学位論文　（要約）

Molecular Systematics of the Order Phyllobothriidea (Platyhelminthes: Cestoda) from the Coastal Seas of Japan

（日本周辺海域における吸葉目（扁形動物門：条虫綱）
の分子系統に基づく分類学的研究）

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Abstract

The order Phyllobothriidea was established based on its molecular phylogeny that separates the family Phyllobothriidae from the order Tetraphyllidea. However, many genera are left *incertae sedis* in Tetraphyllidea, and the order Phyllobothriidea should be revised together with these taxonomically uncertain genera. In this study, the systematics of Phyllobothriidea was revised based on molecular analyses using ssrDNA and lsrDNA. As a result, 17 genera including three new genera, namely *Phyllobothrium*, *Alexandercestus*, *Bilocularia*, *Calliobothrium*, *Calyptrobothrium*, *Chimaerocestos*, *Crossobothrium*, *Mitsukuricestus* n. gen., *Monorygma*, *Orygmatobothrium*, *Pelichnibothrium*, *Scyphophyllidium*, *Symcallio*, *Thysanocephalum*, *Trilocularia*, *Yamaguticestus* n. gen., and *Vertebraeovicestus* n. gen., were recognized in Phyllobothriidea. *Clistobothrium* was a junior synonym of *Pelichnibothrium*, and *Marsupiobothrium*, *Nandocestus*, *Orectolobicestus*, *Paraorygmatobothrium*, and *Ruhnkecestus* were junior synonyms of *Scyphophyllidium*. *Monorygma megacotyla* was a junior synonym of *Ph. squali*, and *Ph. squali* was transferred to *Yamaguticestus*. *Marsupiobothrium gobelinus* was transferred to *Mitsukuricestus*, and *Ph. biacetabulatum* was transferred to *Anthocephalum* of Rhinebothriidea. The sequences of the larval species, namely *Pe. caudatum*, *Ph. delphini*, and *Mo. grimaldii,* were located in the *Pelichnibothrium* clade but did not match those of any adults. These three larval species were considered valid species of *Pelichnibothrium*.

The most important taxonomic characteristics of Phyllobothriidea had been believed to be in its scolex and proglottid, but the morphological characteristics did not reflect the phylogeny. Five types of bothridium on the scolex, namely cup, crumple, divided, flat, and loculate margin, were observed in many lineages, but only sac type was uniquely found in *Sc. giganteum*. The hook of scolex was found to be evolved in multiple lineages. Moreover, it was observed not only in Phyllobothriidea but also in Tetraphyllidea and Onchoproteocephalidea. The presence of laciniate and non-laciniate proglottids was also seen in multiple lineages. Further molecular information is essential to clarify the phylogeny of Phyllobothriidea.

Taxonomic studies of Phyllobothriidea have scarcely been done in the coastal seas of Japan, and only 14 species of four genera have been reported thus far. In this study, I have identified 34 species of 14 genera including 14 new species and three new genera from Japanese waters, of which 12 species and five genera are new to Japan. According to the new systematics in this study, the Phyllobothriidea fauna of the coastal seas of Japan has a total of 47 species of 15 genera.

The life history of Phyllobothriidea has not been studied extensively because identification of its larvae is difficult due to lack of taxonomic characteristics of the larvae. In this study, the identification of phyllobothriidean larvae was attempted by molecular analyses using lsrDNA and mtDNA COI. On investigating 79 species of teleost fishes, mollusks, and decapod crustaceans collected from the coastal seas of Japan, the larvae of Phyllobothriidea or Tetraphyllidea were collected from 25 host species. Molecular analyses of 42 plerocercoids and merocercoids from 25 host species, with the adult and larval species' sequences, revealed plerocercoids of *Pelichnibothrium caudatum* (17 plerocercoids), *Pe. montaukensis* (2), *Pe.* cf. *montaukensis* (2), *Scyphophyllidium carcharhinus* (1), and *Vertebraeovicestus dobukasube* (1) and merocercoids of *Pe. delphini* (2 merocercoids) and *Pe. grimaldii* (2). Only five plerocercoids were identified to be Phyllobothriidea. The other 10 plerocercoids were found to belong to *Anthobothrium* of Tetraphyllidea. On comparison of the morphology between adults and plerocercoids of the same species, the apical sucker on plerocercoids was shown to be lost in their adult stages. The morphology of bothridium also greatly changed in growth from plerocercoids to adult stages. Molecular identification is a very effective method for the exact identification of phyllobothriidean larvae. In this study, a part of the life cycle of three species was revealed by the exact molecular identification of its larvae.

