Pseudopleuronectes herzensteini</i> (Pleuronectidae)*		
	<i>Pseudopleuronectes schrenki</i> (Pleuronectidae)*		
	<i>Pseudopleuronectes obscurus</i> (Pleuronectidae)*		
	<i>Lepidopsetta mochigarei</i> (Pleuronectidae)*		
	<i>Hippoglossus stenolepis</i> (Pleuronectidae)*		
	<i>Myoxocephalus stelleri</i> (Cottidae)*		
	<i>Sebastes trivittatus</i> (Sebastidae)*		
60. <i>Southwellina hispida</i>	<i>Carassius carassius</i> (Cyprinidae)*	Namerikawa (Toyama), Obama (Fukui), Aruji River (Hiroshima),	Amin et al. (2007); Shimizu & Nagasawa (2018); Nagasawa & Kan
	<i>Tanakia lanceolata</i> (Cyprinidae)*	Shika River (Kyoto), Lake Biwa (Shiga), Renjoji River (Ehime),	(2017); Yamaguti (1935, 1939)
	<i>Tanakia limbata</i> (Cyprinidae)*	Okinoerabujima Island (Kagoshima)	
	<i>Nipponocypris sieboldii</i> (Cyprinidae)*		
	<i>Odontobutis obscurus</i> (Odontobutidae)*		
	<i>Rhinogobius</i> sp. (Gobiidae)*		
	<i>Rhinogobius flumineus</i> (Gobiidae)*		
	<i>Coreoperca kawamebari</i> (Percichthyidae)*		
	<i>Micropterus salmoides</i> (Centrarchidae)*		
	<i>Lefua echigonia</i> (Nemacheilidae)*		
	<i>Anguilla marmorata</i> (Anguillidae)*		

* As a paratenic host ** As described in Yamaguti (1935)

Table 2. List of acanthocephalan species in this Ph.D. thesis, except for *Pseudocavisoma chromitidis*, the description of which is based on a syntype specimen borrowed from the US National Museum of Natural History. Locality records for *Echinorhynchus dissimilis* and *E. lotellae* based on specimens deposited at the Meguro Parasitological Museum and the National Museum of Nature and Sciences (Tsukuba) are also not included.

Taxon	Hosts	Locality	Reference
1. Class Eoacanthocephala			
1. Order Neoechinorhynchida			
1. Family Neoechinorhynchidae			
1. <i>Neoechinorhynchus (Hebesoma) yamagutii</i>	<i>Mugil cephalus</i> (Mugilidae)	off Bizen (Okayama, Japan)	this study
2. Class Palaeacanthocephala			
2. Order Echinorhynchida			
2. Family Arhythmacanthidae			
2. <i>Acanthocephaloides neobythitis</i>	<i>Scorpaenopsis cirrosa</i> (Scorpaenidae)	off Sakaiminato (Tottori, Japan)	this study
3. <i>Heterosentis fusiformis</i>	<i>Plotosus japonicus</i> (Plotosidae)	off Matoba (Hiroshima, Japan)	this study
	<i>Istigobius hoshinonis</i> (Gobiidae)		
3. Family Cavisomatidae			
4. <i>Cavisoma magnum</i>	<i>Pentapodus caninus</i> (Nemipteridae)	off Yomitan (Okinawa, Japan)	Kita & Kajihara (2025)
4. Family Echinorhynchidae			
5. <i>Echinorhynchus dissimilis</i>	<i>Physiculus japonicus</i> (Moridae)	off Urakawa (Hokkaido, Japan)	this study
	<i>Zeus faber</i> (Zeidae)	off Ibaraki (Japan)	
6. <i>Echinorhynchus hexagrammi</i>	<i>Liparis</i> sp. (Liparidae)	Akkeshi Bay (Japan)	Kita & Kajihara (2021)
7. <i>Echinorhynchus lotellae</i>	<i>Physiculus japonicus</i> (Moridae)	off Urakawa (Hokkaido, Japan)	this study
	<i>Zeus faber</i> (Zeidae)	off Ibaraki (Japan)	
8. <i>Echinorhynchus sasakiae</i>	<i>Hexagrammos lagocephalus</i> (Hexagrammidae)	Akkeshi Bay (Japan)	Kita & Kajihara (2023)
		off Nemuro (Hokkaido, Japan)	
5. Family Leptorhynchoididae			
9. <i>Metacanthocephalus ovicephalus</i>	<i>Pseudopleuronectes obscurus</i> (Pleuronectidae)	off Iwanai (Hokkaido, Japan)	Kita et al. (2023)
	<i>Pseudopleuronectes schrenki</i> (Pleuronectidae)	off Rausu (Hokkaido, Japan)	
10. <i>Pseudorhadinorhynchus leuciscus</i>	<i>Tribolodon brandtii</i> (Cyprinidae)	off Urakawa (Hokkaido, Japan)	this study
6. Family Micracanthorhynchinidae			
11. <i>Micracanthorhynchina segmentata</i>	<i>Hyporhamphus sajori</i> (Hemirhamphidae)	off Hama-Saroma (Hokkaido, Japan)	this study
12. <i>Pseudocavisoma setoense</i>	<i>Chromis notata</i> (Pomacentridae)	off Ihota (Yamaguchi, Japan)	Kita et al. (2024c)
7. Family Pomphorhynchidae			

13. <i>Pomphorhynchus alemniscus</i>	<i>Acanthogobius flavimanus</i> (Gobiidae) <i>Tridentiger</i> cf. <i>obscurus</i> (Gobiidae)	Kita-Jukken River (Tokyo, Japan)	Kita et al. (2025b)
14. <i>Pomphorhynchus pagrosomi</i>	<i>Branchiostegus japonicus</i> (Maracanthidae) <i>Callionymus</i> sp. (Callionymidae) <i>Pleuronichthys cornutus</i> (Pleuronectidae) <i>Stephanolepis cirrifer</i> (Monacanthidae) <i>Zebrias zebrinus</i> (Soleidae)	off Tamano (Okayama, Japan) off Bizen (Okayama, Japan) off Ijika (Mie, Japan) off Ushitsu (Ishikawa, Japan) off Takojima (Ishikawa, Japan)	this study
8. Family Rhadinorhynchidae			
15. <i>Rhadinorhynchus laterospinosus</i>	<i>Auxis thazard</i> (Scombridae)	off Tosa-Shimizu (Kochi, Japan)	Kita et al. (2024a)
16. <i>Rhadinorhynchus nudus</i>	<i>Euthynnus affinis</i> (Scombridae)	off Hondo (Kumamoto, Japan)	this study
17. <i>Rhadinorhynchus seriolae</i>	<i>Thunnus orientalis</i> (Scombridae)	off Minami-Ise (Mie, Japan)	Kita et al. (2024a)
9. Family Transvenidae			
18. <i>Sclerocollum neorubrimaris</i>	<i>Siganus argenteus</i> (Siganidae)	off Miyakojima Island (Okinawa, Japan)	this study
19. <i>Trajectura ikedai</i>	<i>Pterocaesio digramma</i> (Caesionidae)	off Miyakojima Island (Okinawa, Japan)	this study
3. Order Polymorphida			
10. Family Isthmosacanthidae			
20. <i>Metarhadinorhynchus lateolabracis</i>	<i>Lateolabrax japonicus</i> (Lateolabracidae)	off Oku (Okayama, Japan) Kamo River (Hiroshima, Japan)	Kita et al. (2024b)
11. Family Polymorphidae			
21. <i>Bolbosoma vasculosum</i>	<i>Beryx splendens</i> (Berycidae) <i>Etelis radiosus</i> (Lutjanidae) <i>Malakichthys</i> sp. (Acropomatidae) <i>Pristipomoides argyrogrammicus</i> (Lutjanidae) <i>Pristipomoides sieboldii</i> (Lutjanidae) <i>Trichiurus lepturus</i> (Trichiuridae)	off Naha (Okinawa, Japan) off Awase (Okinawa, Japan) off Nagasaki (Japan) off Minami-Chita (Aichi, Japan) Mikawa Bay (Japan).	Kita et al. (2024d)

Table 3. Morphological comparison between the 13 species in *Acanthocephaloides* Meyer, 1932. Quantitative character states that overlap with those in the present material of *A. neobythitis* Yamaguti, 1939 from Sakaiminato (YK's private collection) are indicated in bold letters.

Species	Proboscis shape	No. of hook rows	No. of hooks per row	Hook shape	Reference
<i>A. claviformis</i>	cylindrical, slightly enlarged in the middle	14	6–8	slightly smaller toward basal hooks	Araki & Machida (1987)
<i>A. cyrusi</i>	claviform	—*	6	anterior 2–3: very long, less curved; posterior 2–3: small	Bray et al. (1988)
<i>A. delamuri</i>	cylindrical	16	8	posterior 1: small	Paruchin (1989)
<i>A. distinctus</i>	cylindrical	12	6–8	posterior 3: small	Golvan (1969)
<i>A. geneticus</i>	cylindrical	12	6	posterior 2: small	de Buron et al. (1986)
<i>A. ichiharai</i>	cylindrical	12–16	10–13	slightly smaller toward basal hooks	Araki & Machida (1987)
<i>A. irregularis</i>	cylindrical, swollen in the middle	12	5	larger toward middle; posterior 2: small	Amin et al. (2011c)
<i>A. neobythitis</i>	cylindrical	16–18	11–13	posterior 2–3: small	Yamaguti (1939); this study
<i>A. nickoli</i>	claviform	18	14	slightly smaller toward basal hooks	Kumar (1992b)
<i>A. plagiuseae</i>	cylindrical, short	14–16	6–7	posterior 3: small	Santana-Piñeros et al. (2013)
<i>A. propinquus</i>	cylindrical, oval	12	6–8	posterior 3: small	Dujardin (1845); Golvan (1969)
<i>A. rhinoplagusiae</i>	cylindrical	14	10	slightly smaller toward basal hooks	Yamaguti (1935)
<i>A. spinicaudatus</i>	cylindrical	10	13	posterior 4: small	Cable & Quick (1954)

*Not mentioned.

Table 4. Morphological comparison between the 17 species in *Heterosentis* Van Cleave, 1931. Quantitative character states that overlap with those in the present material of *H. fusiformis* (Yamaguti, 1935) from off Matoba (YK's private collection) are indicated in bold letters.

Species	Apical hook circular rows arrangement	No. of basal hook rows	No. of basal hooks per row	Trunk spine distribution	Reference
<i>H. brasiliensis</i>	1 apical, 2 subapical	10	3–4	anterior, ventral	Vieira et al. (2009)
<i>H. fusiformis</i>	1 apical, 1 subapical	14	2–3	whole trunk, posteriorly sparse	Yamaguti (1935); this study
<i>H. heteracanthus</i>	1 apical, 1 subapical	10	6	anterior half of the trunk	von Linstow (1895); Van Cleave (1931b)
<i>H. hirstus</i>	1 apical, 1 subapical	14	5	anterior trunk	Pichelin & Cribb (1999)
<i>H. holospinus</i>	1 apical, 1 subapical	14	3–5	whole trunk	Amin et al. (2011b)
<i>H. martini</i>	1 apical, 3 subapical	10	7–8	anterior trunk: ventral spine larger	Lanfranchi & Timi (2011)
<i>H. mongcai</i>	1 apical, 1 subapical	14	3–4	anterior trunk	Amin et al. (2014)
<i>H. mysturi</i>	1 apical, 3 subapical	10–14*	3	anterior trunk	Amin et al. (2011b)
<i>H. overstreeti</i>	1 apical, 1 subapical	12	2–3	whole trunk	Schmidt & Paperna (1978)
<i>H. paraholospinus</i>	1 apical, 1 subapical	11	3	anterior trunk	Amin et al. (2018d)
<i>H. paraplagusiarum</i>	1 apical (apicalmost hook smaller), 1 subapical	14	3–4	anterior trunk	Nickol (1972)
<i>H. parasiluri</i>	1 apical, 3 subapical	13–14	2–3	anterior trunk	Yin & Wu (1984)
<i>H. plotosi</i>	1 apical, 1 subapical	14	3–4	anterior trunk	Yamaguti (1935)
<i>H. pseudobagri</i>	1 apical, 2 subapical	12	2	anterior trunk	Wang & Zhang (1987)
<i>H. septacanthus</i>	1 apical, 1 subapical	13–14	3–4	anterior trunk, including anterior cone	Golvan (1969)
<i>H. thapari</i>	1 apical, 2 subapical	10–12	4–5	anterior trunk, including anterior cone	Gupta & Fatma (1979)
<i>H. zdzitowieckii</i>	1 apical, 2 subapical	14	3–4	anterior trunk	Kumar (1992a)

* Range indicated in the key of Amin et al. (2011b).

Table 5. Morphological comparison of *Echinorhynchus sasakiae* Kita & Kajihara, 2023 with other congeners from Japanese marine waters, along with *E. veli* George & Nadakal, 1978, in which the proboscis shape is similar to the new species. Quantitative character states that overlap with those in *E. sasakiae*, as well as qualitative character states that are the same as in *E. sasakiae*, are indicated in bold letters.

Species	Proboscis shape	No. of hook rows	No. of hooks per row	Variation in the shape of hooks	References
<i>E. dissimilis</i>	subcylindrical; swollen in middle	22–31	10–11	subapical hooks slightly larger than others	Yamaguti (1939); Araki & Machida (1987)
<i>E. gadi</i>	cylindrical; elongate	18–22	10–13	basal hook smallest	Golvan (1969)
<i>E. hexagrammi</i>	cylindrical; elongate	12–16	9–12	apical hook largest; basal two hooks slender	Katahira & Nagasawa (2011); Kita & Kajihara (2021)
<i>E. kushiroensis</i>	cylindrical; short; apically flat	24	8	–	Fujita (1921)
<i>E. lotellae</i>	cylindrical; elongate	16	16	basal hooks slightly slender	Yamaguti (1939); Araki & Machida (1987)
<i>E. sasakiae</i>	subcylindrical; swollen in middle	14–15	7–10	anterior 3–5 hooks short, strongly curved, with large root; posterior 4–5 hooks long, weakly curved, with very short root	Kita & Kajihara (2023)
<i>E. theragrae</i>	cylindrical; elongate	17	22	root of basal hooks not developed	Didenko (1992)
<i>E. veli</i>	cylindrical; swollen in middle ; apical flat	12–15	10–14	basal hooks smaller than apical	Sheema et al. (2017)
<i>E. yamagutii</i>	cylindrical; elongate	18–20	12–14	–	Golvan (1969)

Table 6. Morphological comparison among *Indorhynchus* Golvan, 1969 species.

Species	Hooks × rows	Number of cement glands	Host	References
<i>I. arii</i>	21–22 × 24	8	<i>Arius falcarius</i> (= <i>Arius arius</i>) (Ariidae) <i>Pseudobagrus fulvidraco</i> (= <i>Tachysurus fulvidraco</i>) (Bagridae)	Wang (1966)
<i>I. bilqeesae</i>	12–13 × 18–20	8	<i>Tachysurus nenga</i> (= <i>Nemapteryx nenga</i>) (Ariidae)	Naidu (2012)
<i>I. echeneisi</i>	12 × 16	8	<i>Echeneis naucrates</i> (Echeneidae)	Gupta & Sinha (1991)
<i>I. indicus</i>	14 × 18–22	8	<i>Tachysurus jella</i> (= <i>Arius jella</i>) (Ariidae) <i>Osteogeneiosus militaris</i> (Ariidae)	Golvan (1969); Naidu (2012)
<i>I. thapari</i>	18 × 26	8	<i>Arius platystomus</i> (= <i>Plicofollis platystomus</i>) (Ariidae)	Gupta & Gupta (1975)

Table 7. Comparison among different reports of *Neotegorhynchus cyprini* (Yin in Zhang, 1961).

Hooks × rows	Host	Locality	Reference
18–25 × 12	<i>Cyprinus carpio</i> (Cyprinidae) <i>Barbus caldwelli</i> (= <i>Spinibarbus caldwelli</i>) (Cyprinidae) <i>Ctenopharyngodon idella</i> (Cyprinidae)	Fuzhou (Fukien, China); Wuchang (Hubei, China)	Yin (1961); Wang (1966, 1986)
20–22 × 12	<i>Cyprinus carpio</i> (Cyprinidae)	Haicheng (Liaoning, China); Taian (Liaoning, China)	Yin & Wu (1984)
19–23 × 14	<i>Cyprinus carpio</i> (Cyprinidae)	Taihu Lake (Jiangsu, China)	Lisitsyna et al. (2022)*

*Designated a neotype.

Table 8. Morphological comparison among the genus *Micracanthorhynchina* Strand, 1936, and the present materials. Characteristics shared with the present materials are shown in bold.

Species	No. of proboscis hook rows	No. of hooks per row	No. of cement glands	References
<i>Allorhadinorhynchus segmentatum</i>	12	10–11	2	Yamaguti (1959)
<i>Micracanthorhynchina atherinomori</i>	10	8–9	4	Smales (2014a)
<i>M. brevelemniscus</i>	12	8–9	6	Lisitsyna et al. (2023)
<i>M. chandrai</i>	6	10–11	4	Bhattacharya (2007)
<i>M. cynoglossi</i>	14	8–9	6	Wang (1980)
<i>M. dakusuiensis</i>	12	9	6	Harada (1938)
<i>M. golvani</i>	14–15	16–22	4	Gupta & Sinha (1992)
<i>M. hemiculterus</i>	12	12	4	Demshin (1965)
<i>M. hemirhamphi</i>	12	9–11	4	Baylis (1944)
<i>M. kuwaitensis</i>	12	13–15	6	Amin & Sey (1996)
<i>M. lateolabracis</i>	14	9	6	Wang (1980)
<i>M. motomurai</i>	12	8–9	4	Harada (1935)
<i>M. segmentata</i>	12	9–10	4	Araki & Machida (1987)
<i>M. sinipercae</i>	12	6–7	6	Wang et al. (1983)
the present materials	12	10–12	4	this study

Table 9. Morphological comparison among former *Longicollum* Yamaguti, 1935 species before Zhao et al. (2025).

Species	Arrangement of proboscis hooks (rows × hooks)	Proboscis shape	Strength of neck twisting	Neck width	References
<i>P. alemniscus</i>	11–12 × 9–11	swollen at the anterior half, but slightly tapered at the tip, posterior half cylindrical (= “Kolben-like”)	strongly twisted	uniformly cylindrical	Harada (1935); Fukui & Morisita (1937a); this study
<i>P. cadenati</i>	10–12 × 11–12	club shape	twisted	not mentioned*	Gupta & Naqvi (1984)
<i>P. chabanaudi</i>	12 × 13–15	anterior half spheroids, posterior half cone-like	not mentioned	fusiform	Dollfus & Golvan (1963)
<i>P. dattai</i>	14 × 14	club shaped	not mentioned	not mentioned*	Saxena et al. (2008)
<i>P. engraulisi</i>	14 × 13–14	anteriorly and basally broad, middle narrow	spirally twisted	slightly swollen or expanded towards convex side	Gupta & Fatma (1985)
<i>P. indicum</i>	14 × 15	long, claviform	spirally twisted	not mentioned*	Gupta & Gupta (1970)
<i>P. lutiani</i>	12–13 × 14–15	clavate	not mentioned	not mentioned*	Jain & Gupta (1980)
<i>P. noellae</i>	14 × 13–14	anteriorly and basally broad, middle narrow	not mentioned	fusiform	Golvan (1969)
<i>P. pagrosomi</i>	11–15 × 9–12	short, cylindrical, round in front	spirally twisted	conspicuously expanded on the convex side	Yamaguti (1935); Li et al. (2017b); this study
<i>P. psettodesai</i>	14–16 × 10–12	not mentioned**	twisted	not mentioned*, very long	Gupta & Gupta (1980)
<i>P. quiloni</i>	14–16 × 16–17	cylindrical to claviform	twisted	not mentioned***, very long	Gupta & Naqvi (1984)
<i>P. riouxi</i>	14–16 × 9–10	club shape	not mentioned	fusiform, short	Golvan (1969)

*Seemed to be uniformly cylindrical, based on their line drawings. **Seemed to be “anteriorly and basally broad, middle narrow”, based on their line drawings. ***Seemed to be fusiform, based on their line drawings.

Table 10. Measurements comparison among all records of *Pomphorhynchus alemniscus* (Harada, 1935). Measurements are given in micrometers, otherwise noted.

Chacacteristics	Harada (1935) as <i>Spirorhynchus alemniscus</i>	Fukui & Morisita (1936) as <i>Longicollum minor</i>	Fukui & Morisita (1937a) as <i>Longicollum alemniscus</i>	Kita et al. (2025b)
Trunk length (mm)	6	5	6–9	2.89–3.87 (male), 2.74–3.40 (female)
Trunk width (mm)	1.1	0.277–0.434	1–1.8	0.62–1.02 (male), 0.65–0.92 (female)
Neck length (mm)	8	–	8	1.87–3.46 (male), 1.82–2.81 (female)
Neck width (mm)	0.7	–	0.7	0.18–0.37 (male), 0.22–0.32 (female)
Proboscis length	700	554	930	446.0–656.4 (male), 610.3–703.5 (female)
Proboscis width	350	–	620	203.9–293.8 (male), 260.4–296.8 (female)
Number of hook rows	11	10–11	11	11–12
Number of hooks per row	11	11–12	11–12	9–10
Proboscis receptacle length	–	697.5 (only including region within trunk)	1990	2386.6–3959.1 (male), 2837.7–3744.0 (female)
Proboscis receptacle width	–	–	320	96.2–140.7 (male), 97.1–151.7 (female)
Lemniscus length	–	–	–	102.0–221.1 (male), 111.1–205.3 (female)
Anterior testis length	–	480 (unknown whether anterior or posterior)	1030	282.2–475.6
Anterior testis width	–	–	610	184.3–317.1
Posterior testis length	–	–	–	306.0–524.0

Posterior testis width	—	—	—	170.4–325.7
Saeftigen's pouch length	—	—	1100	215.1–349.6
Copulatory bursa width	—	—	—	334.4
Uterus length	—	—	—	626.3–921.0
Egg length	79	—	77	—
Egg width	23	—	14	—

Table 11. Morphological comparison among species of *Sclerocollum* Schmidt & Paperna, 1978 compared to *Sclerocollum neorubrimaris* Amin et al., 2018, in this study. Characteristics shared with *S. neorubrimaris* in this study are shown in bold.

Species	Hook rows / hooks per row	Position of cephalic ganglion	Lemnisci length (L) vs receptacle length (R)	Position of testes	References
<i>S. australe</i>	14–16 / 10–12	middle	L = R	posterior	Pichelin et al. (2016)
<i>S. neorubrimaris</i>	14 / 9–10	posterior	R < L < 2R	middle	Amin et al. (2018c)
<i>S. robustum</i>	14 / 12–13	middle	L < R	middle	Edmonds (1964)
<i>S. rubrimaris</i>	12–15 / 7–10	middle	L = R	middle	Schmidt & Paperna (1978); Amin et al. (1984)
<i>S. saudii</i>	14 / 8–9	middle	R < L < 2R	middle	Al-Jahdali (2010)
<i>S. neorubrimaris</i> (this study)	13–14 / 9–10	posterior	R < L < 2R	middle	This study

Table 12. Morphological comparison among *Metarhadinorhynchus* Yamaguti, 1959 species. Characteristics that are similar to or the same as those in *M. lateolabracis* Yamaguti, 1959 are in bold.

Species	Proboscis shape	Hooks × rows	Trunk spine distribution	Significant narrowing of trunk spine distribution area	Number of cement glands	Hosts	References
<i>M. bullocki</i>	claviform	16–18 × 24–26	not separated	present	6	<i>Caranx hippos</i> (Carangidae)	Cable & Mafarachisi (1970)
<i>M. cablei</i>	claviform	14–18 × 24–26	not separated	absent	—*	<i>Caranx kalla</i> (= <i>Alepis djebada</i>) (Carangidae)	Gupta & Fatma (1987)
<i>M. cribbi</i>	claviform	21–22 × 30	separated	present	6	<i>Seriola hippos</i> (Carangidae)	Smales (2014b)
<i>M. elongatus</i>	claviform	18–20 × 28	separated	present	—*	<i>Caranx crysos</i> (Carangidae)	Cable & Linderroth (1963)
<i>M. epinepheli</i>	claviform	16 × 26–28	not separated	absent	—*	<i>Epinephelus awoara</i> (Serranidae)	Wang (1986)
<i>M. gnathanodontos</i>	claviform	16 × 24–26	not separated	present	6	<i>Gnathanodon speciosus</i> (Carangidae)	Smales (2014b)
<i>M. golvani</i>	claviform	Anterior hooks: 1214 spiral rows × 5–7 hooks; posterior hooks: 1012 spiral rows × 12–14 hooks	not separated	absent	—*	<i>Saurida tumbil</i> (Synodontidae) <i>S. undosquamis</i> (Synodontidae) <i>Harpadon nehereus</i> (Synodontidae) <i>Johnius aneus</i> (= <i>Pennahia aneus</i>) (Sciaenidae) <i>Pe. argentata</i> (Sciaenidae) <i>Pterotolithus maculatus</i> (Sciaenidae) <i>Kathala axillaris</i> (Sciaenidae)	Chandra et al. (1984)

<i>M. indicus</i>	claviform	10–16 × 20–26	not separated	present	6	<i>Upeneus vittatus</i> (Mullidae)	
<i>M. lateolabracis</i>	claviform	18–20 × 23–25	not separated	present	6	<i>Megalaspis cordyla</i> (Carangidae)	Bhattacharya & Banerjee (2003)
<i>M. lateolabri</i>	claviform	16–17 × 24–26	not separated	present	6	<i>Lateolabrax japonicus</i> (Lateolabracidae)	Yamaguti(1959); this study
<i>M. lintoni</i>	claviform	17–22 × 28	separated	present	6	<i>Lateolabrax japonicus</i> (Lateolabracidae)	Yin & Wu (1984)
<i>M. orientalis</i>	claviform	16–18 × 26	not separated	—*	—*	<i>Seriola lalandi</i> (Carangidae)	Cable & Mafarachisi (1970)
<i>M. pseudocarangis</i>	claviform	16–17 × 27–28	not separated	present	6	<i>Lateolabrax japonicus</i> (Lateolabracidae)	Wang (1966)
<i>M. queenslansensis</i>	claviform	20–22 × 28–30	separated	present	6	<i>Pseudocaranx dentex</i> (Carangidae)	Huston & Smales (2021)
<i>M. valiyathuræ</i>	claviform	10–12 × 18–22	not separated	present	6	<i>Seriola lalandi</i> (Carangidae)	Smales (2014b)
						<i>Caranx melampygus</i> (Carangidae)	Nadakal et al. (1990)
						<i>C. malabaricus</i> (= <i>Carangoides malabaricus</i>) (Carangidae)	
						<i>C. nigripinnis</i> (= <i>Alepes melanoptera</i>) (Carangidae)	

*Not mentioned.

Table 13. Comparison of the species obtained in this study with other *Bolbosoma* Porta, 1908 species, including larvae from around Japan in previous studies. Characteristics in boldface type are identical to those of the specimens in this study.

Taxon	Stage	Locality	Host	Hook arrangement (hooks × rows)	Distribution of spines	Reference
<i>Bolbosoma australis</i>	adult	Antarctic	<i>Balaenoptera borealis schlegeli</i> , <i>Eubalaena</i>	6–8 × 20–24	not separated	Skrjabin (1972)
<i>Bolbosoma balaenae</i>	adult	Capri Island (Tyrrhenian Sea) northern Atlantic Australia	<i>Balaenoptera physalus</i> , <i>Balaena</i> sp., <i>Balaenoptera</i> sp., <i>Hyperodon</i> sp., <i>Megaptera</i> sp.	7–8 × 24	not separated	Yamaguti (1963); Santoro et al. (2021)
<i>Bolbosoma bobrovoi</i>	adult	Tjulenij Island (Okhotsk Sea)	<i>Callorhinus ursinus</i> , <i>Eumetopias jubatus</i>	4–5 × 14–16	not separated	Krotov & Delyamure (1952); Yamaguti (1963)
<i>Bolbosoma brevicolle</i>	adult	northern Atlantic southern Africa South Georgia (Ross Sea)	<i>Balaenoptera</i> spp., <i>Physter catodon</i>	8 × 16–18 5 × 24–25	not separated	Shipley (1899); Yamaguti (1963)
<i>Bolbosoma caenoforme</i>	adult	northern Pacific	<i>Uria aelge inornata</i>	6 × 18–20	not separated	Kihara (1959d); Yamaguti (1963)
<i>Bolbosoma capitatum</i> (= <i>B. vasculosum</i>)	adult	northern Pacific Atlantic Australia	<i>Globicephala macrorhynchus</i> , <i>Globiocephalus melaena</i> , <i>Physeter</i> <i>macrocephalus</i> , <i>Pseudorca crassidens</i> , <i>Steno</i> <i>rostratus</i> , <i>Physeter catodon</i>	8–9 × 16–18	separated	Amin & Margolis (1998); Kikuchi & Nakajima (1993)
<i>Bolbosoma hamiltoni</i>	adult	South Georgia (Ross Sea)	<i>Balaenoptera physalus</i> , <i>Balaenoptera</i> <i>musculus</i>	7–8 × 26	not separated	Baylis (1929)
<i>Bolbosoma nipponicum</i>	adult	northern Pacific	<i>Balaenoptera acutorostrata</i> , <i>Callorhinus</i> <i>urcinus</i>	5–6 × 17–23	not separated	Yamaguti (1939); Ru et al. (2022b)
<i>Bolbosoma scomberomori</i>	adult	off Fujian (China)	<i>Delphinus delphis</i>	7–8 × 26–28	not separated	Wang (1980)

<i>Bolbosoma tuberculata</i>	adult	southern Atlantic Indian Ocean	<i>Balaenoptera borealis</i> , <i>Physter catodon</i>	8 × 25–26	not separated	Skrjabin (1970)
<i>Bolbosoma turbinella</i>	adult	northern Atlantic Pacific	<i>Hyperodon rostratum</i> , <i>Hyperodon ampullatus</i> , <i>Balaenoptera borealis</i> , <i>Balaenoptera musculus</i> , <i>Balaenoptera physalus</i> , <i>Balaenoptera sieboldii</i> , <i>Megaptera nodosa</i>	5–8 × 18–22	not separated	Diesing (1851); Measure (1992); Yamaguti (1963)
<i>Bolbosoma vasculosum</i>	adult	Atlantic Pacific	<i>Delphinus delphis</i> , <i>Mesoplodon bidens</i> , <i>Arctocephalus pusillus pusillus</i>	8–9 × 18–22	separated	Yamaguti (1963); Costa et al. (2000); Halajian et al. (2020)
<i>Bolbosoma</i> sp.	larva	Sagami Bay (Japan)	<i>Lophotus capellei</i>	7–8 × 24	— ^a	Kamegai (1962a)
<i>Bolbosoma</i> sp.	larva	Sagami Bay (Japan)	<i>Beryx splendens</i>	8 × 17–18	separated	Ichihara (1964a)
<i>Bolbosoma</i> sp.	larva	Sagami Bay (Japan)	<i>Promethichthys prometheus</i>	8 × 17–18	separated	Ichihara (1964b)
<i>Bolbosoma</i> sp.	larva	off Miyazu (Kyoto, Japan)	<i>Regalecus russelii</i>	7–9 × 22	not separated, asymmetry	Steinauer et al. (2019)
<i>Bolbosoma vasculosum</i>	larva	off Nagasaki (Japan)	<i>Trichiurus lepturus</i>	8 × 18	separated	Present study
<i>Bolbosoma vasculosum</i>	larva	off Naha (Okinawa, Japan)	<i>Pristipomoides sieboldii</i>	9–10 × 18–19	separated	Present study
<i>Bolbosoma vasculosum</i>	larva	off Naha (Okinawa, Japan)	<i>Etelis radius</i>	8 × 18	separated	Present study
<i>Bolbosoma vasculosum</i>	larva	off Awase (Okinawa, Japan)	<i>Pristipomoides sieboldii</i>	8–10 × 18–19	separated	Present study
<i>Bolbosoma vasculosum</i>	larva	Mikawa Bay (Japan)	<i>Beryx splendens</i>	9 × 18	separated	Present study

<i>Bolbosoma vasculosum</i>	larva	off Minami- Chita (Aichi, Japan)	<i>Malakichthys</i> sp.	8 × 18	separated	Present study
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Table 14. The list of acanthocephalan taxa and their INSDC accession numbers used in the molecular analyses in this study: the sequences obtained from the materials used in Chapter II were shown in **bold** type; the sequences newly obtained in this study without accession numbers are indicated as “NR”.

Taxon	cox1	18S	28S	mtgenome	References
[Ingroup]					
Palaeacanthocephala					
Echinorhynchida					
Arhythmacanthidae					
<i>Acanthocephaloides neobythitis</i>	NR	NR	NA	NA	this study
<i>Acanthocephaloides propinquus</i>	DQ089713	AY830149	AY829110	NA	García-Varela & Nadler (2006) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Calakmulrhynchus amini</i>	NA	EU732662	EU732661	NA	García-Varela & Andrade-Gómez (2021)
<i>Heterosentis</i> sp.	MN692676	MN705825	MN705845	NA	Huston et al. (2020)
<i>Heterosentis fusiformis</i>	NR	NR	NR	NA	this study
<i>Heterosentis holospinus</i>	MN715352	NA	NA	PQ675784	Amin et al. (2019c) for cox1; Chen et al. (2025) for mtgenome
<i>Heterosentis pseudobagri</i>	NA	OP286859	OP286594	OP278658	Gao et al. (2023)
Cavisomatidae					
<i>Caballerorhynchus lamothei</i>	PX132614	PX139054	PX139057	NA	Aguilar-Aguilar et al. (2025)
<i>Cavisoma magnum</i>	LC881782	LC881783	LC881784	MN562586	Kita & Kajihara (2025) for cox1, 18S, and 28S; Muhammad et al. (2020c) for mtgenome
Diplosentidae					
<i>Sharpilosentis peruviansis</i>	KP967562	NA	NA	NA	Lisitsyna et al. (2015)
Echinorhynchidae					
<i>Echinorhynchus bothniensis</i>	KP261018	NA	KM656146	NA	Wayland et al. (2015)
<i>Echinorhynchus brayi</i>	KP261015	NA	KM656151	NA	Wayland et al. (2015)
<i>Echinorhynchus cictulus</i>	KP261014	NA	KM656142	NA	Wayland et al. (2015)
<i>Echinorhynchus cotti</i>	NA	MW172280	MW172287	NA	García-Varela & Andrade-Gómez (2021)
<i>Echinorhynchus dissimilis</i>	NR	NR	NR	NA	this study
(Urakwa)					
<i>Echinorhynchus dissimilis</i>	NR	NR	NR	NA	this study
(Ibaraki)					
<i>Echinorhynchus gadi</i>	NR	NR	NR	NR	this study
<i>Echinorhynchus gymnocyprii</i>	MT169741	MT162018	NA	ON960151	Lei et al. (2020) for cox1 and 18S; Li & He (unpublished)

<i>Echinorhynchus hexagrammi</i>	LC625885	LC757490	LC757491	NA	Kita & Kajihara (2021) for cox1; Kita & Kajihara (2023) for 18S and 28S
<i>Echinorhynchus lotellae</i> (Urakawa)	NA	NR	NR	NA	this study
<i>Echinorhynchus lotellae</i> (Ibaraki)	NR	NR	NA	NA	this study
<i>Echinorhynchus salmonis</i>	KP261017	NA	KM656145	NA	Wayland et al. (2015)
<i>Echinorhynchus sasakiae</i>	LC757487	LC757488	LC757489	NR	Kita & Kajihara (2023) for cox1, 18S, 28S; this study for mtgenome
<i>Echinorhynchus truttae</i>	KP261013	AY830156	AY829097	FR856883	Wayland et al. (2015) for cox1; García-Varela & Nadler (2005) for 18S and 28S; Weber et al. (2013) for mtgenome
<i>Echinorhynchus veli</i>	NA	KP260659	NA	NA	Sheema et al. (unpublished)
Filisomatidae					
<i>Filisoma argusum</i>	MK305841	NA	NA	NA	Kaur et al. (2021)
<i>Filisoma bucerium</i>	DQ089722	AF064814	AY829110	NA	García-Varela & Nadler (2006) for cox1; García-Varela et al. (2000) for 18S; García-Varela & Nadler (2005) for 28S
<i>Filisoma caudata</i>	MH004408	MH004443	MH004455	NA	Costa Fernandes et al. (2019)
<i>Filisoma filiforme</i>	MN692678	MN705826	MN705846	NA	Huston et al. (2020)
<i>Filisoma rizalinum</i>	NA	JX014229	NA	NA	Verweyen et al. (2011)
Heteracanthocephalidae					
<i>Aspersentis</i> sp.	OQ947286	OQ942219	NA*	NA	Bennett et al. (2023)
<i>Aspersentis megarhynchus</i>	NA	MW916821	NA	PP965112	Amin et al. (2021) for 18S; Xie et al. (2024) for mtgenome
Leptorhynchoididae					
<i>Brentisentis yangtzensis</i>	NA	NA	NA	MK651258	Song et al. (2019)
<i>Dentitruncus truttae</i>	JX460887	JX460860	NA	NA	Smrzlić et al. (2013)
<i>Dollfusentis bravoae</i>	OR883559	OR886453	OR886456	NA	García-Varela et al. (2024)
<i>Dollfusentis chndleri</i>	DQ320484	NA	NA	NA	Baker & Sotka (unpublished)
<i>Dollfusentis lenti</i>	MK294054	MK282744	MK282748	NA	Keidel et al. (2019)
<i>Dollfusentis mayae</i>	OR883550	OR886452	OR886455	NA	García-Varela et al. (2024)
<i>Illiosentis</i> sp.	DQ089705	AY830158	AY829092	NA	García-Varela & Nadler (2006) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Illiosentis cetratus</i>	ON184031	ON180690	OR166369	NA	Amin et al. (2023)

<i>Koronacantha pectinaria</i>	DQ089707	AF092433	AY829094	NA	García-Varela & Nadler (2006) for cox1; García-Varela et al. (2000) for 18S; García-Varela & Nadler (2005) for 28S
<i>Koronacantha mexicana</i>	DQ089708	AY830157	AY829095	NA	García-Varela & Nadler (2006) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Leptorhynchoides thecatus</i>	AY690487	AF001840	AY829093	AY562383	Steinauer et al. (2007) for cox1; Near et al. (1998) for 18S; García-Varela & Nadler (2005) for 28S; Steinauer et al. (2005) for mtgenome
<i>Metacanthocephalus ovicephalus</i> (Iwanai)	LC730869	LC730868	LC730868	NR	Kita et al. (2023) for cox1, 18S, and 28S; this study for mtgenome
<i>Metacanthocephalus ovicephalus</i> (Rausu)	LC730878	NA	LC730867	NA	Kita et al. (2023)
<i>Pseudoleptorhynchoides lamotiei</i>	EU090949	EU090950	EU090951	NA	García-Varela & González-Oliver (2008)
<i>Pseudorhadinorhynchus leuciscus</i>	LC717943	NA	LC717942	NA	this study
Micracanthorhynchinidae					
<i>Micracanthorhynchina brevelemniscus</i>	OR625528	OR625654	NA	NA	Lisitsyna et al. (2023)
<i>Micracanthorhynchina dakusuiensis</i>	NA	OP133175	OP133174	OP131911	Gao et al. (2022)
<i>Micracanthorhynchina hemirhamphi</i>	NA	NA	NA	PV590120	Xie et al. (2025b)
<i>Micracanthorhynchina segmentata</i>	NA	NR	NR	NA	this study
<i>Pseudocavisoma setoense</i>	LC835834	LC835835	LC835836	NA	Kita et al. (2024c)
Paracanthocephalidae					
<i>Acanthocephalus anguillae</i>	MN416027	MN394412	MN394417	NA	Amin et al. (2019b)
<i>Acanthocephalus clavula</i>	AM039866	MW172278	MW172285	NA	Benesh et al. (2006) for cox1; García-Varela & Andrade-Gómez (2021) for 18S and 28S
<i>Acanthocephalus dirus</i>	DQ089718	AY830151	AY829106	NA	García-Varela & Nadler (2006) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Acanthocephalus lucii</i>	MT682949	AY830152	AY829101	NA	Reier et al. (2020) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Acanthocephalus nanus</i>	LC100070	LC129889	NA	NA	Nakao (2016)
<i>Acanthocephalus ranae</i>	PV655166	PV648453	NA	NA	Dmitrieva (unpublished)

<i>Acanthocephalus rhinensis</i>	NA	MW172279	MW172286	NA	García-Varela & Andrade-Gómez (2021)
Pomphorhynchidae					
<i>Pomphorhynchus</i> sp.	NA	NA	NA	JQ824372	Pan & Nie (unpublished)
<i>Pomphorhynchus alemniscus</i>	PV436855	PV436859	PV657853	NA	Kita et al. (2025b)
<i>Pomphorhynchus bulbocolli</i>	NA*	AF001841	AY829096	JQ824371	Near et al. (1998) for 18S; García-Varela & Nadler (2005) for 28S; Pan & Nie (unpublished) for mtgenome
<i>Pomphorhynchus laevis</i>	AY423348	AY423346	NA	JQ809446	Perrot-Minnot (2004) for cox1 and 18S; Pan & Nie (unpublished) for mtgenome
<i>Pomphorhynchus pagrosomi</i> (Ijika)	NR	NR	NR	NR	this study
<i>Pomphorhynchus pagrosomi</i>	NA	NA	NA	OR215045	Ren et al. (2025)
<i>Pomphorhynchus rocci</i>	NA	NA	NA	JQ824373	Pan & Nie (unpublished)
<i>Pomphorhynchus tereticollis</i>	OQ569523	OQ581789	NA	JQ809451	Smrzlić et al. (2024) for cox1 and 18S; Pan & Nie (unpublished) for mtgenome
<i>Pomphorhynchus zhoushanensis</i> (= <i>P. pagrosomi</i>)	KY490045	KY490049	NA	MN602447	Li et al. (2017a) for cox1 and 18S; Zhao (unpublished) for mtgenome
<i>Tenuiproboscis</i> sp.	JF694273	JF694275	NA	NA	Sanil et al. (unpublished)
Pseudoacanthocephalidae					
<i>Pseudoacanthocephalus bufonis</i>	PP477056	PP447266	NA	MZ958236	C-H Zhao et al. (2024) for cox1 and 18S; T-Y Zhao et al. (2023) for mtgenome
<i>Pseudoacanthocephalus lucidus</i>	LC100062	LC129279	NA	NA	Nakao (2016)
<i>Pseudoacanthocephalus nguyenthileae</i>	PP476964	PP447460	NA		C-H Zhao et al. (2024)
<i>Pseudoacanthocephalus previatesticulus</i>	PP481149	PP455352	PP471559	NA	C-H Zhao et al. (2024)
<i>Pseudoacanthocephalus sadoensis</i>	LC853426	LC853427	NA	NA	Kita et al. (2025a)
<i>Pseudoacanthocephalus sichuanensis</i>	PP469226	PP454074	PP471560		C-H Zhao et al. (2024)
<i>Pseudoacanthocephalus toshimai</i>	LC100044	LC129278	NA	NA	Nakao (2016)
Rhadinorhynchidae					
<i>Rhadinorhynchus carangis</i>	MN692684	MN705830	MN705850	NA	Huston et al. (2020)
<i>Rhadinorhynchus decapteri</i> **	KJ590125	KJ590123	KJ590124	NA	Braicovich et al. (2014)

<i>Rhadinorhynchus dorsoventrospinosus</i>	MN267180	NA***	NA	NA	Chaudhary et al. (2020b)
<i>Rhadinorhynchus gerberi</i>	MN104898	MN105739	MN105747	NA	Lisitsyna et al. (2019)
<i>Rhadinorhynchus hiansi</i>	MN203138	MN203134	NA	NA	Amin et al. (2020a)
<i>Rhadinorhynchus johnstoni</i>	MN692680	MN705827	MN705847	NA	Huston et al. (2020)
<i>Rhadinorhynchus laterospinosus</i>	MK572744	MK457183	NA	PV590110	Amin et al. (2019a) for cox1 and 18S; Xie et al. (2025b) for mtgenome
<i>Rhadinorhynchus laterospinosus</i> (Tosa-Shimizu)	LC777823	LC777824	LC841944	NR	Kita et al. (2024a) for cox1 and 18S; Kita et al. (2024c) for 28S; this study for mtgenome
<i>Rhadinorhynchus mariserpentis</i> (= <i>R. nudus</i>)	MK012666	MK014866	MK014867	NA	Steinauer et al. (2019)
<i>Rhadinorhynchus nudus</i>	MG838935	MG838945	NA	NA	Li et al. (2019)
<i>Rhadinorhynchus nudus</i> (Hondo)	NR	NR	NA	NA	this study
<i>Rhadinorhynchus seriola</i>	LC777825	LC777826	NA	NA	Kita et al. (2024a)
<i>Rhadinorhynchus trachinoti</i>	PQ541025	PQ549641	PQ549643	NA	Grano-Maldonado et al. (2025)
<i>Rhadinorhynchus villalobosi</i>	PQ374012	PQ373610	PQ373609	NA	Martínez-Flores et al. (2025)
Spinulacorpidae					
<i>Spinulacarpus biforme</i>	MN692683	MN705829	MN705849	NA	Huston et al. 2020
Transvenidae					
<i>Darwinorhynchus bajacaliforniaensis</i>	PX132612	PX139052	PX139055	NA	Aguillar-Aguillar et al. (2025)
<i>Pararhadinorhynchus magnus</i>	NA	MN395027	MN820614	NA	Chaudhary et al. (2020a)
<i>Pararhadinorhynchus sodwanensis</i>	NA	MN105738	MN105744	NA	Lisitsyna et al. (2019)
<i>Paratrajectura longcementglandatus</i>	MK770615	MK770616	NA	NA	Sharifdini et al. (2020)
<i>Sclerocollum australe</i>	MN692686	MN705831	MN705851	NA	Huston et al. (2020)
<i>Sclerocollum neorubrimaris</i>	LC757485	NR	NR	NR	this study
<i>Sclerocollum robustum</i>	MN692687	MN705832	MN705852	NA	Huston et al. (2020)
<i>Trajectura ikedai</i>	NR	NA	NA	NA	this study
<i>Transvena annulospinosa</i>	DQ089711	AY830153	AY829098	NA	García-Varela & Nadler (2006) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Transvena pichelinae</i>	MN104895	MN105736	MN105742	NA	Lisitsyna et al. (2019)
Polymorphida					