Comparison of the phyllobothriidean lineage with the host lineage suggested that both host-switch and host-range expansion occurred frequently in the evolution of Phyllobothriidea. These events may play important roles in the diversification of Phyllobothriidea.

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DISCLAIMER: The present study is not issued for the permanent scientific record, and no part of it is to be considered published within the meaning of the International Code of Zoological Nomenclature (see Code, Art. 8b).

General introduction

Cestodes, which infest sharks, skates, and rays (Chondrichthyes: Elasmobranchii), have long attracted parasitologists' attention, probably due to their species diversity and unique morphological characteristics. Therefore, many taxonomic studies have been accumulated to date. However, taxa with unsettled taxonomy have been widely recognized. This is due to species diversity and unique morphological characteristics of cestodes resident in elasmobranchs. For example, the order Tetraphyllidea previously considered as the most diverse, included four families: Onchobothriidae, Phyllobothriidae, Lecanicephalidae, and Ichthyotaeniidae. Subsequently, twenty families were recognized in this order (Table 1). Recent phylogenic analyses employing morphology (Euzet et al., 1981; Brooks et al., 1991; Hoberg et al., 1997; Caira et al., 1999; 2001) and biomolecular markers (Mariaux, 1998; Olson & Caira, 1999; Kodedová et al., 2000; Olson et al., 2001; Waeschenbach et al., 2007, 2012) revealed that the order Tetraphyllidea was, in fact, polyphyletic.

The order Phyllobothriidea was recently elected from one of the families of the polyphyletic order Tetraphyllidea, based on molecular phylogenetic analysis by Caira et al. (2014). They examined 134 species representing 97 genera across the 15 cestode orders. However, the statistical support for the inclusion of Phyllobothriidea was relatively weak compared with support for that of other orders including Litobothriidea, Lecanicephalidea, Rhinebothriidea, Cathetocephalidea, and Onchoproteocephalidea. Moreover, they also withheld to dismantle the order Tetraphyllidea and remained several uncertain genera in polyphyletic Tetraphyllidea. These uncertainties seem to be consequent to inadequate sampling density (and hence statistical power) across the Tetraphyllidea.

Elasmobranch fauna in the waters around Japan are relatively abundant, comprising 205 species (Nakabo, 2013) which correspond to approximately 1/5 of all elasmobranch species overall. In contrast to the diversity of host elasmobranchs, investigations of parasitic cestode fauna in the coastal seas of Japan have been limited to only 14 species and several unidentified forms from 11 host species, which have been detailed in five reports to date (Yoshida, 1917; Yamaguti, 1934, 1952, 1960; Yamaguchi et al., 2000; Table 2). It is strongly suggested that diverse cestodes, including new species, must infect elasmobranchs in the coastal seas of Japan.

As detailed in Chapter I of the present study, the author conducted several molecular phylogenetic analyses on a wide variety of cestodes using newly collected specimens through intensive and extensive parasitological investigations on elasmobranchs in the coastal seas of Japan. The sequence data examined by Caira et al. (2014) was augmented to elucidate the precise nature of species diversity and phylogeny of elasmobranch cestodes with special reference to the order Phyllobothriidea. The most accurate, up-to-date statistical analytical techniques were also employed.

Phyllobothriidean cestodes have two or more intermediate hosts for larval development in addition to a final host for adult stages (Euzet, 1952; Caira, 1990). The parasites migrate from an intermediate host to the advanced-stage host through the food chain during their life cycle. Adult worms occupy the spiral intestines of elasmobranchs and chimaeras, and eggs are released into sea water. The eggs hatch and develop into hexacanth embryos, which are usually consumed by copepods or euphausiids, representing the first intermediate host wherein they develop into procercoid larvae. The first intermediate host is consumed by the second intermediate host, which is typically an invertebrate of one of the seven phyla, teleosts, and cetaceans, and procercoids grow to merocercoid or plerocercoid larvae (Caira & Reyda, 2005). When the second intermediate host animals are eaten by elasmobranchs and chimaeras, merocercoids and plerocercoids mature into adult worms. Cestode larvae are frequently found during parasitological surveys of marine fishes, marine mammals, and marine invertebrates. However, these larvae can barely be identified because potentially-distinguishing morphological characteristics are not yet known. This has obstructed detailed characterization of intermediate hosts and life cycle stages for not only phyllobothriidean cestodes but also marine parasites in general.

Molecular methods, i.e., molecular sequence comparisons between adults and larvae should be effective in linking larvae to adults. In Chapter II of the present study, the author employs such molecular techniques in efforts to identify a wide variety of larval cestodes collected from marine fishes, marine mammals, and marine invertebrates, using the sequence data obtained from adults.

Chapter I
Taxonomic revision of the order Phyllobothriidea based on molecular analysis

1. Introduction

Recent taxonomic and phylogenetic studies on cestodes parasitizing in elasmobronchs have been focused on solving polyphyly of the order Tetraphyllidea. Olson & Caira (2001) resurrected the order Litobothriidea and transferred the family Litobothriidae from Tetraphyllidea to Litobothriidea. Caira et al. (2005) resurrected the order Cathetocephalidea and transferred the families Cathetocephalidae and Disculicipitidae from Tetraphyllidea to Cathetocephalidea. Healy et al. (2009) elected a new order Rhinebothriidea and transferred a part of Phyllobothriidae from Tetraphyllidea to Rhinebothriidea. These taxonomical decisions were successful, but polyphyly of Tetraphyllidea was not resolved.

Recently, Ruhnke (2011) re-examined 78 genera historically associated with the family Phyllobothriidae and reported that only *Phyllobothrium* was unambiguously valid, 16 genera were provisionally valid, five genera were *nomina dubia*, one genus was *nomen ad interium*, nine genera were *genera inquirendae*, and 17 genera were *incertae sedis* within the family Phyllobothriidae (Table 3). He transferred eight valid, nine provisionally valid, and one *increate sedis* genera to the order Rhinebothriidea. In addition, he transferred two valid genera and two genera *inquirenda* to the other tetraphyllidean family Serendipidae (Table 3). He also synonymized the remaining seven genera to some other tetraphyllidean or rhinebothriidean genera. Later, a new genus *Alexandercestus* was elected in Phyllobothriidae by Ruhnke & Workman (2013), and the family Phyllobothriidae included the following 18 genera: *Phyllobothrium*, *Alexandercestus*, *Bibursibothrium*, *Calyptrobothrium*, *Cardiobothrium*, *Clistobothrium*, *Crossobothrium*, *Doliobothrium*, *Flexibothrium*, *Marsupiobothrium*, *Monorygma*, *Nandocestus*, *Orectolobicestus*, *Orygmatobothrium*, *Paraorygmatobothrium*, *Ruhnkecestus*, *Scyphophyllidium*, and *Thysanocephalum* (Ruhnke, 2011; Ruhnke & Workman, 2013).