Centrorhynchidae					
<i>Centrorhynchus aluconis</i>	NA	MN057695	MN057699	KT592357	García-Varela et al. (2020b) for 18S and 28S; Gazi et al. (2016) for mtgenome
<i>Centrorhynchus clitorideus</i>	MN661370	MN661371	MN661374	MT113355	Zhao et al. (2020) for cox1, 18S and 28S; Muhammad et al. (2020b) for mtgenome
<i>Centrorhynchus globirostris</i>	NA	KM588206	KM588207	NA	Amin et al. (2015)
<i>Centrorhynchus globocaudatus</i>	MT992255	MN057696	MN057700	NA	Amin et al. (2020b) for cox1; García-Varela et al. (2020b) for 18S and 28S
<i>Centrorhynchus magnus</i>	LC713290	LC713278	LC713284	NA	Sasaki et al. (unpublished)
<i>Centrorhynchus microcephalus</i>	NA	AF064813	MT161664	NA	García-Varela et al. (2000) for 18S; García-Varela et al. (2020a) for 28S
<i>Centrorhynchus milvus</i>	NA	NA	NA	MK922344	Muhammad et al. (2019b)
<i>Centrorhynchus nahuelhuapensis</i>	NA	MK411249	MK411250	NA	Steinauer et al. (2020)
<i>Centrorhynchus nickoli</i>	NA	MT161621	MT161666	NA	García-Varela et al. (2020a)
<i>Sphaerirostris lanceoides</i>	MG931939	NA	MT110677	MT476588	Kang & Li (2018) for cox1 and 28S; Muhammad et al. (2020a) for mtgenome
<i>Sphaerirostris picae</i>	NA*	NA	NA	MK471355	Muhammad et al. (2019a)
Isthmosacanthidae					
<i>Gorgorhynchus lepidus</i>	OR826977	NA	NA	NA	Martínez-Aquino et al. (2023)
<i>Gorgorhynchus medius</i>	OR883561	OR886454	OR886457	NA	García-Varela et al. (2024)
<i>Metarhadinorhynchus bullocki</i>	DQ089715	AY830154	AY829103	NA	García-Varela & Nadler (2006) for cox1; García-Varela & Nadler (2005) for 18S and 28S
<i>Metarhadinorhynchus gnathanodontos</i>	MN692697	MN705839	MN705859	NA	Huston et al. (2020)
<i>Metarhadinorhynchus lateolabraxis</i>	LC804744	LC804746	LC804747	NR	Kita et al. (2024b) for cox1, 18S and 28S: this study for mtgenome
<i>Metarhadinorhynchus pseudocarangis</i>	MN692699	MN705840	MN705860	NA	Huston et al. (2020)
<i>Metarhadinorhynchus queenslandensis</i>	MN692696	MN705838	MN705858	NA	Huston et al. (2020)
<i>Serrasentis sagittifer</i>	MN692700	MN705841	MN705861	NA	Huston et al. (2020)
<i>Serrasentis gibsoni</i>	OR826956	NA	NA	NA	Martínez-Aquino et al. (2023)
<i>Serrasentis nadakali</i>	KC291712	KC291715	NA	NA	Paul et al. (unpublished)
Plagiorhynchidae					

<i>Lueheia azteca</i>	NA	MT161620	MT161666	NA	García-Varela et al. (2020a)
<i>Plagiorhynchus aznari</i>	NA	MN057693	MN057697	NA	García-Varela et al. (2020b)
<i>Plagiorhynchus crassicolis</i>	NA	MW367669	MW367671	NA	Capasso et al. (2021)
<i>Plagiorhynchus cylindraceus</i>	DQ089714	AF001839	AY829102	NA	García-Varela & Nadler (2006) for cox1; Near et al. (1998) for 18S; García-Varela & Nadler (2005) for 28S
<i>Plagiorhynchus transversus</i>	NA	MN057694	MN057698	KT447549	García-Varela et al. (2020b) for 18S and 28S; Gazi et al. (2016) for mtgenome
Polymorphidae					
<i>Andracantha grvida</i>	EU267822	EU267802	EU267814	NA	García-Varela et al. (2009)
<i>Andracantha leucocarboi</i>	MF527025	NA	MF401623	NA	Presswell et al. (2017)
<i>Andracantha phalacrocoracis</i>	LC465396	NA	LC461973	NA	Sasaki et al. (2019)
<i>Andracantha sigma</i>	MF527027	NA	MF401624	NA	Presswell et al. (2017)
<i>Arhythmorhynchus brevis</i>	JX442194	JX442171	JX442183	NA	García-Varela et al. (2013)
<i>Arhythmorhynchus frassoni</i>	JX442188	JX442164	JX442176	NA	García-Varela et al. (2013)
<i>Bolbosoma balaenae</i>	MZ047272	MZ047221	MZ047231	MZ357084	Santoro et al. (2021) for cox1, 18S, and 28S; García-Gallego et al. (2023) for mtgenome
<i>Bolbosoma caenoforme</i>	KF156891	KF156879	NA	NA	Malyarchuk et al. (2014)
<i>Bolbosoma capitatum</i> (= <i>B. vasculosum</i>)	NA	MZ358110	MZ366746	MZ357085	García-Gallego et al. (2023)
<i>Bolbosoma nipponicum</i>	ON359908	ON358429	ON359841	OR468096	Ru et al. (2022b) for cox1, 18S, and 28S; Li et al. (2024) for mtgenome
<i>Bolbosoma turbinella</i>	NA	MZ358111	MZ366747	MZ357086	García-Gallego et al. (2025)
<i>Bolbosoma vasculosum</i>	PX278699	PX273926	PX274206	MZ357087	García-Gallego et al. (2023)
<i>Bolbosoma vasculosum</i> (Naha)	LC786500	LC786494	NA	NA	Kita et al. (2024d)
<i>Corynosoma australe</i>	JX442191	JX442168	JX442180	NA	García-Varela et al. (2013)
<i>Corynosoma bullosum</i>	NA*	NA*	NA	PQ516697	Xie et al. (2025a)
<i>Corynosoma enhydri</i>	DQ089719	AF001837	AY829107	NA	García-Varela & Nadler (2006) for cox1; Near et al. (1998) for 18S; García-Varela & Nadler (2005) for 28S
<i>Corynosoma evae</i>	ON881146	ON890393	ON890395	PQ516696	Hernández-Orts et al. (2022) for cox1, 18S and 28S; Xie et al. (2025a) for mtgenome
<i>Corynosoma semerme</i>	LC465311	NA	LC461963	NA	Sasaki et al. (2019)
<i>Corynosoma strumosum</i>	LC465328	NA	LC461964	NA	Sasaki et al. (2019)
<i>Corynosoma villosum</i>	LC465335	NA	LC461968	OR468095	Sasaki et al. (2019)
<i>Heterospinus mccordi</i>	PQ219553	NA	PQ285816	NA	Rothman et al. (2025)

<i>Hexaglandula corynosoma</i>	EU189485	EU267808	EU267817	NA	Guillén-Hernández et al. (2008) for cox1; García-Varela et al. (2009) for 18S and 28S
<i>Ibirhynchus dimorpha</i>	GQ981438	GQ981436	GQ981437	NA	García-Varela et al. (2011)
<i>Polymorphus minutus</i>	EF467865	EU267806	EU267819	MN646175	García-Varela & Pérez-Ponce de León (2008) for cox1; García-Varela et al. (2009) for 18S and 28S; Sarwar et al. (2021) for mtgenome
<i>Polymorphus obtusus</i>	JX442195	JX442172	JX442184	NA	García-Varela et al. (2013)
<i>Polymorphus phippsi</i>	OL676687	NA	ON667751	NA	Diumina et al. (2024)
<i>Polymorphus trochus</i>	JX442196	JX442173	JX442185	NA	García-Varela et al. (2013)
<i>Profilicollis altmani</i>	DQ089720	AF001838	AY829108	NA	García-Varela & Nadler (2006) for cox1; Near et al. (1998) for 18S; García-Varela & Nadler (2005) for 28S
<i>Profilicollis botulus</i>	EF467862	EU267805	EU267818	NA	García-Varela & Pérez-Ponce de León (2008) for cox1; García-Varela et al. (2009) for 18S and 28S
<i>Pseudocorynosoma anatarium</i>	EU267821	EU267801	EU267813	NA	García-Varela et al. (2009)
<i>Pseudocorynosoma constrictum</i>	EU267820	EU267800	EU267812	NA	García-Varela et al. (2009)
<i>Southwellina hispida</i>	EF467866	EU267807	EU267810	KJ869251	García-Varela & Pérez-Ponce de León (2008) for cox1; García-Varela et al. (2009) for 18S and 28S; Gazi et al. (2015) for mtgenome
<i>Tenuisoma tarapungi</i>	MN688202	MN688257	MN688256	NA	Presswell et al. (2020)
Pyriproboscidae					
<i>Pyriproboscis heronensis</i>	MN692703	MN705842	MN692703	NA	Huston et al. (2020)
[Outgroup]					
Eoacanthocephala					
Gyracanthocephala					
Quadrigyridae					
<i>Acanthogyrus (Acanthosentis) bilaspurensis</i>	NA	OM262040	OM333893	MT476589	Ru et al. (2022a) for 18S and 28S; Muhammad et al. (2023) for mtgenome
<i>Pallisentis (Pallisentis) celatus</i>	NA	NA	NA	JQ943583	Pan & Nie (2013)
Neoechinorhynchida					
Neoechinorhynchidae					
Neoechinorhynchidae sp.****	NA	NA	NA	MT345686	Pan (unpublished)
<i>Neoechinorhynchus (Hebesoma) violentus</i>	NA*	KF156881	NA	KC415004	Malyarchuk et al. (2014) for 18S; Pan & Nie (2014) for mtgenome

<i>Neoechinorhynchus (Hebesoma) yamagutii</i>	NA	NR	NR	NR	this study
<i>Neoechinorhynchus (Neoechinorhynchus) qinghaiensis</i>	NA	MW144440	NA	MW851291	Pan (unpublished)
Tenuisentidae					
<i>Paratenuisentis ambiguus</i>	NA	AF469414	NA	FR856885	Herlyn et al. (2003) for 18S; Weber et al. (2013) for mtgenome
Polyacanthorhynchida					
Polyacanthorhynchidae					
<i>Polyacanthorhynchus caballeroi</i>	DQ089724	AF388660	DQ089738	KT592358	García-Varela & Nadler (2006) for cox1 and 28S; García-Varela et al. (2002) for 18S; Gazi et al. (2016) for mtgenome
Archiacanthocephala					
Moniliformida					
Moniliformidae					
<i>Moniliformis</i> sp.	NA	OM388438	NA	OP413683, OK415026	Dai et al. (2022); Ma (unpublished) for mtgenome
Oligacanthorhynchida					
Oligacanthorhynchidae					
<i>Macracanthorhynchus hirudinaceus</i>	LC350021	LC350001	LC350001	FR856886	Kamimura et al. (2018) for cox1, 18S, and 28S; Weber et al. (2013) for mtgenome
<i>Oncicola luehei</i>	NA	NA	NA	JN710452	Gazi et al. (2012)
Rotifera					
<i>Seison</i> sp.	NA	NA	NA	KP742964	Siellaff et al. (2016)
<i>Rotaria rotatoria</i>	NA	DQ089736	DQ089743	GQ304898	García-Varela & Nadler (2006) for 18S and 28S; Min & Park (2009) for mtgenome
<i>Philodina citrina</i>	NA	JX494790	NA	FR856884	Tang et al. (2012) for 18S; Weber et al. (2013) for mtgenome

*Data available but insufficient length or low quality. **Secondary homonym of *Rhadinorhynchus decapteri* Paruchin & Kovalenko, 1976. ***Only contaminated sequences are available. ****Registered as “*Acanthocephalus* sp.”

Table 15. The list of the optimal substitution models determined by Modelfinder/Partitionfinder for each of the three datasets. Each partition of nucleotide sequences is indicated as “[gene name]_pos#” (e.g., atp6_pos2 means the second codon of atp6 codon frame).

Dataset	Models (Modelfinder)	Partitions (Modelfinder)	Models (Partitionfinder)	Partitions (Partitionfinder)
AA	MTINV + F + I + R6	atp6, cox3, nad1, nad2, nad3, nad4, nad4l, nad5, nad6	LG + I + G	atp6, nad1, cox1, nad2, nad3, nad4
	MTINV + F + R6	<i>cox1, cox2, cytb</i>	WAG + I + G	<i>cox2, cox3, cytb, nad5, nad6</i>
DNA	GTR + F + I + G4	atp6_pos1, cox3_pos3, nad2_pos3, nad4_pos1, cox1_pos2, cox2_pos3	WAG + G GTR + I + G	<i>nad4l</i> atp6_pos1–3, cox1_pos1–3, cox2_pos1–3, cox3_pos1–3, cytb_pos1–3, nad1_pos1–3, nad2_pos1–3, nad3_pos1–3, nad4_pos1–3, nad4l_pos2, nad5_pos1–3
	TVM + F + I + G4	atp6_pos2, nad4l_pos3, cytb_pos2, nad1_pos1, nad3_pos3	GTR + G	nad4l_pos1, nad4l_pos3, nad6_pos1, nad6_pos2, nad6_pos3
	GTR + F + I + R4	atp6_pos3, cox3_pos1, nad1_pos2, nad2_pos1, nad3_pos1, nad5_pos2, cox1_pos1, cox2_pos2, cytb_pos1		
	TIM3 + F + I + R4	cox1_pos3, cox2_pos1, cytb_pos3		
	TVM + F + I + R5	cox3_pos2, nad5_pos1, nad5_pos3		
	TIM2 + F + I + R4	nad1_pos3, nad2_pos2, nad3_pos2		
	GTR + F + I + R5	nad4_pos2, nad4_pos3, nad4l_pos2		

DNA+R	TIM3 + F + G4	nad4l_pos1, nad6_pos3, nad6_pos1, nad6_pos2	GTR + I + G	atp6_pos1–3, cox1_pos1–3, cox2_pos1–3, cox3_pos1–3, cytb_pos1–3, nad1_pos1–3, nad2_pos1–3, nad3_pos1–3, nad4_pos1–3, nad4l_pos2, nad5_pos1–3, 12S, 16S nad4l_pos1, nad4l_pos3, nad6_pos1, nad6_pos2, nad6_pos3
	GTR + F + I + G4	atp6_pos1, cox3_pos3, nad2_pos3, nad4_pos1, cox1_pos2, cox2_pos3		
	TVM + F + I + R5	atp6_pos2, cox3_pos2, nad4l_pos3, nad5_pos1, nad5_pos3	GTR + G	
	GTR + F + I + R4	atp6_pos3, cox3_pos1, nad2_pos1, nad3_pos1, cox1_pos1, cox2_pos2, cytb_pos1		
	TIM3 + F + I + R4	cox1_pos3, cox2_pos1, cytb_pos3, nad1_pos2, nad5_pos2		
	TVM + F + I + G4	cytb_pos2, nad1_pos1, nad3_pos3		
	TIM2 + F + I + R4	nad1_pos3, nad2_pos2, nad3_pos2, nad4l_pos2		
	GTR + F + R5	nad4_pos2, nad4_pos3, nad6_pos1, nad6_pos2		
DNA+RR	TIM3 + F + G4	nad4l_pos1, nad6_pos3	GTR + I + G	atp6_pos1–3, cox1_pos1–3, cox2_pos1–3, cox3_pos1–3, cytb_pos1–3, nad1_pos1–3, nad2_pos1–3, nad3_pos1–3, nad4_pos1–3,
	GTR + F + I + R5	16S, 12S		
	TIM + F + I + R4	atp6_pos1, nad4_pos1, nad6_pos1, nad6_pos2		

			nad4l_pos2, nad5_pos1-3, 12S, 16S, 18S, 28S
TVM + F + I + G4	atp6_pos2, cox3_pos2, nad4l_pos3, cox1_pos2, cox2_pos3, cytb_pos2, nad1_pos1, nad3_pos3	GTR + G	nad4l_pos1, nad4l_pos3, nad6_pos1, nad6_pos2, nad6_pos3
GTR + F + I + R4	atp6_pos3, cox3_pos1, nad2_pos1, nad3_pos1, cox1_pos1, cox2_pos2, cytb_pos1		
TIM3 + F + I + R4	cox1_pos3, cox2_pos1, cytb_pos3, nad1_pos2, nad5_pos2		
TVM + F + R6	cox3_pos3, nad2_pos3, nad5_pos1, nad5_pos3		
TIM2 + F + I + R4	nad1_pos3, nad2_pos2, nad3_pos2, nad4l_pos2		
GTR + F + I + R5	nad4_pos2, nad4_pos3, 16S, 12S		
TIM3 + F + G4	nad4l_pos1, nad6_pos3		
GTR + F + I + G4	18S, 28S		

Table 16. Profile of annotated mitochondrial genes of *Echinorhynchus gadi* Zoega in Müller, 1776.

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1545	1545
<i>trnG</i>	1545	1597	53
<i>trnY</i>	1640	1692	53
16S	1693	2663	971
<i>trnL</i>	2614	2667	54
<i>nad6</i>	2782	3288	507
<i>atp6</i>	3285	3863	579
<i>nad3</i>	3877	4230	354
<i>trnW</i>	4211	4271	61
<i>trnV</i>	5963	6025	63
<i>trnE</i>	6074	6127	54
<i>trnT</i>	6129	6183	55
<i>nad4l</i>	6237	6512	276
<i>nad4</i>	6530	7798	1269
<i>trnH</i>	7798	7855	58
<i>nad5</i>	7853	9511	1659
<i>trnL</i>	9511	9563	53
<i>trnP</i>	9572	9623	52
<i>CYTB</i>	9618	10742	1125
<i>ND1</i>	10746	11642	897
<i>trnS</i>	11713	11768	56
<i>trnI</i>	11997	12050	54
<i>trnM</i>	12054	12110	57
12S	12111	12698	588
<i>trnF</i>	12691	12743	53
<i>cox2</i>	12744	13406	663
<i>trnC</i>	13393	13444	52
<i>COX3</i>	13413	14183	771
<i>trnA</i>	14182	14234	53
<i>trnN</i>	14285	14340	56
<i>trnS</i>	14333	14389	57
<i>nad2</i>	14389	15300	912

Table 17. Profile of annotated mitochondrial genes of *Echinorhynchus sasakiae* Kita & Kajihara, 2023.

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1545	1545
<i>trnG</i>	1545	1597	52
<i>trnY</i>	1640	1692	54
16S	1750	2613	864
<i>trnL</i>	2615	2668	54
<i>nad6</i>	2783	3301	519
<i>atp6</i>	3295	3876	582
<i>nad3</i>	3869	4243	351
<i>trnW</i>	4224	4284	61
<i>trnK</i>	5397	5467	71
<i>trnE</i>	5456	5507	52
<i>trnV</i>	6261	6323	63
<i>trnT</i>	6373	6427	55
<i>nad4l</i>	6453	6758	306
<i>nad4</i>	6776	8044	1269
<i>trnH</i>	8043	8100	58
<i>nad5</i>	8171	9757	1587
<i>trnL</i>	9756	9808	53
<i>trnP</i>	9816	9868	53
<i>cytb</i>	9870	10988	1119
<i>nad1</i>	11004	11888	885
<i>trnI</i>	12250	12316	67
<i>trnM</i>	12309	12365	57
12S	12435	12944	510
<i>trnF</i>	12945	12997	53
<i>cox2</i>	13023	13661	639
<i>trnC</i>	13647	13698	52
<i>cox3</i>	13668	14438	771
<i>trnA</i>	14436	14506	71
<i>trnN</i>	14528	14590	63
<i>trnS</i>	14586	14642	57
<i>nad2</i>	14662	15555	894

Table 18. Profile of annotated mitochondrial genes of *Metarhadinorhynchus lateolabracis* Yamaguti, 1959.

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1539	1539
<i>trnG</i>	1538	1590	53
<i>trnY</i>	1632	1684	53
16S	1757	2607	851
<i>trnL</i>	2595	2648	54
<i>nad6</i>	2646	3098	453
<i>trnD</i>	3089	3141	53
<i>atp6</i>	3123	3818	696
<i>nad3</i>	3834	4190	357
<i>trnW</i>	4165	4224	60
<i>trnI</i>	4310	4371	62
<i>trnV</i>	5421	5481	61
<i>trnE</i>	5485	5536	52
<i>trnT</i>	6417	6466	50
<i>trnS</i>	6466	6516	51
<i>nad4l</i>	6519	6803	285
<i>nad4</i>	6780	8095	1316
<i>trnH</i>	8080	8131	52
<i>nad5</i>	8135	9778	1644
<i>trnL</i>	9780	9846	67
<i>trnP</i>	9835	9887	53
<i>cytb</i>	9900	11018	1119
<i>nad1</i>	11018	11908	891
<i>trnM</i>	12540	12594	55
12S	12659	13178	520
<i>trnF</i>	13179	13219	40
<i>cox2</i>	13220	13864	645
<i>trnC</i>	13864	13918	55
<i>cox3</i>	13939	14649	711
<i>trnA</i>	14648	14715	68
<i>trnR</i>	14700	14761	62
<i>trnS</i>	14801	14858	58

<i>nad2</i>	14876	15763	888
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Table 19. Profile of annotated mitochondrial genes of *Pomphorhynchus pagrosomi* (Yamaguti, 1935).

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1548	1548
<i>trnG</i>	1549	1603	55
16S	1791	2629	839
<i>trnL</i>	2605	2660	56
<i>nad6</i>	2601	3095	495
<i>atp6</i>	3122	3796	675
<i>nad3</i>	3850	4197	348
<i>trnW</i>	4142	4203	62
<i>trnV</i>	5273	5334	62
<i>trnE</i>	5388	5439	52
<i>trnT</i>	5440	5502	63
<i>nad4l</i>	5503	5811	309
<i>nad4</i>	5829	7103	1275
<i>nad5</i>	7175	8857	1683
<i>trnL</i>	8820	8885	66
<i>trnP</i>	8874	8925	52
<i>cytb</i>	8929	10047	1119
<i>nad1</i>	10050	10979	930
<i>trnM</i>	11255	11311	57
12S	11375	11896	522
<i>trnF</i>	11889	11939	51
<i>cox2</i>	11958	12593	636
<i>cox3</i>	12642	13373	732
<i>trnA</i>	13372	13424	53
<i>trnN</i>	13469	13525	57
<i>trnS</i>	13545	13600	56
<i>nad2</i>	13604	14496	893

Table 20. Profile of annotated mitochondrial genes of *Metacanthocephalus ovicephalus* (Zhukov, 1960).

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1591	1591
<i>trnG</i>	1531	1586	56
<i>trnY</i>	1626	1679	54
16S	1799	2588	790
<i>trnL</i>	2585	2638	54
<i>nad6</i>	2660	3079	420
<i>trnD</i>	3075	3129	55
<i>atp6</i>	3237	3800	564
<i>nad3</i>	3800	4150	351
<i>trnW</i>	4141	4200	60
<i>trnV</i>	5307	5367	61
<i>trnK</i>	5366	5427	62
<i>trnE</i>	5417	5468	52
<i>trnT</i>	5469	5542	74
<i>nad4l</i>	5569	5817	249
<i>nad4</i>	5821	6978	1158
<i>trnH</i>	7082	7132	51
<i>nad5</i>	7160	8776	1617
<i>trnL</i>	8772	8826	55
<i>trnP</i>	8826	8877	52
<i>cytb</i>	8905	10020	1116
<i>nad1</i>	10011	10904	894
<i>trnI</i>	10908	10968	61
<i>trnM</i>	11254	11311	58
12S	11259	11891	633
<i>trnF</i>	11884	11938	55
<i>cox2</i>	11900	12586	687
<i>trnC</i>	12585	12640	56
<i>cox3</i>	12668	13390	723
<i>trnA</i>	13390	13442	53
<i>trnR</i>	13443	13504	62
<i>nad2</i>	13512	14513	1002

Table 21. Profile of annotated mitochondrial genes of *Neoechinorhynchus (Hebesoma) yamagutii* Tkach et al., 2014.

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1539	1539
<i>trnG</i>	1541	1592	52
16S	1941	2598	657
<i>trnL</i>	2559	2613	55
<i>nad6</i>	2593	3042	450
<i>atp6</i>	3224	3742	519
<i>nad3</i>	3749	4066	318
<i>trnW</i>	4065	4127	63
<i>trnV</i>	4494	4545	52
<i>trnS</i>	4691	4740	50
<i>nad4l</i>	4696	4986	291
<i>nad4</i>	5025	6230	1206
<i>nad5</i>	6277	7851	1575
<i>trnL</i>	7859	7912	54
<i>trnP</i>	7913	7968	56
<i>cytb</i>	7968	9077	1110
<i>nadI</i>	9058	9930	873
<i>trnM</i>	10252	10311	60
12S	10370	10911	542
<i>trnF</i>	10906	10956	51
<i>cox2</i>	10957	11571	615
<i>trnC</i>	11575	11633	59
<i>cox3</i>	11709	12404	696
<i>trnA</i>	12364	12429	66
<i>trnR</i>	12418	12476	59
<i>trnN</i>	12460	12537	78
<i>trnS</i>	12518	12569	52
<i>nad2</i>	12555	13350	796

Table 22. Profile of annotated mitochondrial genes of *Rhadinorhynchus laterospinosus* Amin et al., 2011.

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1539	1539
<i>trnG</i>	1537	1591	55
<i>trnY</i>	1888	1938	51
16S	1939	2892	954
<i>trnL</i>	2855	2906	52
<i>nad6</i>	2901	3335	435
<i>trnS</i>	3494	3546	53
<i>atp6</i>	3496	4008	513
<i>nad3</i>	4028	4384	357
<i>trnW</i>	4344	4409	66
<i>trnE</i>	4843	4894	52
<i>nad4l</i>	4968	5231	264
<i>nad4</i>	5318	6640	1323
<i>nad5</i>	7066	8346	1281
<i>trnL</i>	8346	8397	52
<i>trnP</i>	8398	8448	51
<i>cytb</i>	8449	9579	1131
<i>nad1</i>	9564	10490	927
<i>trnM</i>	10481	10570	90
12S	10621	11099	479
<i>trnF</i>	11093	11141	49
<i>cox2</i>	11142	11765	624
<i>cox3</i>	12081	12500	420
<i>trnA</i>	12508	12562	55
<i>nad2</i>	12715	13566	852

Table 23. Profile of annotated mitochondrial genes of *Sclerocollum neorubrimaris* Amin et al., 2018.

Gene	Start	End	Length (bp)
<i>coxI</i>	1	1542	1542
<i>trnG</i>	1540	1594	55
<i>trnY</i>	1955	2027	73
16S	2028	2936	908
<i>trnL</i>	2914	2965	52
<i>nad6</i>	2954	3394	441
<i>atp6</i>	3385	4083	699
<i>nad3</i>	4064	4438	375
<i>trnW</i>	4419	4480	62
<i>trnM</i>	4954	5037	84
<i>trnE</i>	5122	5172	51
<i>nad4l</i>	5167	5502	336
<i>nad4</i>	5445	6662	1218
<i>trnV</i>	6663	6733	71
<i>trnK</i>	6711	6775	65
<i>nad5</i>	6939	8564	1626
<i>trnL</i>	8560	8611	52
<i>trnP</i>	8611	8651	41
<i>cytb</i>	8622	9776	1155
<i>nad1</i>	9715	10701	987
12S	10821	11314	494
<i>trnF</i>	11308	11374	67
<i>cox2</i>	11217	11999	783
<i>cox3</i>	11974	12744	771
<i>trnA</i>	12742	12799	58
<i>nad2</i>	12917	13792	876

FIGURES

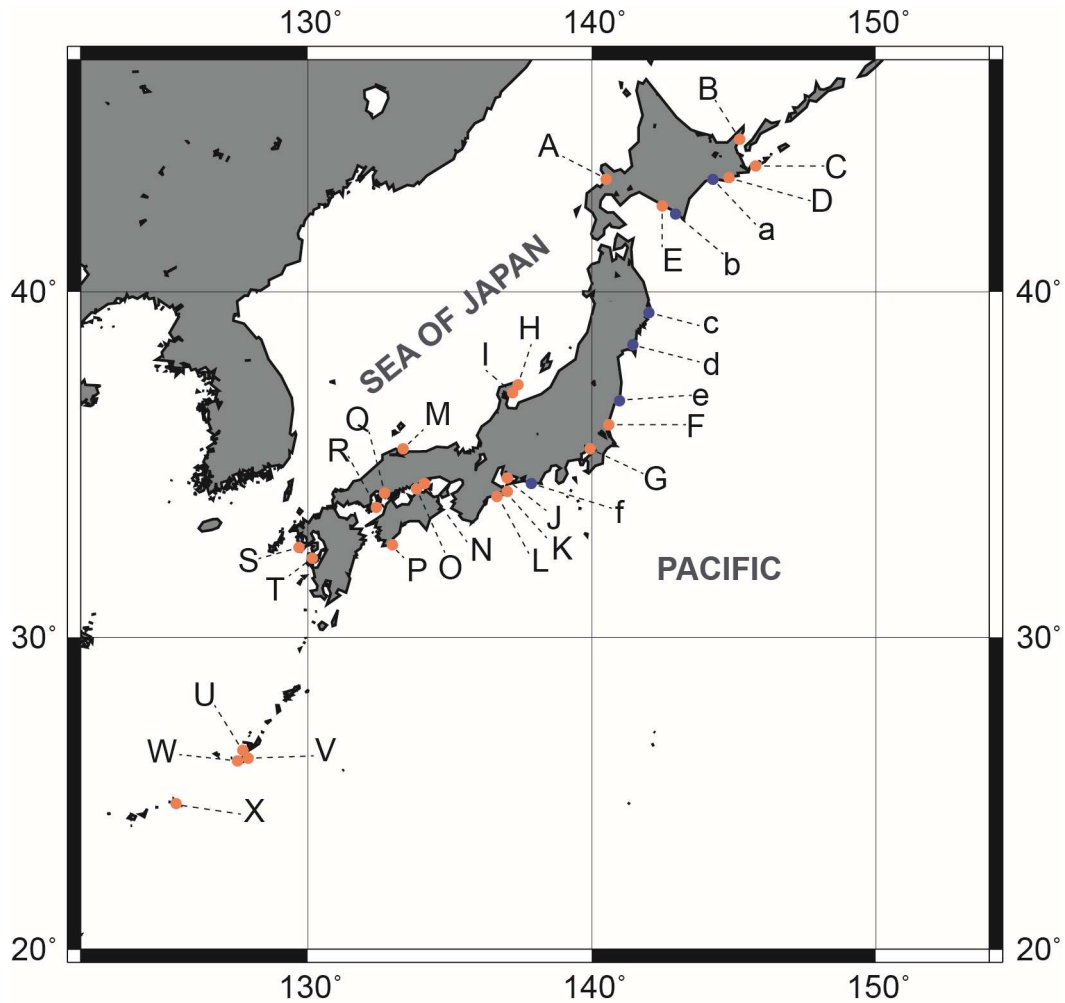


Fig. 1. Sampling sites of acanthocephalan specimens used in this study. Orange dots: sampling sites where specimens were newly obtained. Blue dots: localities where the specimens deposited in MPM and NMNS were originally collected. A, Iwanai; B, Rausu; C, Nemuro; D, Akkeshi Bay; E, Urakawa; F, Ibaraki; G, Kita-Jukken River; H, Takojima; I, Ushitsu; J, Minami-Chita; K, Ijika; L, Minami-Ise; M, Sakaiminato; N, Bizen and Oku; O, Tamano; P, Tosa-Shimizu; Q, Matoba; R, Ihota; S, Nagasaki; T, Hondo; U, Yomitan; V, Awase; W, Naha; X, Miyakojima Island; a, Kushiro; b, Samani; c, Otsuchi; d, Kesennuma; e, Onahama; f, Maisaka.

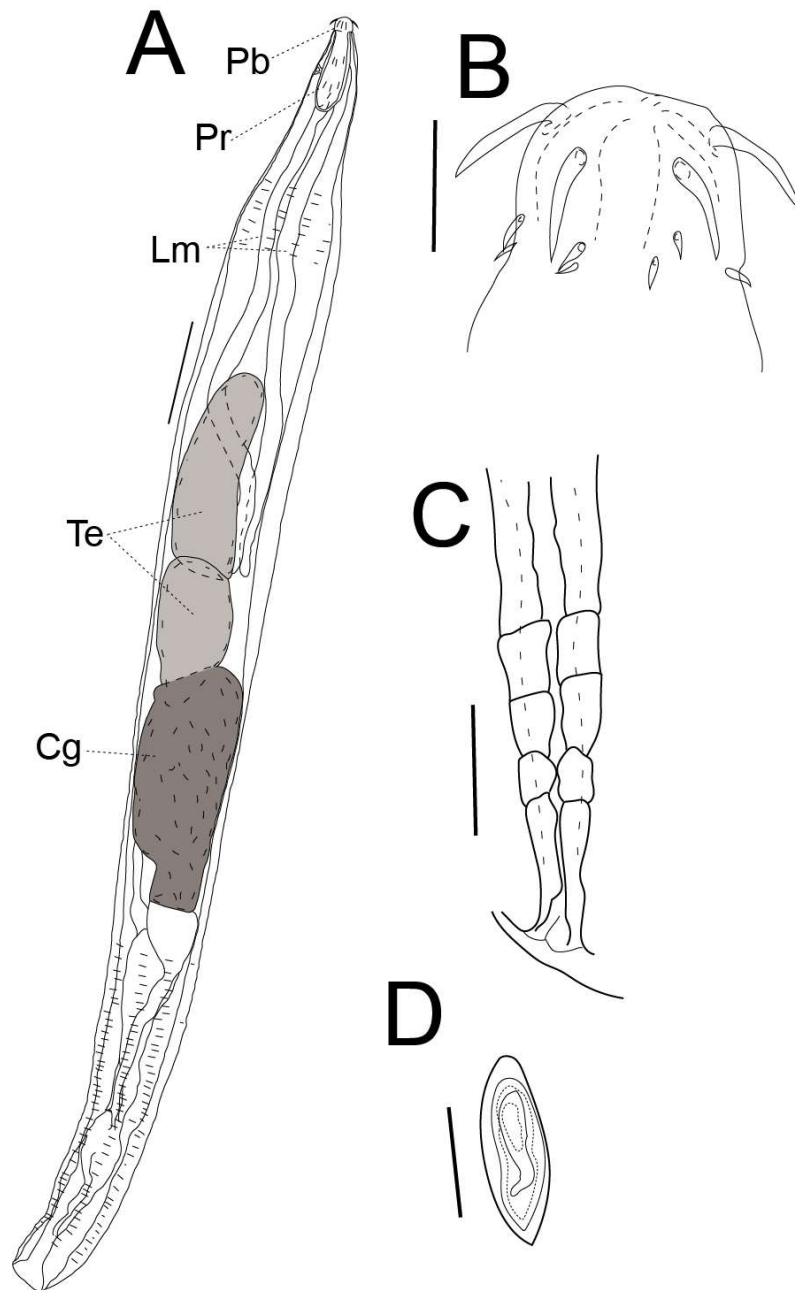


Fig. 2. *Neoechinorhynchus (Hebesoma) yamagutii* Tkach et al., 2014 (YK's private collection). A, Whole body of male; B, proboscis; C, genital pore of female; D, egg. Scale bars: 1 mm (A); 100 μ m (B, C); 10 μ m (D). Abbreviations: Cg, cement gland; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Te, testes. After Kita (unpubl.).

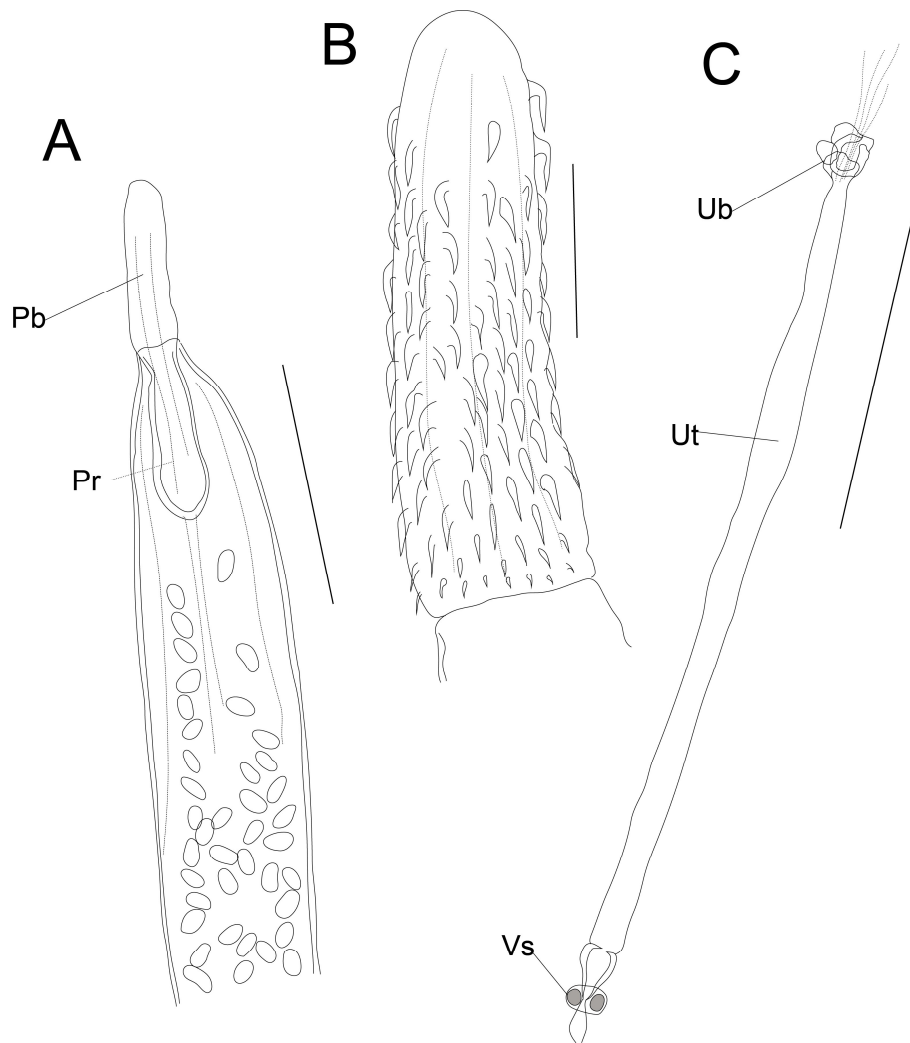


Fig. 3. *Acanthocephaloides neobythitis* Yamaguti, 1939 from Sakaiminato (YK's private collection). A, Anterior part of the specimen; B, proboscis; C, female genital organ. Scale bars: 1 mm (A); 200 μ m (B); 400 μ m (C). Abbreviations: Pb, proboscis; Pr, proboscis receptacle; Ub, uterine bell, Ut, uterus; Vs, vaginal sphincter. After Kita (unpubl.).

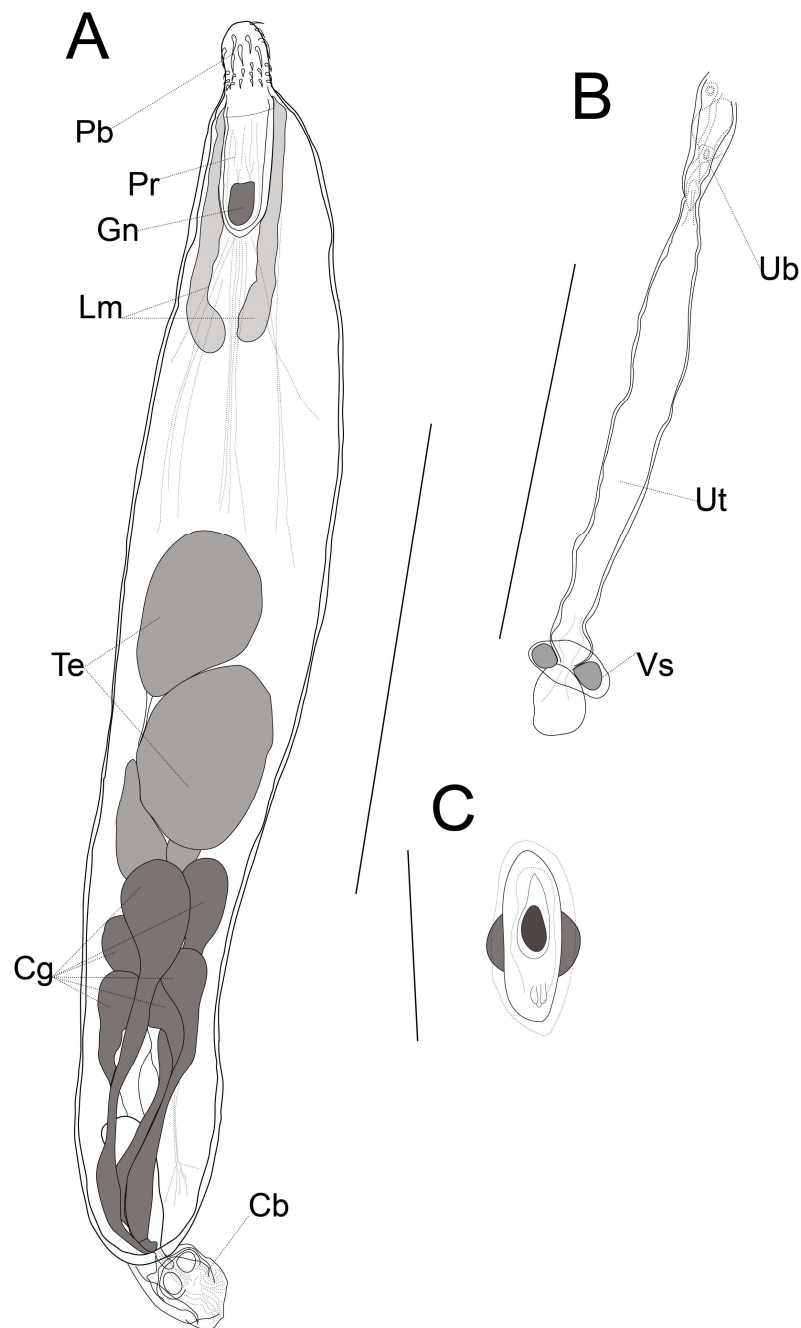


Fig. 4. *Heterosentis fusiformis* (Yamaguti, 1935) from off Matoba (YK's private collection). A, Whole body of male; B, genital organ of a female; C, egg. Scale bars: 1 mm (A); 400 μ m (B); 30 μ m (C). Abbreviations: Cb, copulatory bursa; Cg, cement glands; Gn, cerebral ganglion; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Te, testes; Ub, uterine bell; Ut, uterus; Vs, vaginal sphincter. After Kita (unpubl.)

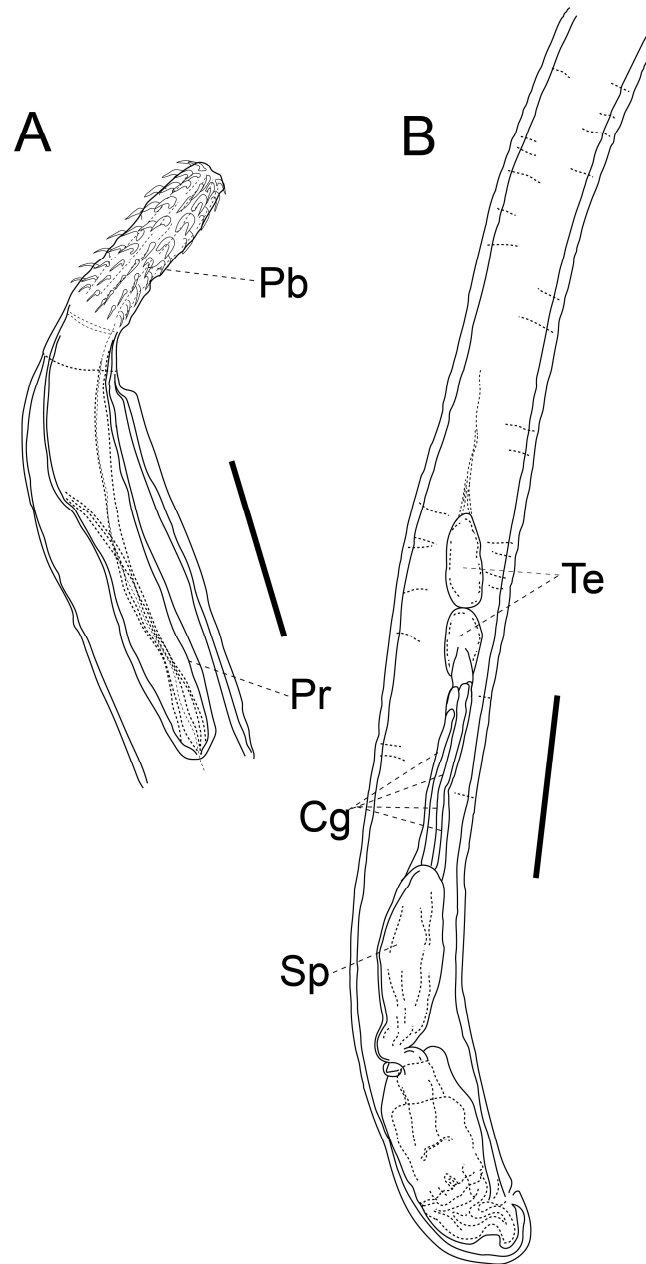


Fig. 5. *Cavisoma magnum* (Southwell, 1927) from Yomitan (Okinawa, Japan) (non-type, ICHUM 9053). A, Anterior part of the specimen; B, posterior part of the specimen. Scale bars: 1 mm. Abbreviations: Cg, cement glands; Pb, proboscis; Pr, proboscis receptacle; Te, testes; Sp, Saeftigen's pouch. After Kita & Kajihara (2025, fig. 2).