Recently, Bayesian Inference (BI) analyses of various combinations of complete small subunit ribosomal DNA (ssrDNA) sequences and complete or partial large subunit ribosomal DNA (lsrDNA) sequences that included 134 species representing 97 genera across the 15 eucestode orders, were conducted by Caira et al. (2014). A monotypic clade consisted of 11 genera, of which 10 genera corresponded to those in the family Phyllobothriidae *sensu* Ruhnke (2011), emerged through an analysis of the complete ssrDNA along with the partial lsrDNA (D1–D3) sequences of 134 taxa. They raised the clade to the new order Phyllobothriidea elected from a part of Phyllobothriidae and Chimaerocestidae of Tetraphyllidea. Another new order Onchoproteocephalidea was also elected from the order Proteocephalidea and a part of from the family Onchobothriidae.

A monophyletic order Phyllobothriidea was first recognized on a molecular basis by Caira et al. (2014), although the statistical significance was low when comparing with other orders. However, the family Phyllobothriidae, revised by Ruhnke (2011), has not been completely examined on a molecular basis and *incertae sedis* still remains within the family. Moreover, the polyphyly of the order Tetraphyllidea remains unclear because many uncertain genera in polyphyletic Tetraphyllidea remained in the study by Caira et al. (2014).

In Chapter I, 419 specimens of cestodes were obtained and intensive and extensive parasitological investigations were performed on elasmobranchs, teleosts, and mammals in the coastal seas of Japan. The specimens were identified, described, illustrated, and sequenced for molecular analysis. In addition to the original data, data examined by Caira et al. (2014) were also included in the present analysis to precisely elucidate the species diversity and phylogeny of the order Phyllobothriidea and related taxa including the order Tetraphyllidea.

2. Materials and Methods

2.1 Specimens

Elasmobranchs were widely caught in the coastal seas of Japan, including the Ogasawara and Yaeyama Islands (Fig. 1, Table 4). Elasmobranchs and other host animals were collected using scientific research vessels and fishing boats and were also obtained from fishes at fishing ports.

Parasite investigations were performed on a total of 921 individuals obtained from 76 elasmobranch species of 51 genera from 31 families, two teleost species of two genera from two families, and one cetacean species (Table 5). Hosts were preserved on ice or sometimes frozen until examination and dissected to collect cestodes under a stereomicroscope.

2.2 Treatment of specimens

Cestodes were washed and immersed in elasmobranch saline (NaCl, 2 g; KCl, 0.1 g; $CaCl_2$, 0.02 g; $NaHCO_3$, 0.002 g; urea, 2.5 g; and distilled water, 100 ml). Specimens were mounted on microscopic slides under coverslips with slight pressure and then fixed in alcohol, formaldehyde, and acetic acid (AFA) fixative (70% ethanol, 40% formaldehyde, and acetic acid glacial at a 20:1:1 ratio) for morphological observations. A part of proglottids of some specimens were separately preserved in 99.5 % ethanol for molecular analyses.

Specimens on slides were stained with Heidenhain's iron hematoxylin or alum carmine. Heidenhain's iron hematoxylin staining was performed as follows: specimens were immersed in 70% ethanol for 1 h, distilled water for 1 h, and 4% ferric ammonium alum for 12h; washed with running water for a half day; stained using Heidenhain's iron hematoxylin from 3–6 h; washed with running water for a half day; immersed in 1 or 2% ammonium ferric ammonium alum until the color was adequate for observation; washed in running water for a half day; dehydrated in graded ethanol series (70%, 90%, 99.5%, and 100%) for one day each; and cleared in creosote for over 3 days. For alum carmine staining, specimens were immersed in 70% ethanol for 1 h and distilled water for 1 h, stained using alum carmine for 3 days, washed with running water for a half day, with 70% ethanol containing 1% HCl until the color was adequate for observations, washed with running water for half a day, dehydrated in graded ethanol series (70%, 90%, 99.5%, and 100%) for one day each, and cleared in xylene for over 3 days. The stained specimens were then mounted in Canada balsam or Entellan new (Merck). Specimens were deposited in the National Museum of Nature and Science (NSMT-Pl).