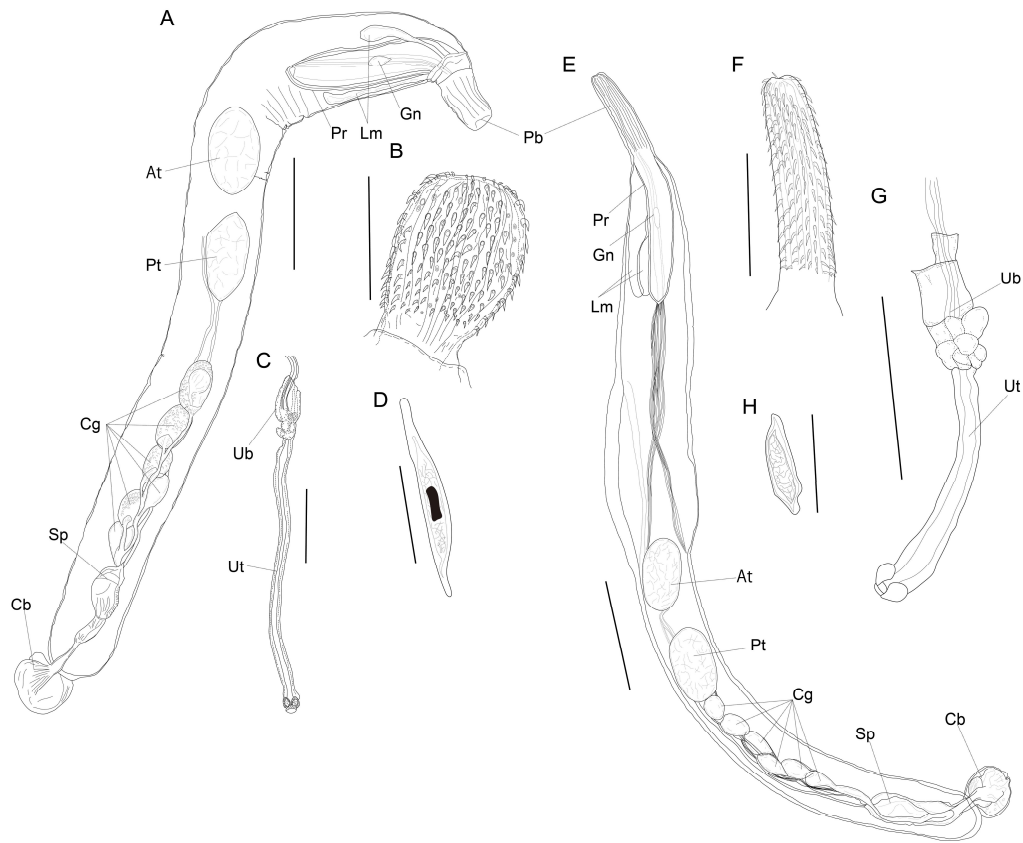


Fig. 6. *Echinorhynchus dissimilis* Yamaguti, 1939 (A–D) and *E. lotellae* Yamaguti, 1939 (E–H). A, Whole body, male (YK's private collection); B, proboscis, female (YK's private collection); C, genital organs, female (YK's private collection); D, egg (YK's private collection); E, whole body, male (YK's private collection); F, proboscis, male (YK's private collection); G, genital organs, female (YK's private collection); H, egg (YK's private collection). Abbreviations: At, anterior testis; Cb, copulatory bursa; Cg, cement glands; Gn, cephalic ganglion; Lm, lemnisci; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch; Ub, uterine bell; Ut, uterus. Scale bars: 1000 μm (A, E); 500 μm (B, C, F, G); 100 μm (D); 50 μm (H). After Kita (unpubl.).

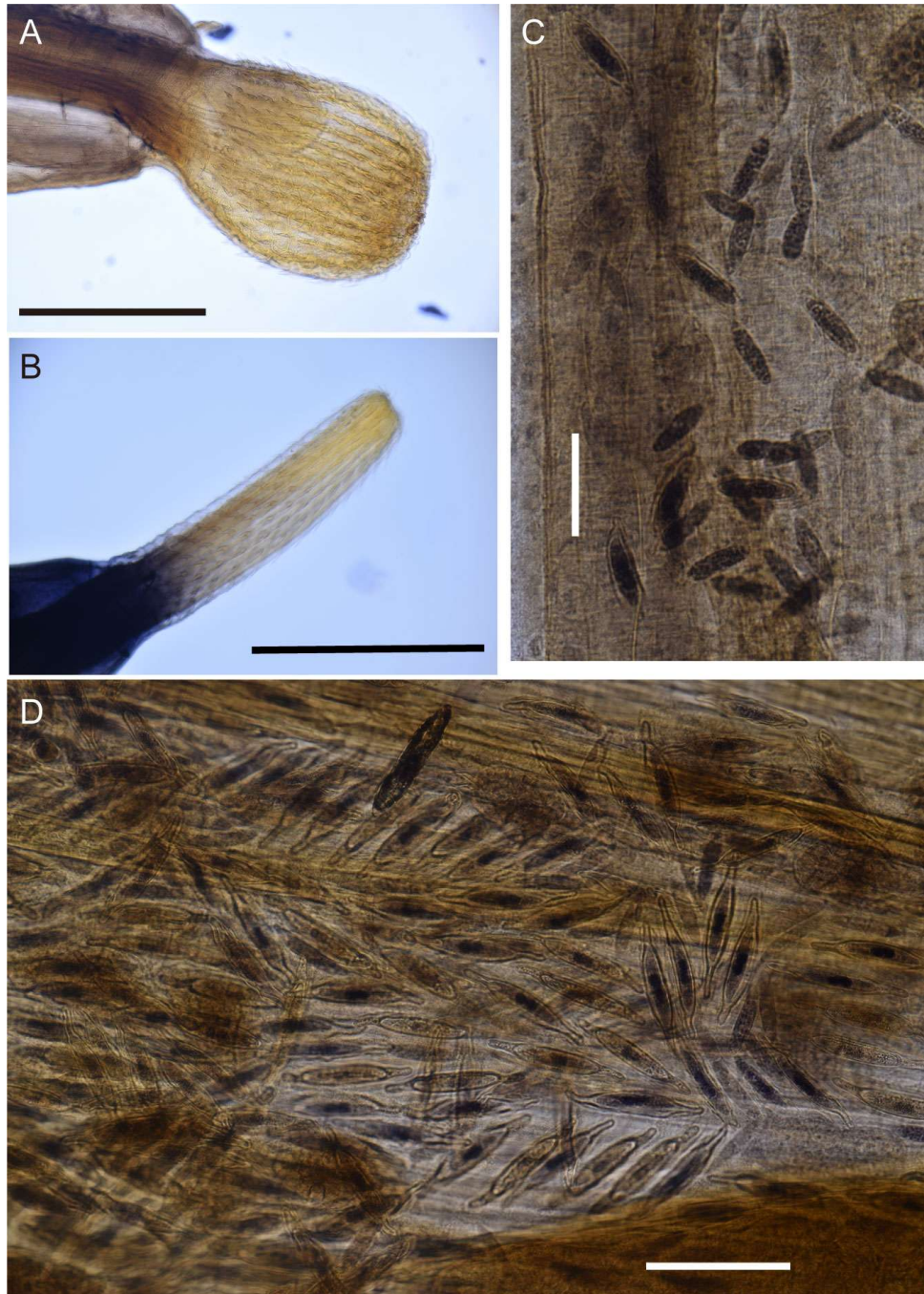


Fig. 7. *Echinorhynchus dissimilis* Yamaguti, 1939 (A, D) and *E. lotellae* Yamaguti, 1939 (B, C). A, B, Proboscis; C, D, eggs. Scale bars: 500 μm (A, B); 100 μm (D); 50 μm (C). After Kita (unpubl.).

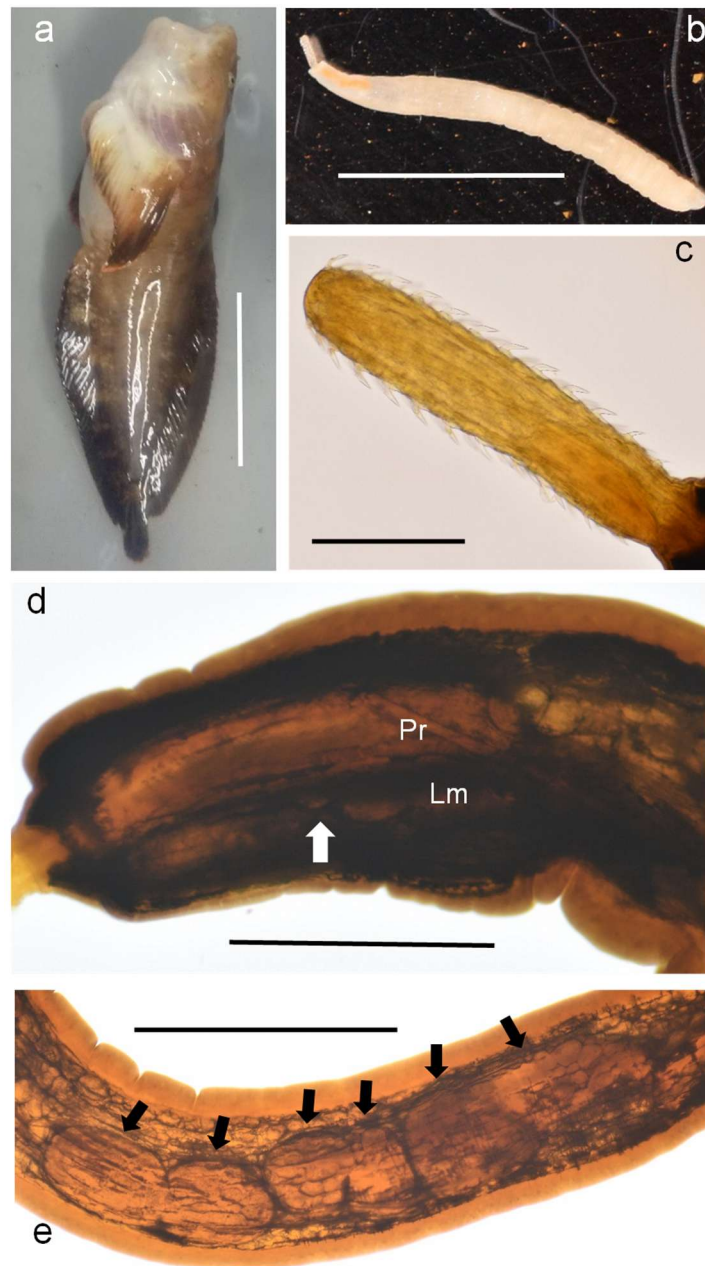


Fig. 8. *Echinorhynchus hexagrammi* Baeva, 1965 and its host, *Liparis* sp. a, *Liparis* sp., a new host of *E. hexagrammi* found in this study, lateral view; b, full body view of *E. hexagrammi* in a living state; c, a micrograph of the proboscis of *E. hexagrammi*; arrows indicate hooks that belong to a row of hooks; d, a micrograph of anterior end of *E. hexagrammi*; arrow indicates cerebral ganglion; e, a micrograph of near posterior end of *E. hexagrammi*; arrows indicate cement glands. Abbreviations: Pr, proboscis receptacle; Lm, lemniscus. Scale bars: a, 4 cm, b, 5000 μm , c, 400 μm , d, 1000 μm , e, 500 μm . After Kita & Kajihara (2021, fig. 1).

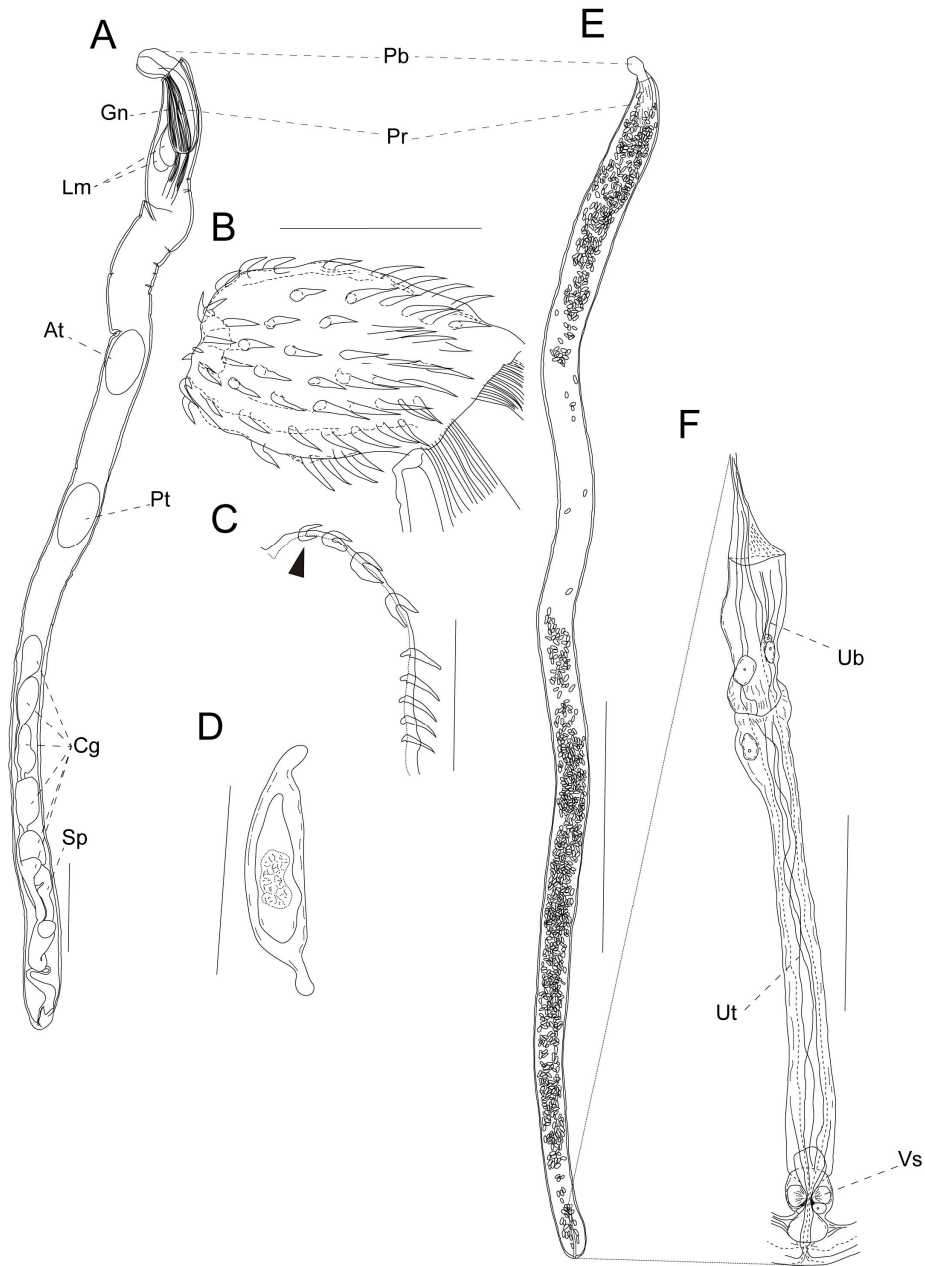


Fig. 9. *Echinorhynchus sasakiae* Kita & Kajihara, 2023, A, Whole body, male (holotype, ICHUM 8526); B, proboscis, male (holotype, ICHUM 8526); C, row of proboscis hooks, female (paratype, ICHUM 8540); arrowhead indicates the apical hook of this row; D, egg, female (paratype, ICHUM 8540); E, whole body, female (paratype, ICHUM 8539); F, genital organ, female (paratype, ICHUM 8539). Abbreviations: At, anterior testis; Cg, cement gland; Gn, cerebral ganglion; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch; Ub, uterine bell; Ut, uterus; Vs, vaginal sphincter. Scale bars: 2 mm (A); 1 mm (B, F); 500 μ m (C); 100 μ m (D); 4 mm (E). After Kita & Kajihara (2023, fig. 1).

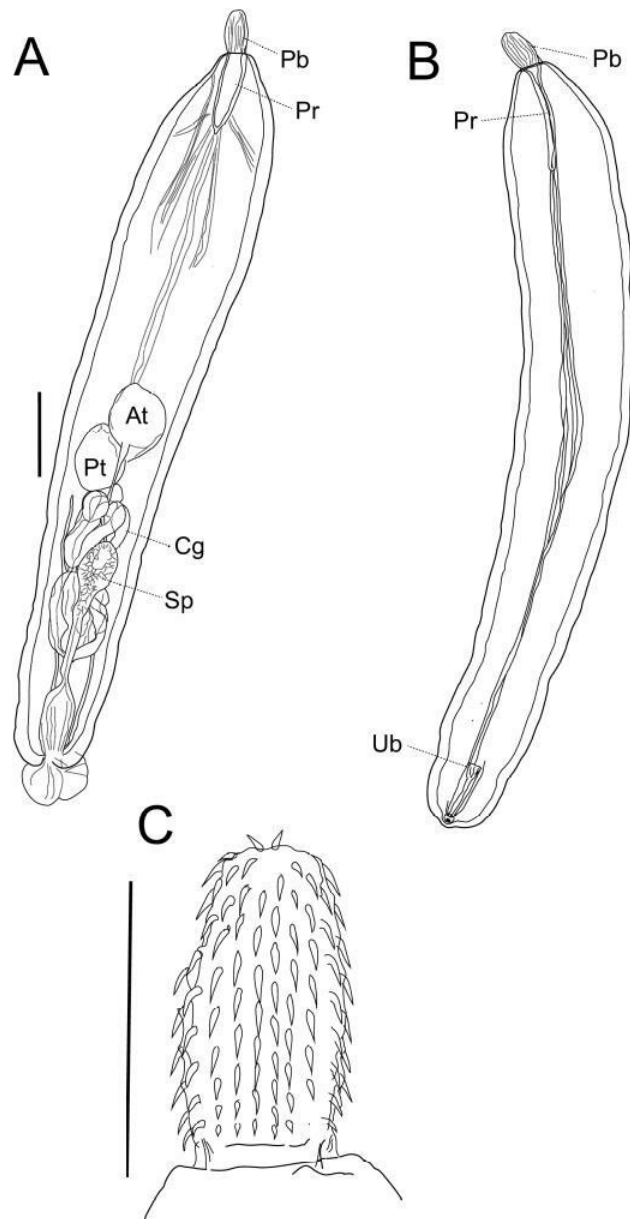


Fig. 10. *Metacanthocephalus ovicephalus* (Zhukov, 1960), line drawings. A. Whole body, male (non-type, ICHUM 8409); B, whole body, female (non-type, ICHUM 8408); C, proboscis, female (non-type, ICHUM 8408). Scale bars: 1 mm (A–C). Abbreviations: At, anterior testis; Cg, cement gland; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch; Ub, uterine bell. After Kita et al. (2023, fig. 2).

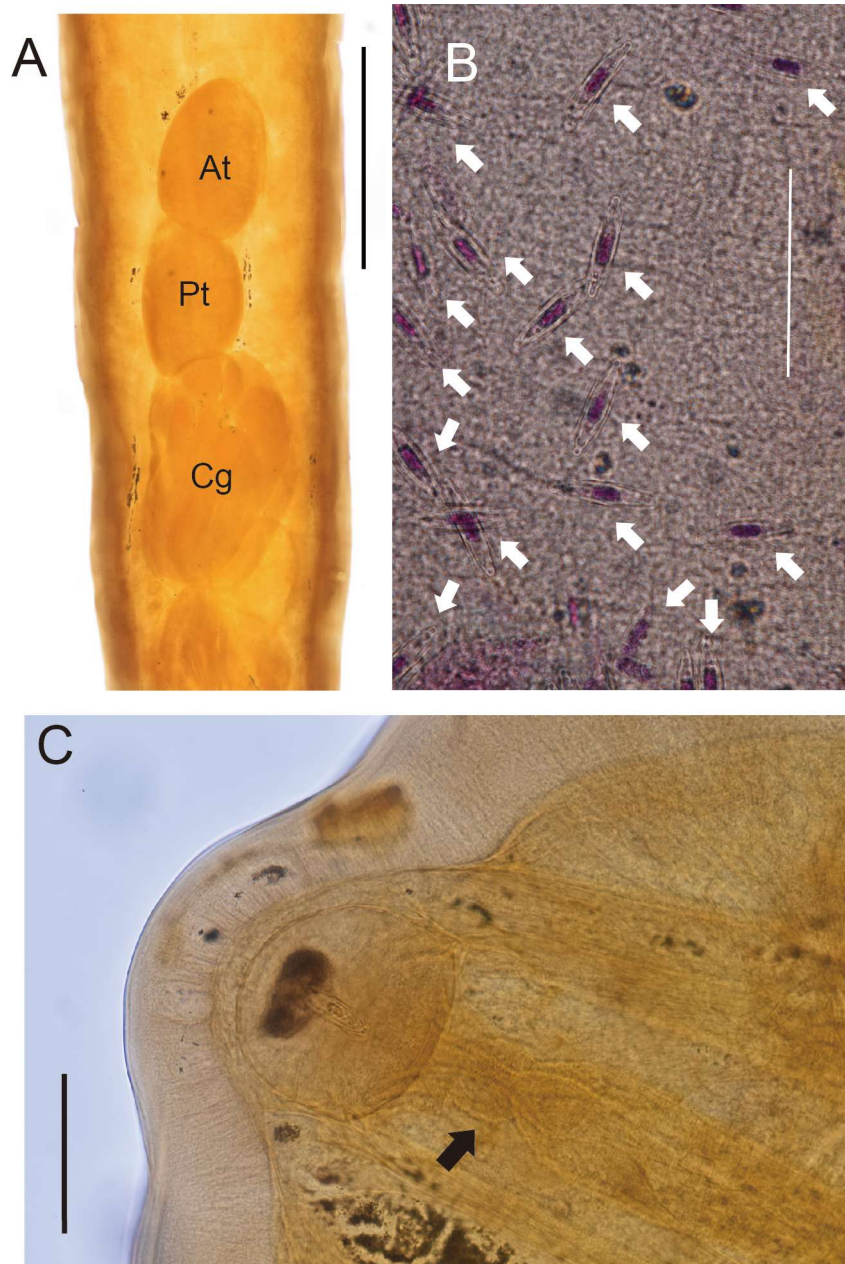


Fig. 11. *Metacanthocephalus ovicephalus* (Zhukov, 1960), photomicrographs. A, Genital organs, male, Heidenhain's iron hematoxylin (non-type, ICHUM 8410); B, eggs (indicated by arrows), alum-carmin (non-type, ICHUM 8411); C, vagina, Heidenhain's iron hematoxylin; the arrow indicates the position of the vaginal sphincter (non-type, ICHUM 8408). Scale bars: 1 mm (A); 100 μ m (B, C). Abbreviations: At, anterior testis; Cg, cement glands; Pt, posterior testis. After Kita et al. (2023, fig. 3).

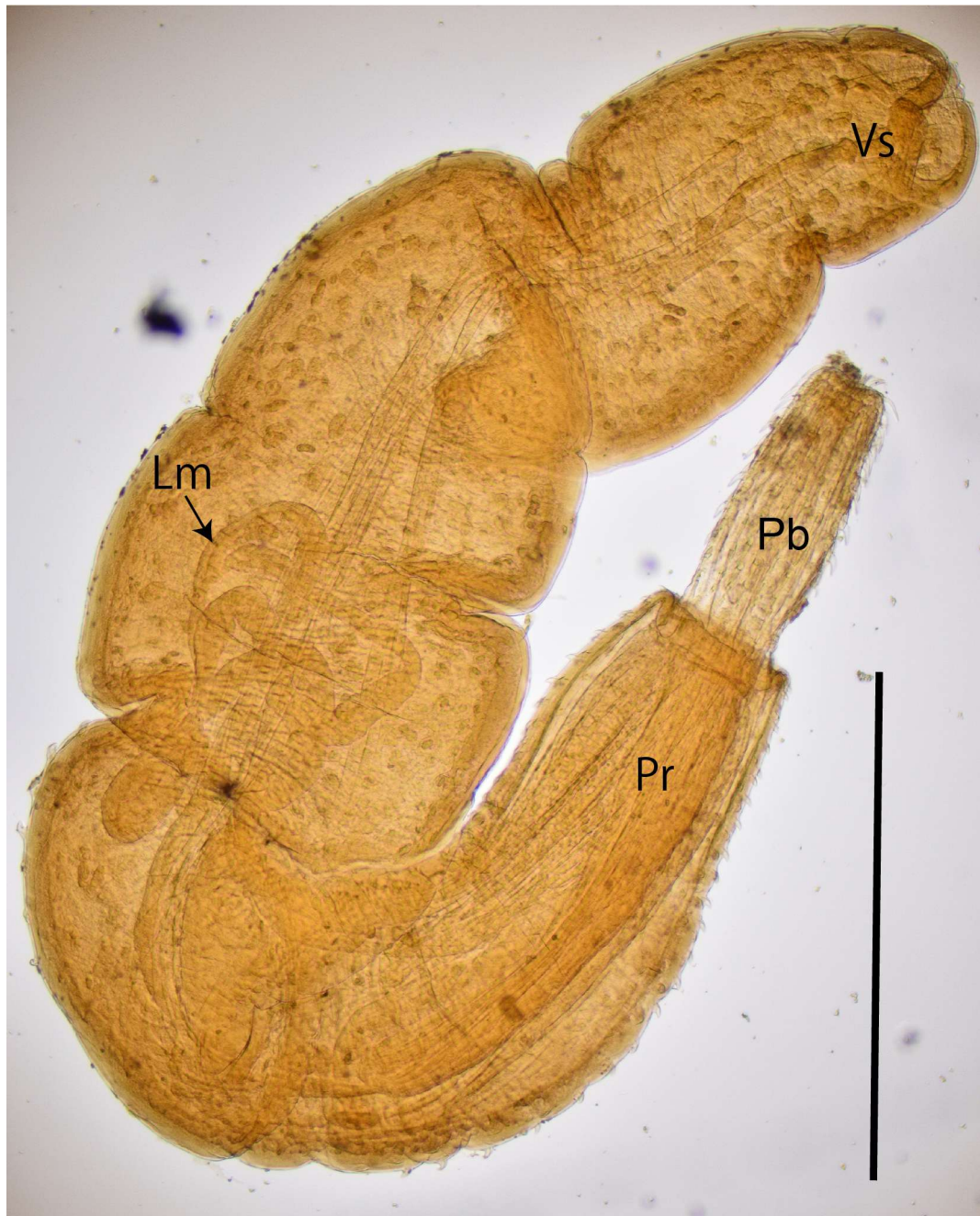


Fig. 12. *Pseudorhadinorhynchus leuciscus* (Krotov & Petrochenko in Petrochenko, 1956) (non-type, ICHUM 8338, immature female), photomicrograph of the whole body, obtained from the intestine of the Pacific redfin *Tribolodon brandtii*. Abbreviations: Lm, lemniscus; Vs, vaginal sphincter; Pb, proboscis; Pr, proboscis receptacle. Scale bar: 500 μ m. After Kita (unpubl.).

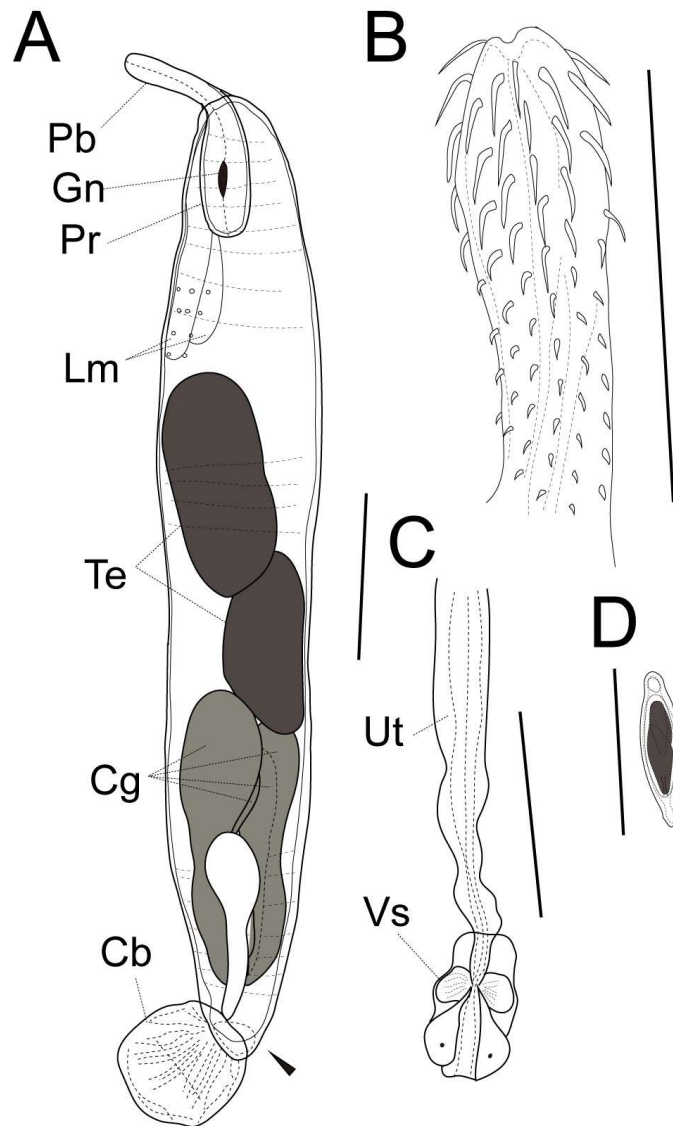


Fig. 13. *Micracanthorhynchina segmentata* (Yamaguti, 1959) from Hama-Saroma (YK's private collection). A, Whole body of a male (arrowhead indicates the muscular bursal cap); B, proboscis; C, genital organ of a female; D, egg. Scale bars: 1 mm (A); 500 μ m (B); 250 μ m (C); 50 μ m (D). Abbreviations: Cb, copulatory bursa; Cg, cement glands; Gn, cerebral ganglion; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Te, testes; Ut, uterus; Vs, vaginal sphincter. After Kita (unpubl.).

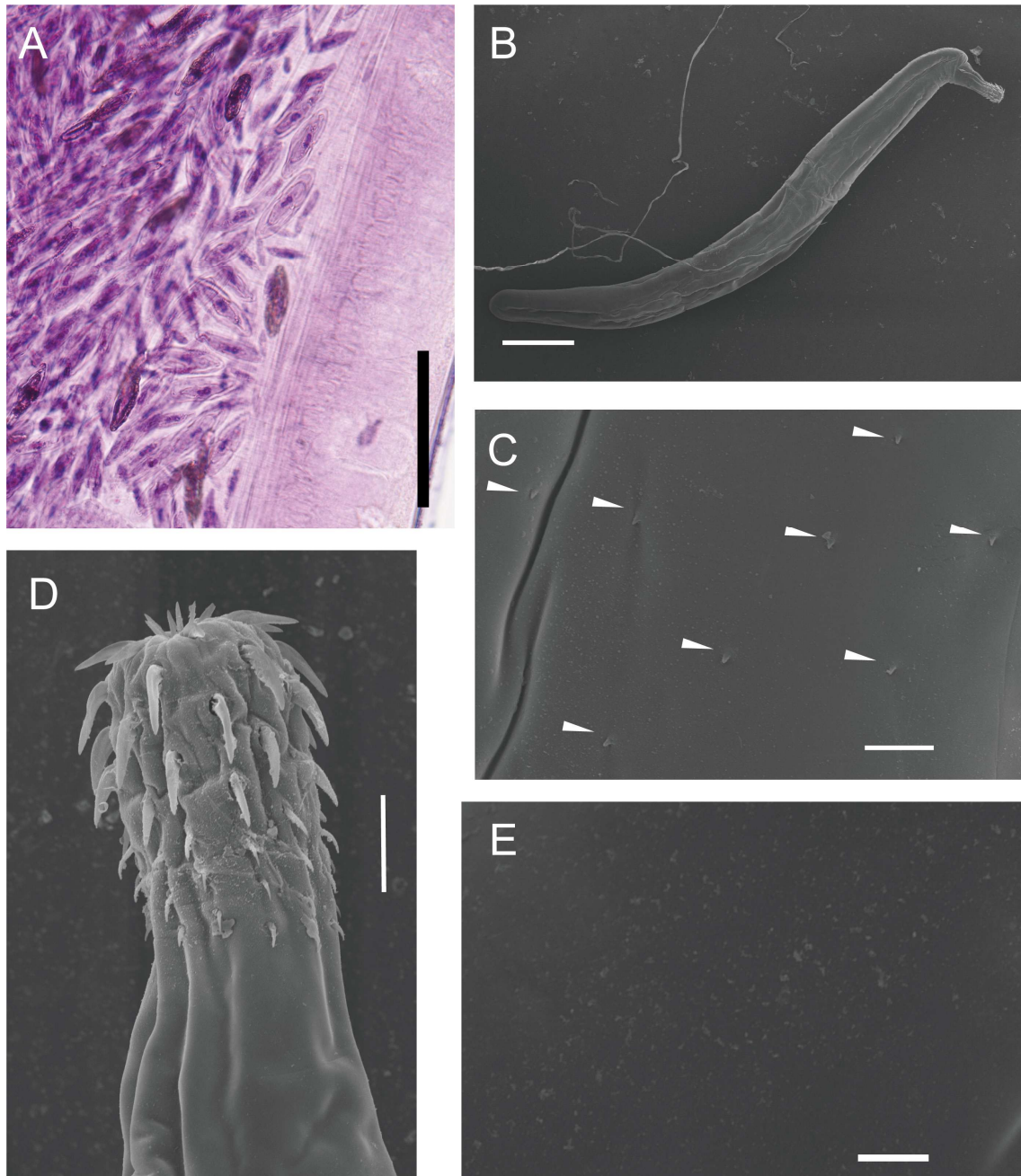


Fig. 14. *Pseudocavisoma setoense* Kita et al., 2024. A, Photomicrograph of eggs (paratype, ICHUM 8901); B, whole body, SEM; C, anterior trunk surface, SEM (arrowheads indicate trunk spines); D, proboscis, SEM; E, posterior trunk surface SEM. Scale bars: 100 μm (A); 500 μm (B); 20 μm (C, E); 50 μm (D). After Kita et al. (2024c, fig. 1).

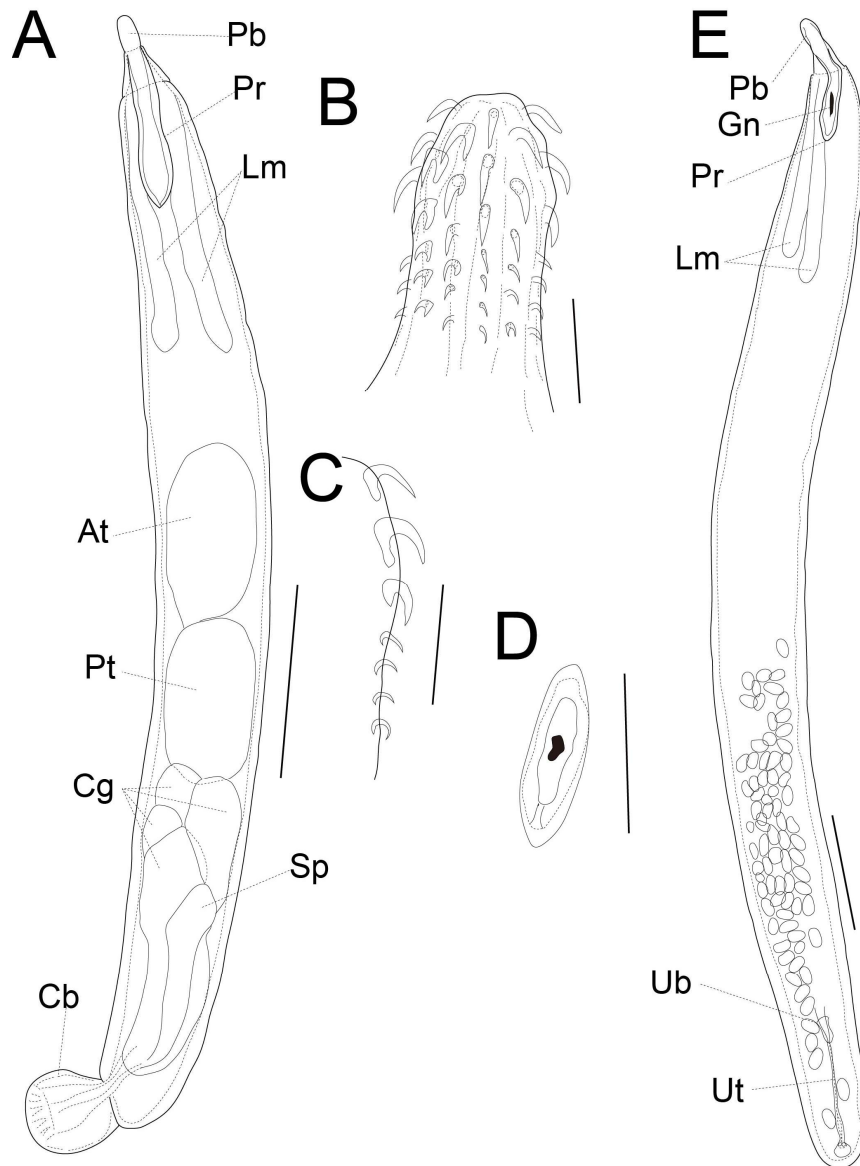


Fig. 15. *Pseudocavisoma setoense* Kita et al., 2024. A, Whole body, male (holotype, ICHUM 8909); B, proboscis (paratype, ICHUM 8901); C, row of hooks on the proboscis (paratype, ICHUM 8901); D, egg (paratype, ICHUM 8901); E, whole body, female (paratype, ICHUM 8918). Scale bars: 1000 μm (A, E); 100 μm (B, C); 50 μm (D). Abbreviations: At, anterior testis; Cb, copulatory bursa; Cg, cement glands; Gn, cephalic ganglion; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch; Ub, uterine bell; Ut, uterus. After Kita et al. (2024c, fig. 2).

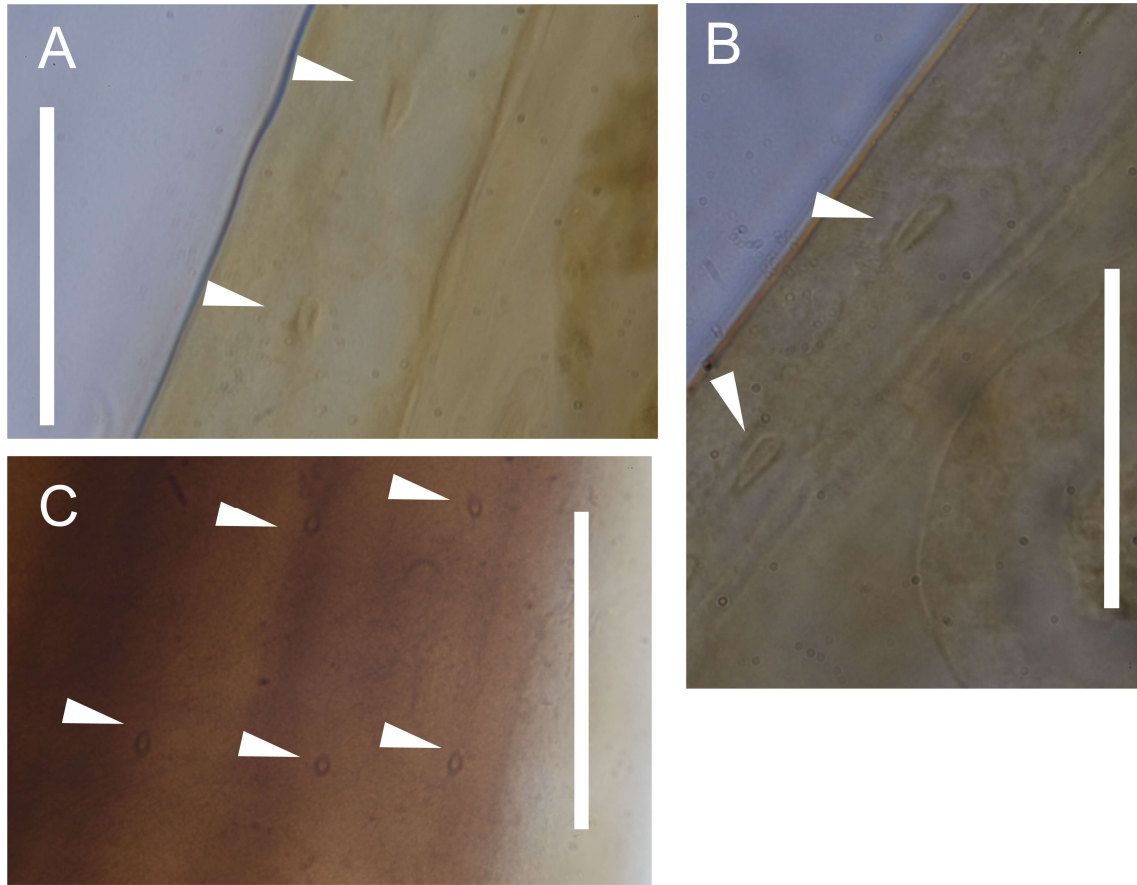


Fig. 16. Trunk spines found on the body surfaces of *Pseudocavisoma chromitidis* (Cable & Quick, 1954) (syntype, USNM 1348243) (A, B) and *Pseudocavisoma setoense* Kita et al., 2024 (paratype, ICHUM 8901) (C). A, Anterior trunk spines; B, posterior trunk spines; C, roots of anterior trunk spines; arrowheads indicate the position of trunk spines or their roots. Scale bars: 50 μm (A–C). After Kita et al. (2024c, fig. 3).

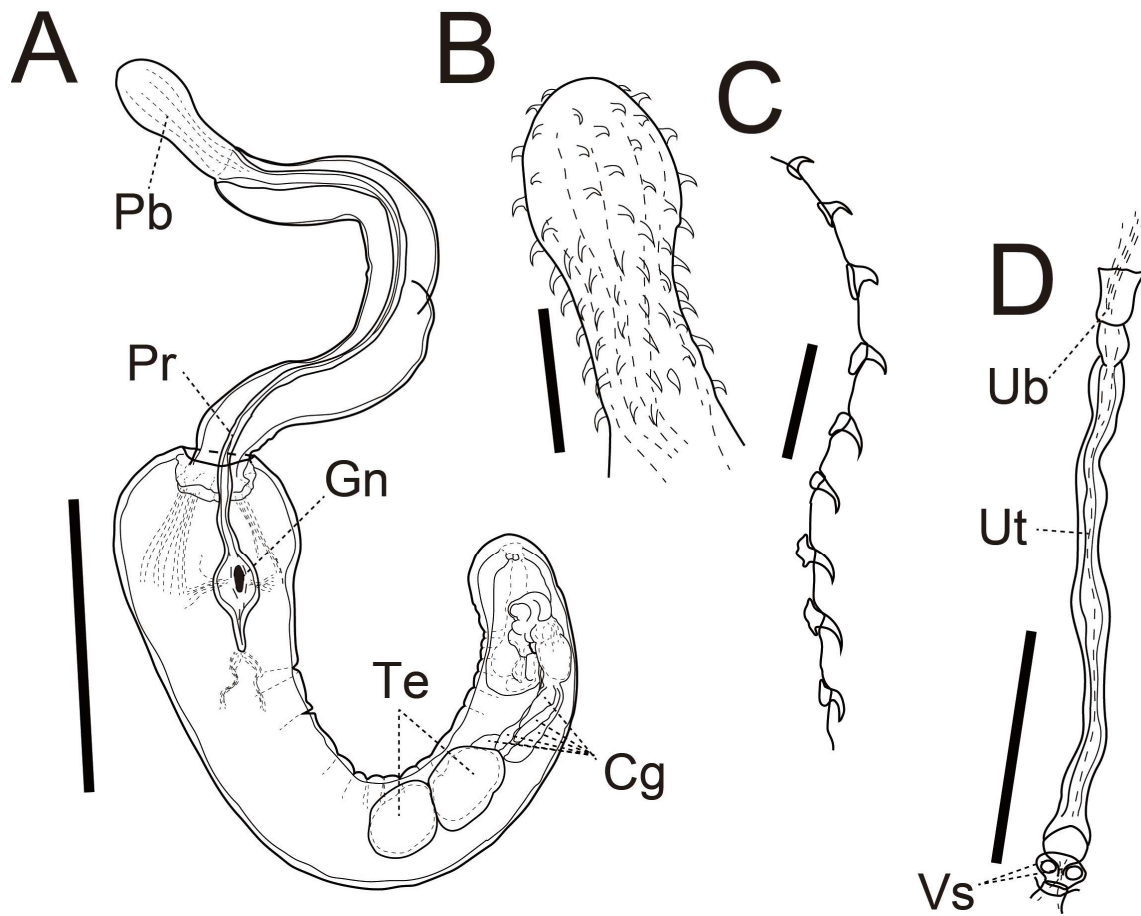


Fig. 17. *Pomphorhynchus alemniscus* (Harada, 1935). A, Whole body, male (non-type, ICHUM 8999); B, proboscis (non-type, ICHUM 8999); C, hook row of the proboscis (non-type, ICHUM 8999); D, genital organ, female (non-type, ICHUM 9000). Abbreviations: Cg, cement glands; Gn, cerebral ganglion; Pb, proboscis; Pr, proboscis receptacle; Te, testes; Ub, uterine bell; Ut, uterus; Vs, vaginal sphincter. Scale bars: 1 mm (A); 200 µm (B, D); 100 µm (C). After Kita et al. (2025b, fig. 1).