2.3 Morphological observations

Prepared specimens were observed under a light microscope. Illustrations were made using a drawing tube or by tracing the photographs of the specimens. Morphological terms followed Chervy (2002) and Ruhnke (2011) (Fig. 2). Measurements of the following body parts were made directly on the specimens using ocular micrometer or on the drawings using ImageJ 1.49 (Rasband, 1997–2014): total length and maximum width, muscle band widths at anterior and posterior proglottid, scolex length and width, accessory sucker length and width, bothridia length and width, apical sucker length and width, stem length and width, neck width, anterior region of scolex length and width, testis length and width, cirrus width, cirrus sac length and width, ovary length and width, uterus length and width, vagina width, vitelline follicles length and width, and egg length and width. The number of proglottids and tesres were also counted. Specimens were identified as species based on the published keys to the cestodes (Khalil et al., 1994) and every original or revised descriptions.

2.4 DNA extraction, PCR amplification, and DNA sequencing

Total genomic DNA was extracted from a total of 43 species (Table 6) of Phyllobothriidea and its related taxa. In the case that the same species was collected from two or more host species, DNA was obtained from cestode specimen from each host species. DNA extraction was performed using DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's protocol.

Complete ssrDNA and partial lsrDNA (D1–D3) were amplified using the primers WormA and WormB, and LSU5 and 1500R, respectively (Waeschenbach et al., 2007; Table 7). PCR amplifications were performed using Premix Taq™ (Ex Taq™ Version 2.0, TaKaRa) or HotStarTaq DNA Polymerase (Qiagen). The total reaction volume was 15 µl containing 7.5 µl of Premix Taq, 0.75 µl of each 0.5 µM primer, and 4.5 µl of Milli-Q water, or 0.075 µl of HotSterTaq DNA Polymerase, 1.5 µl of 10X PCR Buffer, 0.3 µl of 1M dNTP mix, 0.75 µl of each 0.5 µM primer, and 10.125 µl of UPW. Thermal cycling was performed in a Mastercycler® nexus (Eppendorf) or TaKaRa PCR Thermal Cycler Dice® (TaKaRa). PCR reactions were initiated by denaturation at 94°C for 2 min, followed by 40 cycles of the following reactions: denaturation at 94°C for 1 min, annealing at 53°C for 30 s, and extension at 72°C for 2 min, followed by final extension at 72°C for 7 min and completed by preserving the mixture at 10°C. PCR products were loaded on 1.2% agarose gels to confirm amplification and purified by removing excess oligonucleotides using Exo-SAP IT For PCR Product Clean-Up (Affymetrix/USB) following the manufacturer's protocol.

BigDye Terminator version 3.1 Cycle Sequencing Kit (Applied Biosystems) was used for sequencing the purified PCR product. Cycling conditions followed the manufacturer's protocol. PCR and additional sequencing primers (300F, 300R, 930F, 1200F, 1200R, 1270F, 1270R, and 18S-A27 for ssrDNA and 300F, ECD2, and 1200R for lsrDNA; Table 7) were used. Sequencing was conducted for both strands by Applied Biosystems 3500/3500xL Genetic Analyzer (Applied Biosystems). Contigs were assembled using ATGC5 (GENETYX) or GeneStudio Professional (GeneStudio, Inc.).

2.5 Sequence alignment and tree construction

In the present study, 56 operational taxonomic units (OTUs) from the order Phyllobothriidea and its related taxa, which have not yet been analyzed on a molecular basis, were newly sequenced for the phylogenetic analyses (Table 6). In addition, 55 OTU sequences from GenBank, which were used by Caira et al. (2014), were also analyzed (Table 6). The following two datasets were prepared: Dataset 1 contained a suite of all 111 OTU sequences and Dataset 2 was restricted to 73 OTU sequences, excluding data from the fast-evolving taxa and those from the same species (Table 6, see Results). The sequences of complete ssrDNA, partial lsrDNA (D1–D3), and their combined sequences were used for analysis.