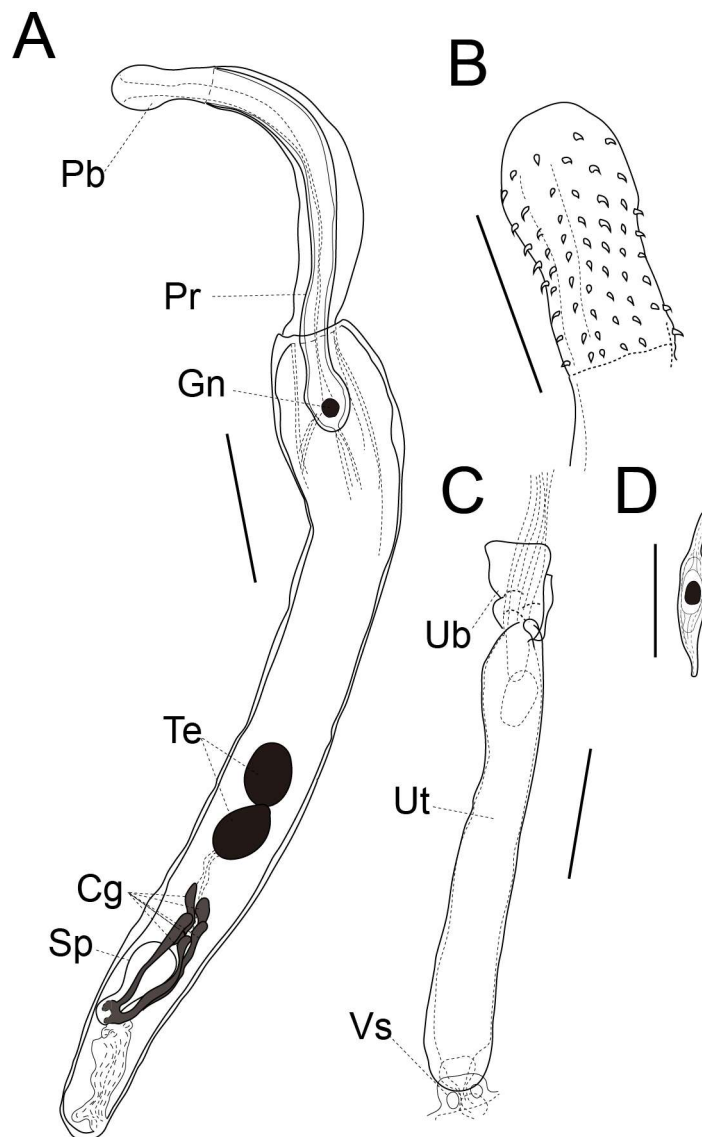


Fig. 18. *Pomphorhynchus pagrosomi* (Yamaguti, 1935) (YK's private collection). A, Whole body, male; B, proboscis; C, genital organ, female; D, egg. Scale bars: 1 mm (A). 500 μ m (B, C). 50 μ m (D). Abbreviations: Cg, cement glands. Gn, cerebral ganglion. Pb, proboscis. Pr, proboscis receptacle. Sp, Saefftigen's pouch. Te, testes. Ub, uterine bell. Ut, uterus. Vs, vaginal sphincter. After Kita (unpubl.).

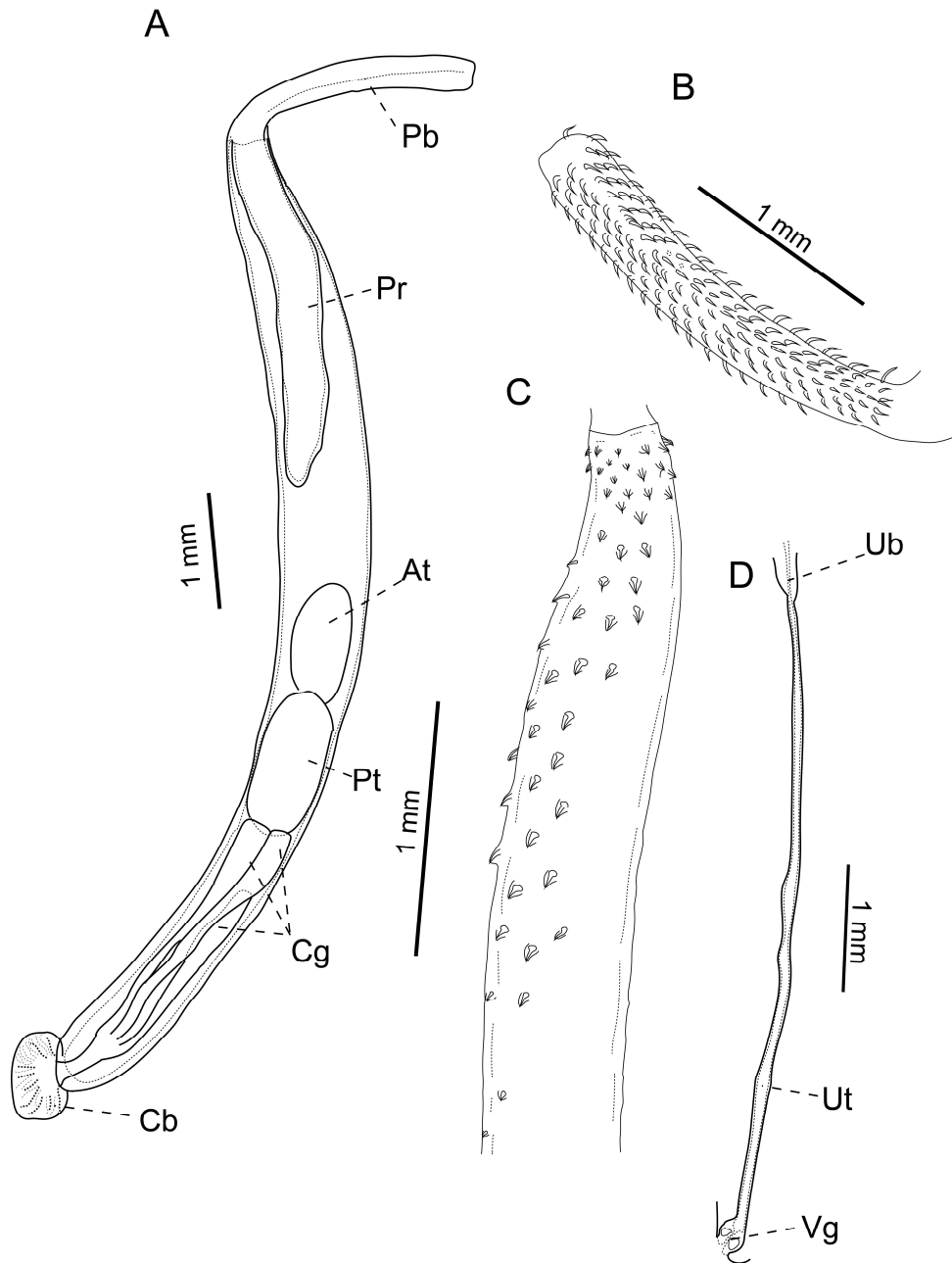


Fig. 19. *Rhadinorhynchus laterospinosus* Amin et al., 2011a. A, Whole body, male (non-type, ICHUM 8572); B, proboscis, male (non-type, ICHUM 8572); C, distribution of trunk spines (non-type, ICHUM 8575); D, female genital organ (non-type, ICHUM 8575). Abbreviations: At, anterior testis; Cb, copulatory bursa; Cg, cement gland; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Ub, uterine bell; Ut, uterus; Vg, vagina. After Kita et al. (2024a, fig. 2).

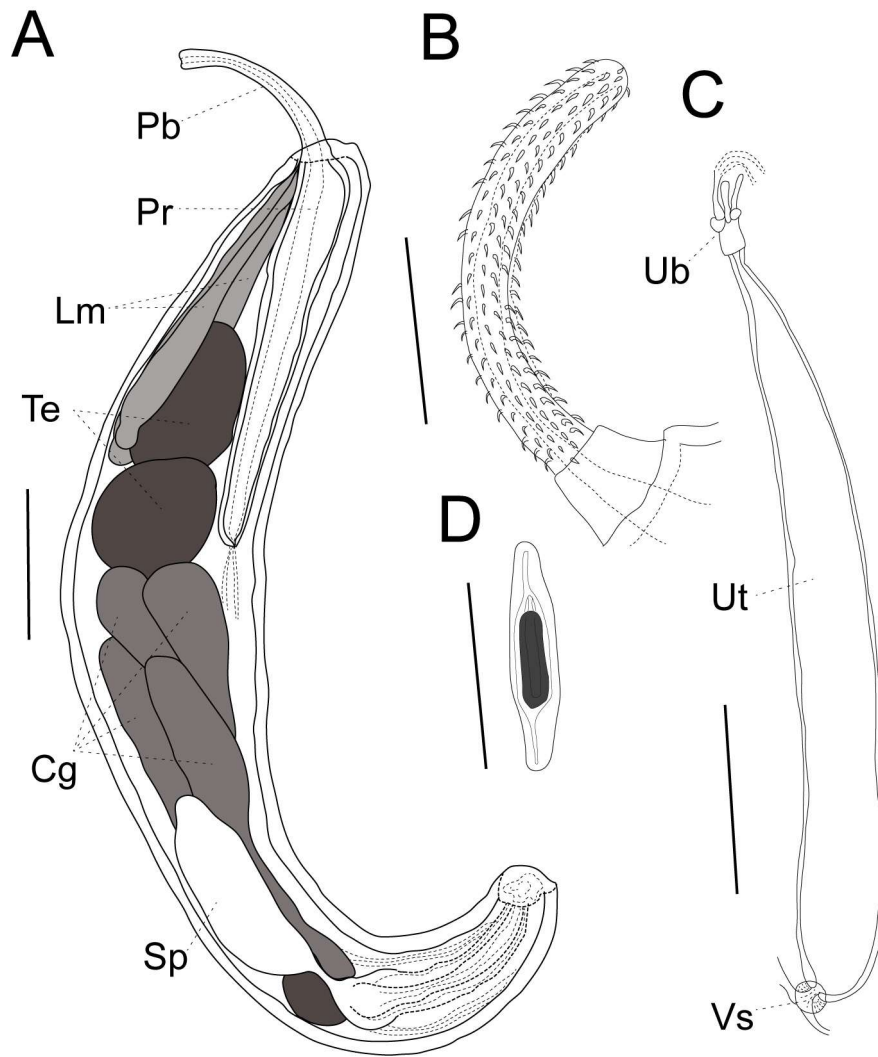


Fig. 20. *Rhadinorhynchus nudus* Harada, 1938 (HK's private collection). A, Whole body, male; B, proboscis; C, genital organ, female; D, egg. Scale bars: 1 mm (A), 500 μ m (B, C), 50 μ m (D). Abbreviations: Cg, cement glands; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Sp, Saefftigen's pouch; Te, testes; Ub, uterine bell; Ut, uterus; Vs, vaginal sphincter. After Kita (unpubl.).

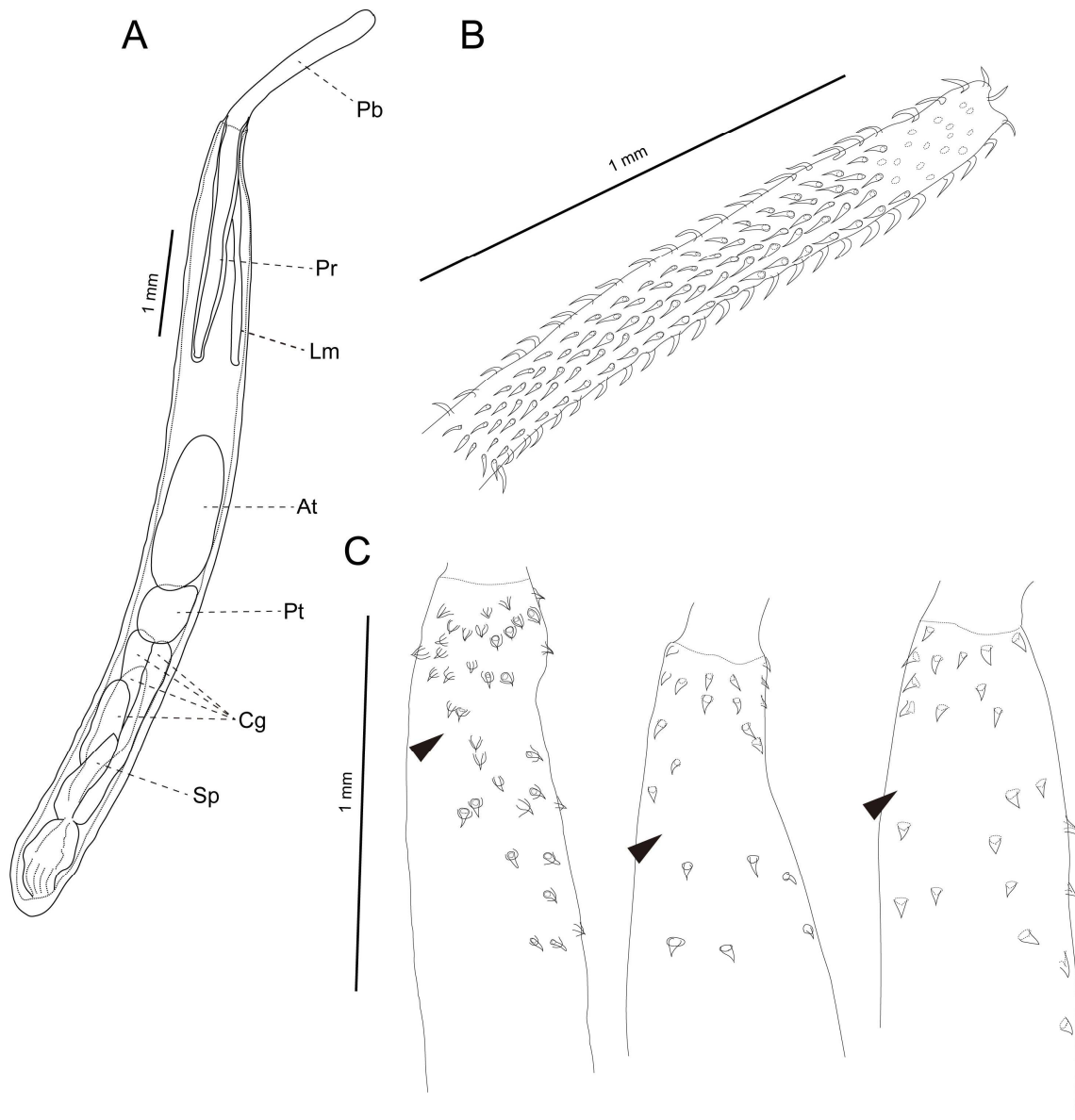


Fig. 21. *Rhadinorhynchus seriolae* (Yamaguti, 1963) (non-type, ICHUM 8571, consisting of three specimens, including a male). A, Whole body (male, one of the three specimens); B, proboscis (male, one of the three specimens); C, trunk spines, arrowhead indicates the border of two regions of trunk spines. Abbreviations: At, anterior testis; Cg, cement glands; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch. After Kita et al. (2024a, fig. 1).

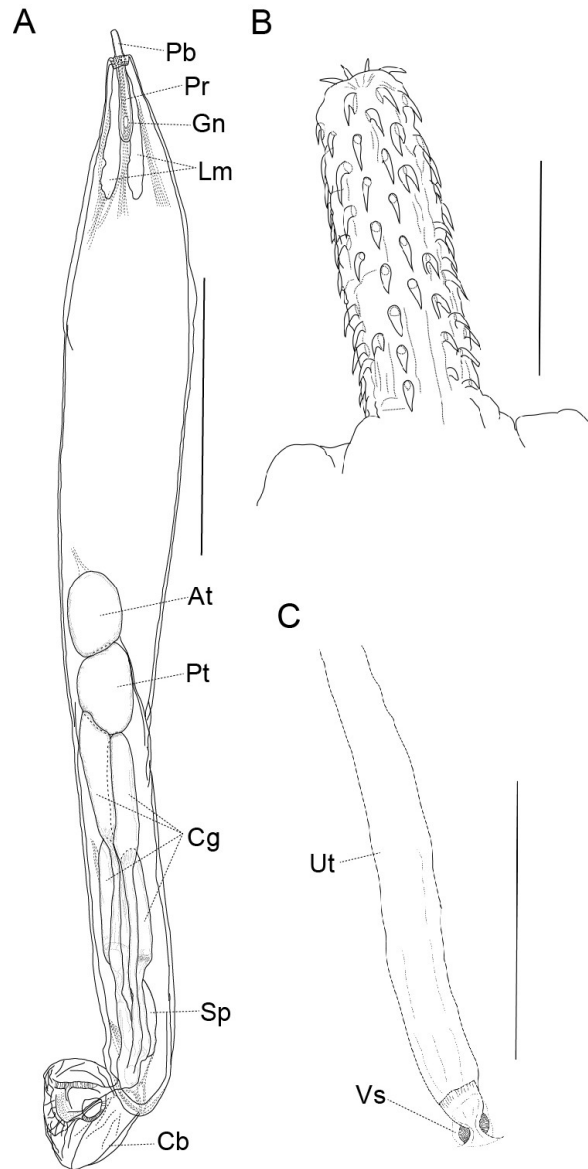


Fig. 22. *Sclerocollum neorubrimaris* Amin et al., 2018c. A, Whole body, male (non-type, ICHUM 8519); B, proboscis, male (non-type, ICHUM 8519); C, genital organs, female (non-type, ICHUM 8520). Abbreviations: At, anterior testis; Cb, copulatory bursa; Cg, cement glands; Gn, cephalic ganglion; Lm, lemnisci; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch; Ut, uterus; Vs, vaginal sphincter. Scale bars: 5 mm (A); 500 μ m (B); 1 mm (C). After Kita (unpubl.).

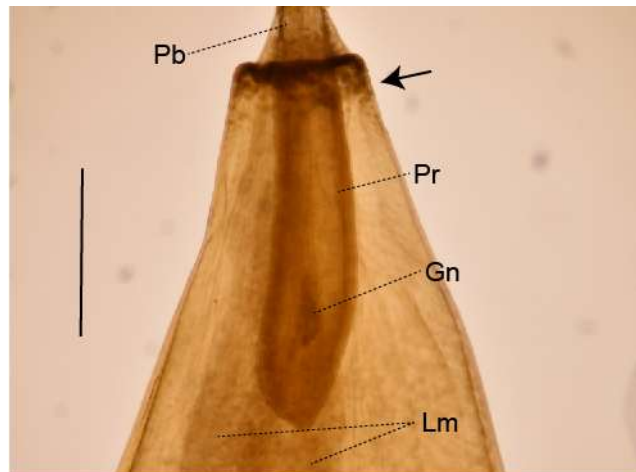


Fig. 23. *Sclerocollum neorubrimaris* Amin et al., 2018c. (non-type, ICHUM 8519), anterior end of the trunk; arrowhead indicates the anterior end of the trunk where sclerotized plaques are present. Abbreviations: Gn, cephalic ganglion; Lm, lemnisci; Pb, proboscis; Pr, proboscis receptacle. Scale bar: 500 μ m. After Kita (unpubl.).

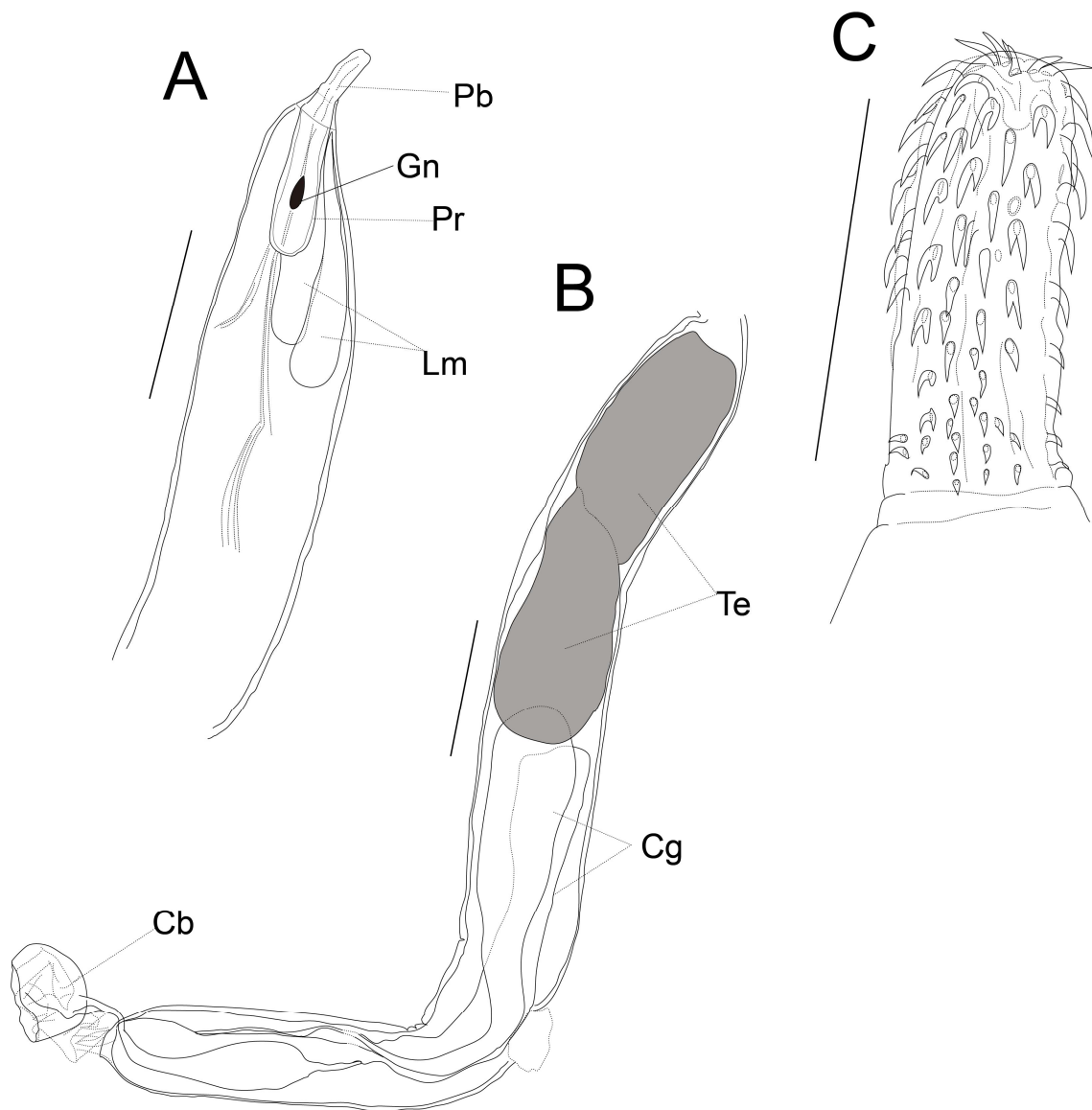


Fig. 24. *Trajectura ikedai* from off Miyakojima Island (YK's private collection). A, Anterior part of trunk; B, posterior part of trunk; C, proboscis. Scale bars: 1 mm (A, B); 300 μ m (C). Abbreviations: Cb, copulatory bursa; Cg, cement glands; Gn, cerebral ganglion; Lm, lemniscus; Pb, proboscis; Pr, proboscis receptacle; Te, testes. After Kita (unpubl.).