By the multiple alignments using MAFFT v7.215 (Katoh & Standley, 2013) with the option L-INS-i, 2,322 positions were aligned from 1,770–2,157 bp of ssrDNA and 1,549 positions from 1,226–1,390 bp of lsrDNA in Dataset 1, whereas 1,905 positions were aligned from 1,816–1,956 bp of ssrDNA and 1,396 positions from 1,225–1,331 bp of lsrDNA in Dataset 2. To remove unreliably aligned regions, including large gaps, Gblocks v0.91b (Castresana, 2000) was employed with the following parameter settings in Dataset 1: minimum number of sequences for a conserved position = 57, minimum number of sequences for a flank position = 95, maximum number of contiguous non-conserved positions = 8, minimum length of a block = 10, allowed gap positions = all, whereas in dataset 2 the following parameter settings were employed: minimum number of sequences for a conserved position = 37, minimum number of sequences for a flank position = 62, maximum number of contiguous non-conserved positions = 8, minimum length of a block = 10, and allowed gap positions = all. Therefore, 1,859 positions of ssrDNA consisting of seven blocks and all 1,386 positions of lsrDNA consisting of nine blocks were selected for reliable regions in Dataset 1, whereas all 1,951 positions of ssrDNA and all 1,378 positions of lsrDNA consisting of two blocks were selected in Database 2.

The phylogenetic trees were constructed using the maximum likelihood (ML) method with IQ-TREE version 1.4.3 (Nguyen et al., 2015) and BI with MrBayes v. 3.2.4 (Ronquist & Huelsenbeck, 2003). The General Time Reversible plus Gamma distributed (GTR + G) model was selected as the best-fitting evolutionary model by IQ-TREE for all analyses. Gaps and missing site characters were treated as unknown characters. In the ML analysis, branch supports with the ultrafast bootstrap (UFBoot) (Minh et al. 2013) were obtained and the Shimodaira-Hasegawa like interpretation of aLRT statistic (SH aLRT) (Guindon et al., 2010) implemented in the IQ-TREE, UFBoot, and SH aLRT were estimated from 1,000 replicates. SH aLRT was only used to estimate for nodes of orders. In the BI analysis, bayesian posterior probabilities (BPP) were obtained. The Markov-chain Monte Carlo (MCMC) process was run until the average standard deviation of split frequencies became less than 0.01. The MCMC process was run with four chains sampled every 100 generations for 6,500,000 generations for the combined sequence, 1,500,000 generations for ssrDNA, and 3,000,000 generations for lsrDNA in Dataset 1, whereas 100 generations for 500,000 generations for the combined sequence and ssrDNA and 1,500,000 generations for lsrDNA were sampled in Dataset 2, and the first 25% trees were discarded as burn-in.

As above mentioned, a total of 12 phylogenetic analyses were conducted and summarized as follows. ML analysis with IQ-TREE in Dataset 1 with a combined sequence of ssrDNA and lsrDNA, a single ssrDNA, and lsrDNA (Analyses 1, 2, and 3, respectively) and in Dataset 2 with a combined sequence of ssrDNA and lsrDNA, a single ssrDNA, and a single lsrDNA (Analyses 4, 5, and 6, respectively) and BI analysis in Dataset 1 with a combined sequence of ssrDNA and lsrDNA, a single ssrDNA, and a single lsrDNA (Analyses 7, 8, and 9, respectively) and in Dataset 2 with a combined sequence of ssrDNA and lsrDNA, a single ssrDNA, and a single lsrDNA (Analyses 10, 11, and 12, respectively).