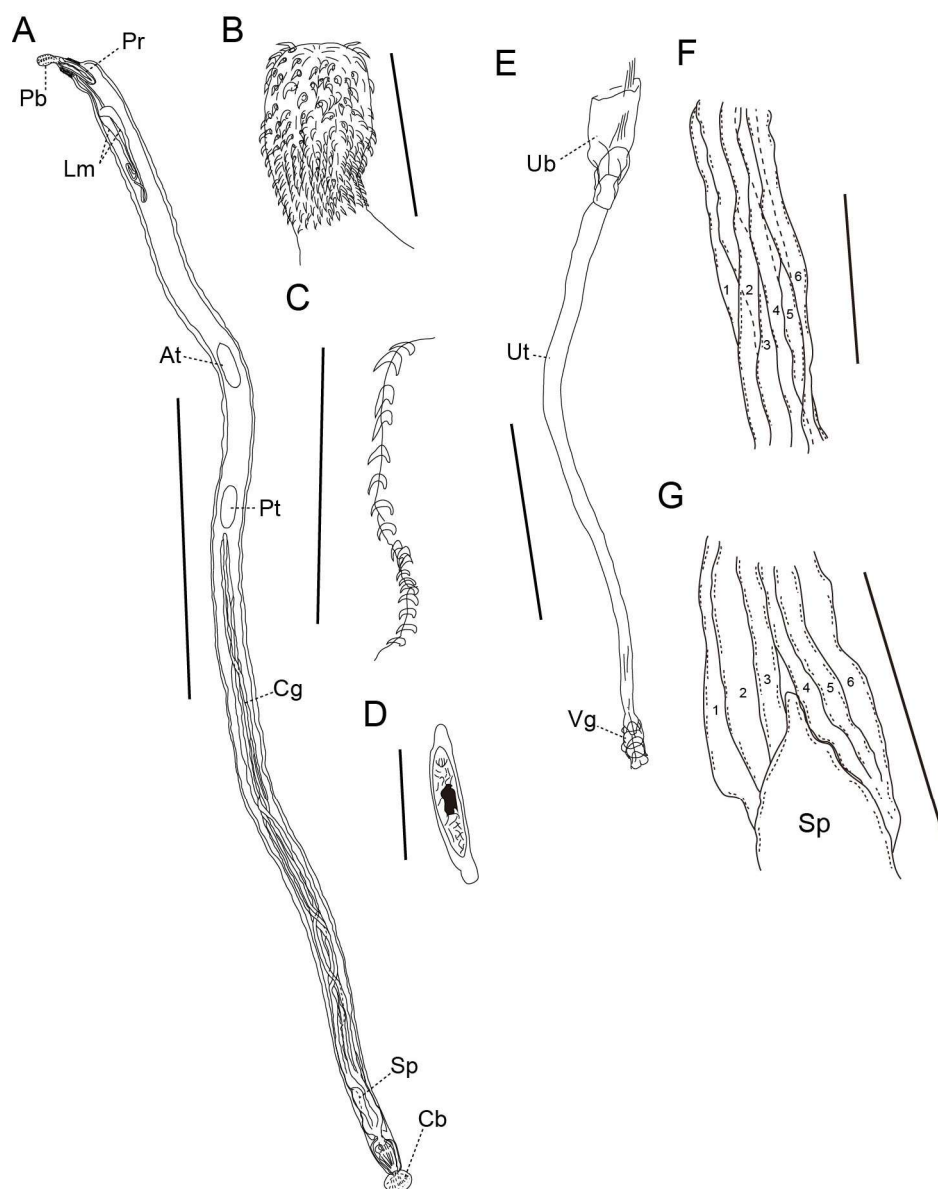


Fig. 25. *Metarhadinorhynchus lateolabracis* Yamaguti, 1959. A, Whole body, male (non-type, ICHUM 8794); B, proboscis (non-type, ICHUM 8794); C, one of the hook rows (non-type, ICHUM 8794); D, one of the eggs (non-type, ICHUM 8797); E, genital organs, female (non-type, ICHUM 8803); F, arrangement of cement glands in the middle (MPM Coll.-No. 22601-SY6970); numbers show each of the glands; G, arrangement of cement glands in the posterior (SY6970); numbers show each of the glands. Abbreviations: At, anterior testis; Cb, copulatory bursa; Cg, cement glands; Lm, lemnisci; Pb, proboscis; Pr, proboscis receptacle; Pt, posterior testis; Sp, Saeftigen's pouch; Ub, uterine bell; Ut, uterus; Vg, vagina. Scale bars: 10 mm (A); 500 µm (B–C, F–G); 50 µm (D); 1 mm (E). After Kita et al. (2024b, fig. 1).

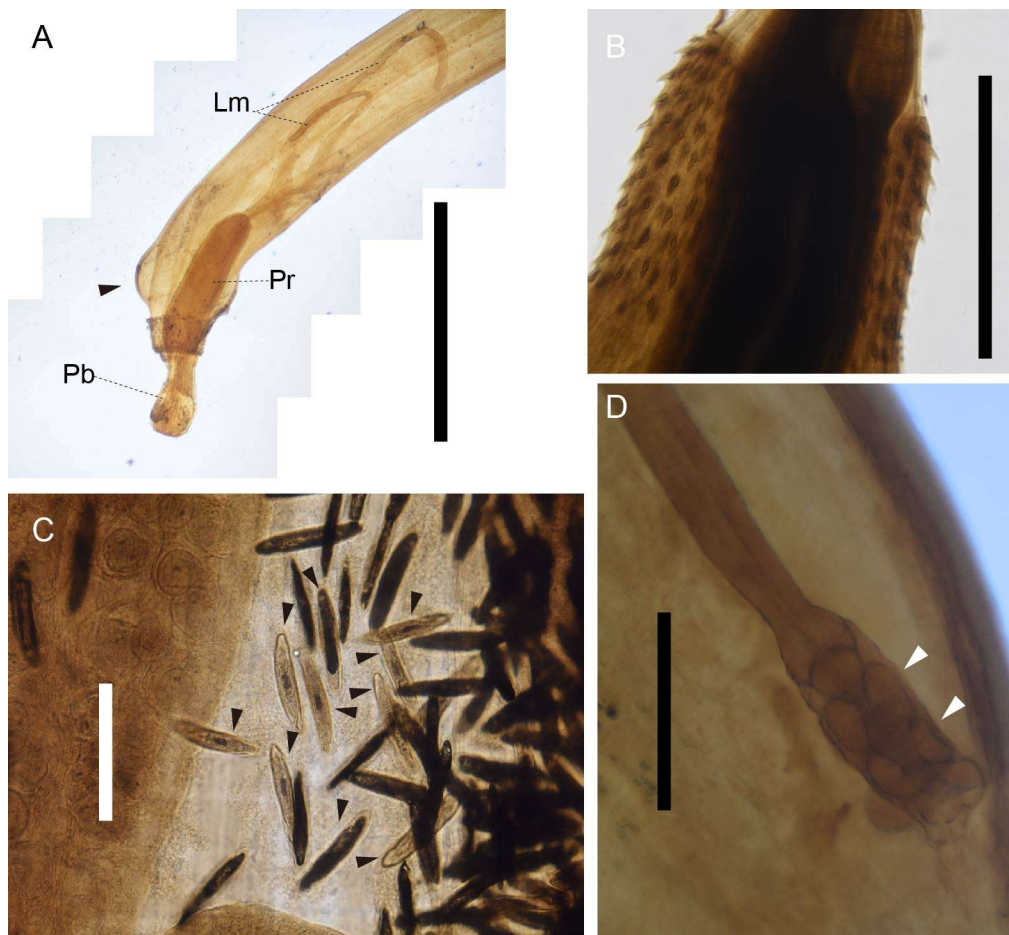


Fig. 26. *Metarhadinorhynchus lateolabracis* Yamaguti, 1959. A, Anterior end of trunk (non-type, ICHUM 8802) (arrowheads indicate the bulbous portion of trunk); B, spinose region on the anterior end of the trunk (non-type, ICHUM 8795); C, eggs (non-type, ICHUM 8797) (arrowheads indicate each egg measured); D, around the genital pore of the female individual (non-type, ICHUM 8803) (arrowheads indicate the two bulbous portions of the vagina). Scale bars: 2 mm (A); 500 μ m (B); 100 μ m (C); 200 μ m (D). After Kita et al. (2024b, fig. 2).

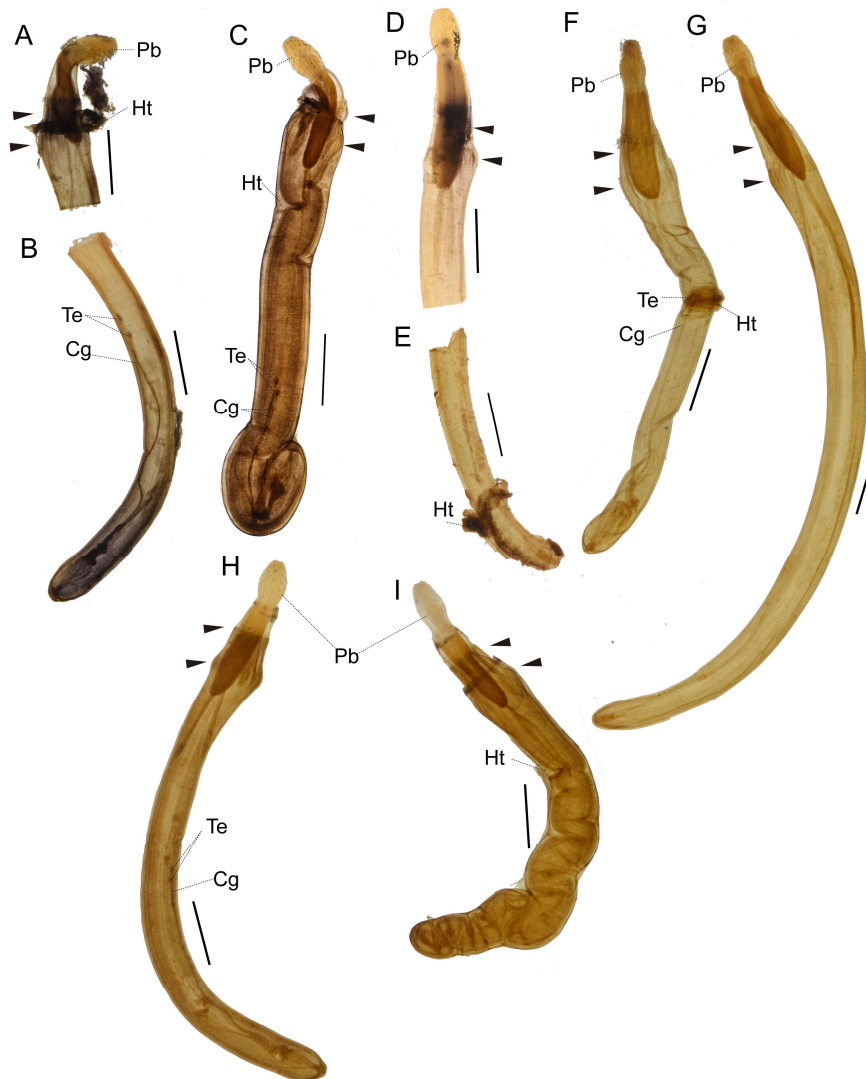


Fig. 27. Cystacanths of *Bolbosoma vasculosum* (Rudolphi, 1819); arrowheads indicate coverage of trunk spines. A, Anterior part, from *Trichiurus lepturus*, Nagasaki, male (ICHUM 8620); B, posterior part, from *Tr. lepturus*, Nagasaki, male (ICHUM 8620); C, whole body, from *Pristipomoides sieboldii*, Naha, male (ICHUM 8618); D, anterior part, from *Etelis radiosus*, Naha, female (ICHUM 8619); E, posterior part, from *E. radiosus*, Naha, female (ICHUM 8619); F, whole body, from *Pr. sieboldii*, Awase, male (ICHUM 8621); G, whole body, from *Pr. sieboldii*, Awase, female (ICHUM 8622); H, whole body, from *Beryx splendens*, Mikawa Bay, male (ICHUM 8623); I, whole body, from *Malakichthys* sp., Minami-Chita, female (ICHUM 8624). Scale bars: 1 mm. Abbreviations: Cg, cement glands; Ht, host tissue; Pb, proboscis; Te, testes. After Kita et al. (2024d, fig. 1).

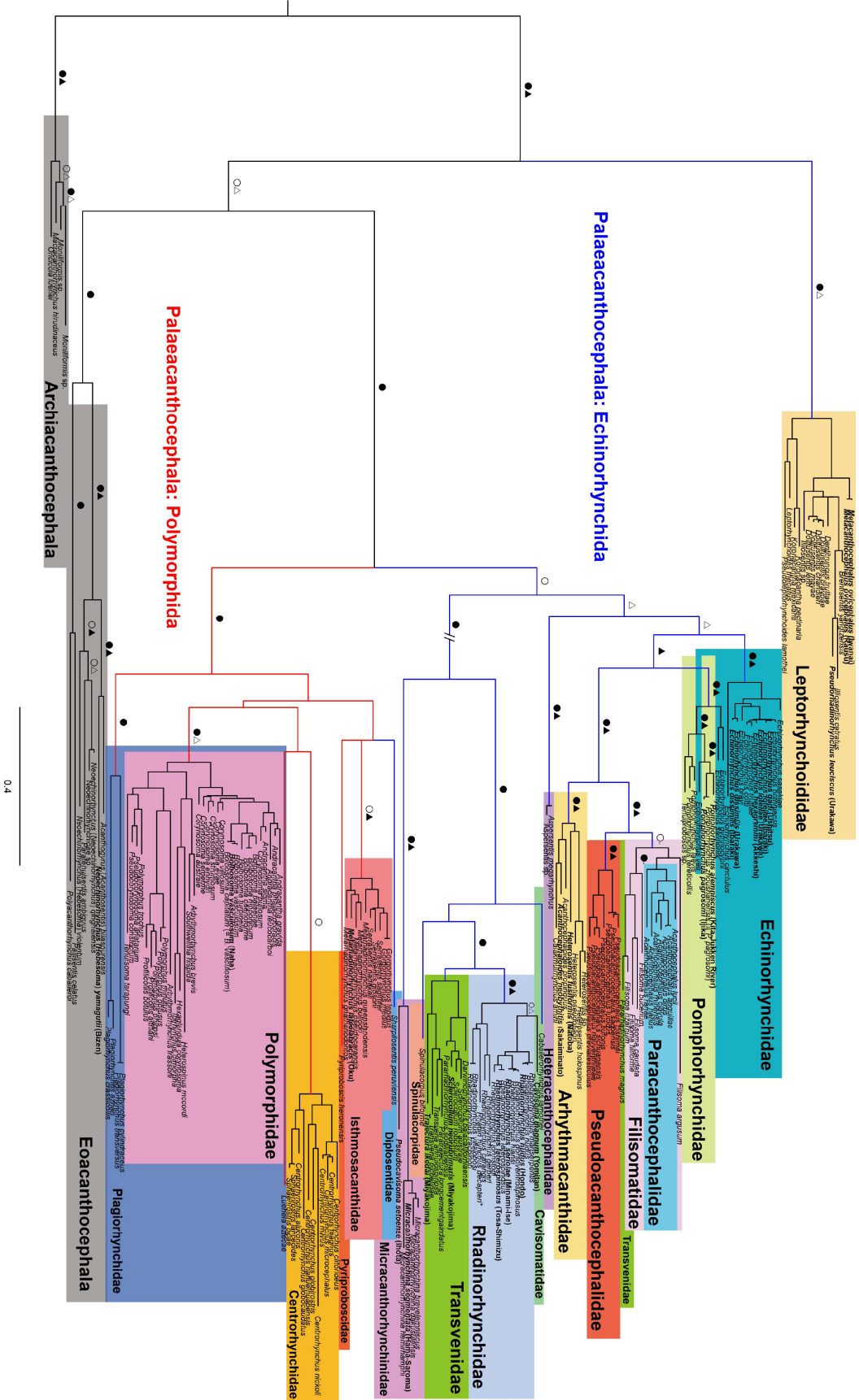


Fig. 28. Molecular phylogenetic tree based on the traditional DNA dataset (cox1 + 18S + 28S) reconstructed by the maximum-likelihood method. Branches marked with solid circles indicate 100% ultrafast bootstrap support (UF), whereas open circles denote 90–99% UF. Solid triangles represent branches with a Bayesian posterior probability (BPP) of 1.00, and open triangles indicate BPP values of 0.95–0.99. Branches without a circle have UF < 90, and those without a triangle have BPP < 0.95.

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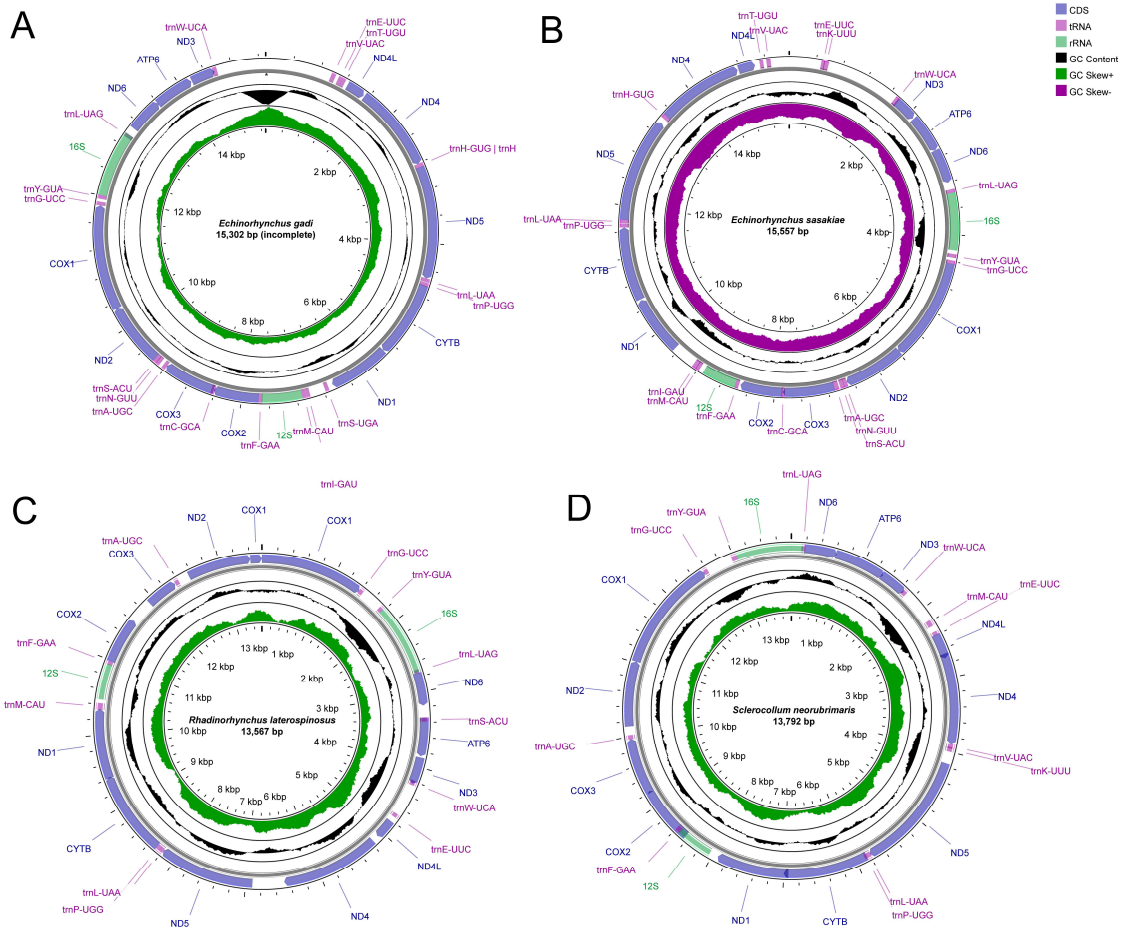


Fig. 30. Circular figures of mitochondrial genes detected in this study. A. *Echinorhynchus gadi*. B. *Echinorhynchus sasakiae*. C. *Rhadinorhynchus laterospinosus*. D. *Sclerocollum neorubrimaris*. An asterisk indicates the non-coding region that could not be determined in this study. GC skew was calculated as $(G - C) / (G + C)$.

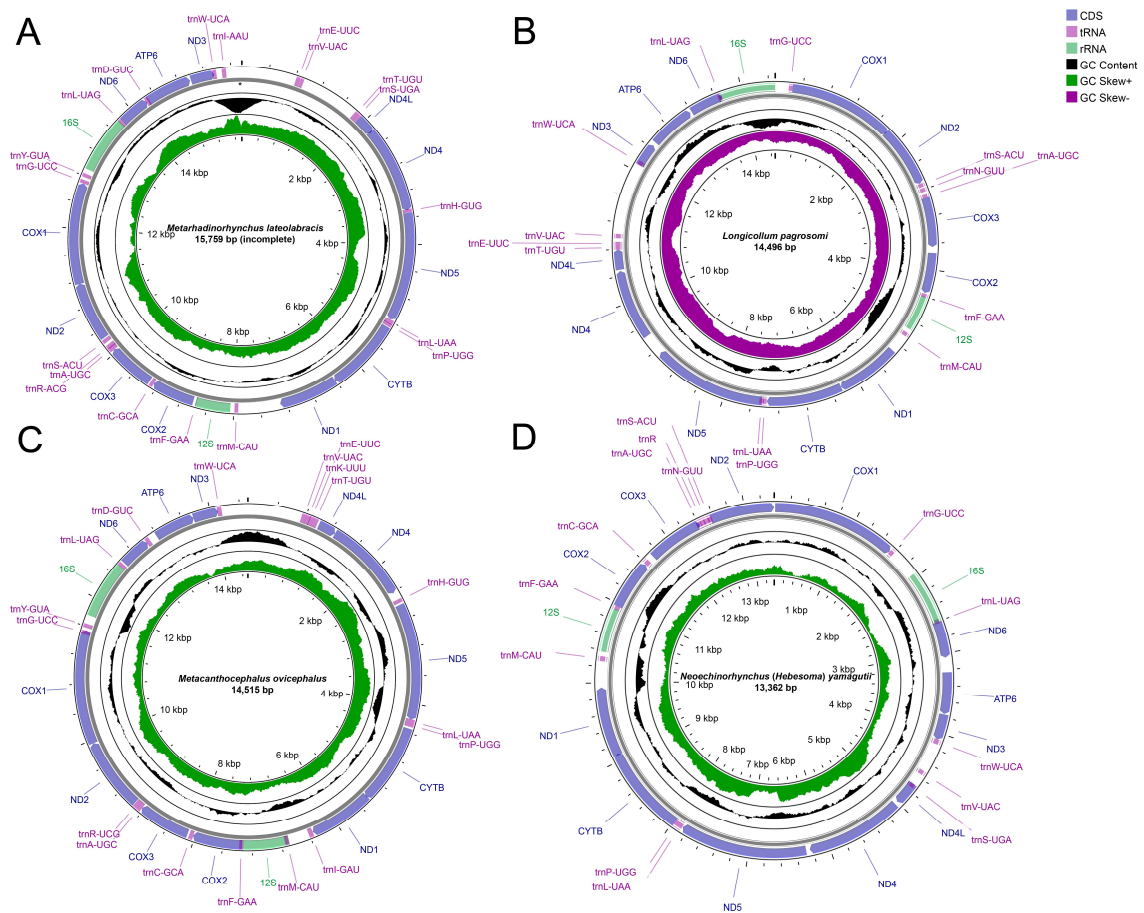


Fig. 31. Circular figures of mitochondrial genes detected in this study. A. *Metarhadinorhynchus lateolabracis*. B. *Longicollum pagrosomi*. C. *Metacanthocephalus ovicephalus*. D. *Neoechinorhynchus (Hebesoma) yamagutii*. The calculation formula of GC skew is the same as Fig. 30.



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