The UFBoot and BPP are shown on each ML and BI tree, respectively. The author interpreted a statistical support as robust when a node was supported by UFBoot ≥95, BPP ≥0.98, or SH aLRT ≥80.0. The members of the order Litobothriidea and Lecanicephalidea were used as outgroups in Analyses 1–3 and 7–9 and those of the order Lecanicephalidea were used as outgroups in Analyses 4–6 and 10–12.

3. Results

3.1 Molecular phylogenetic analysis

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Calliobothrium shirozame n. sp.

Type host: *Mustelus griseus* Pietschmann, 1908 (Carcharhiniformes: Triakidae).
Type locality: off Chigasaki, Kanagawa Prefecture, Japan.
Site of infection: Spiral intestine.
Distribution: Pacific Ocean– off Chigasaki, Kanagawa Prefecture, Japan (this study); off Iburi, Kochi Prefecture, Japan (this study); off Kochi, Kochi Prefecture, Japan (this study).

Etymology: The species is named for Japanese name of its type host.

Material examined: NSMT-Pl 6037 (Holotype: a whole mounted specimen ex *Mu. griseus*, off Chigasaki, Kanagawa Prefecture, Japan, 31. v. 2009); NSMT-Pl 6038–6039 (two whole mounted specimens ex *Mu. griseus*, off Chigasaki, Kanagawa Prefecture, Japan); NSMT-Pl 6044, 6048 (two whole mounted specimens ex *Mu. griseus*, off Chigasaki, Kanagawa Prefecture, Japan, 31. v. 2009); NSMT-Pl 6040–6041, 6051 (four whole mounted specimens ex *Mu. griseus*, off Chigasaki, Kanagawa Prefecture, Japan, vi. 2009); NSMT-Pl 6045 (a whole mounted specimen ex *Mu. griseus*, off Chigasaki, Kanagawa Prefecture, Japan, 24. x. 2009); NSMT-Pl 6042 (a whole mounted specimen ex *Mu. griseus* (host voucher NSMT-P 111875) off Iburi, Kochi Prefecture, Japan, 4. xii. 2012); NSMT-Pl 6043, 6050 (two whole mounted specimens ex *Mu. griseus*, off Iburi, Kochi Prefecture, Japan, 7. xii. 2012); NSMT-Pl 6046–6047 (two whole mounted specimens ex *Mu. griseus*, off Kochi, Kochi Prefecture, Japan, 17. i. 2013).

Description (Fig. 19)

Adults

Based on 17 whole mounted adult specimens.

Worms euapolytic 26.7–108.3 (56.4 mm, N=15) long, with maximum width 596–1,800 (1,062, N=15) at level of mature proglottids, comprised of 240–353 (288, N=15) proglottids (Fig. 19A). Scolex 295–562 (405, N=17) long, bears four bothridia and cephalic peduncle (Fig. 19B). Cephalic peduncle 19–119 (64, N=17) long, gradually widening posteriorly, extends beyond posterior margin of bothridium. Bothridium 257–495 (364, N=16, n=58) long, 129–190 (158, N=14, n=44) wide, each with muscular pad 24–148 (65, N=14, n=29) long, 33–190 (111, N=16, n=34) wide, with central accessory sucker 24–71 (40, N=15, n=41) in diameter and 2 lateral accessory suckers 19–57 (32, N=15, n=44) in diameter, bearing 2 pairs of articulated hooks, divided into 3 loculi by 2 transverse septa. Anterior loculus 105–238 (154, N=16, n=59) long, 81–143 (112, N=13, n=42) wide; middle loculus 33–105 (61, N=16, n=59) long, 62–143 (99, N=13, n=42) wide; posterior loculus 38–100 (61, N=16, n=59) long, 52–129 (80, N=13, n=42) wide.

All hooks hollow. Lateral and medial pair of hooks symmetrical, each tip of prongs extending posteriorly (Fig. 19C). Axial hooks more acutely recurved than abaxial hooks. Lateral hook measurements (Fig. 19D): A, 48–93 (68, N=16, n=53); B, 95–148 (117, N=16, n=53); C, 43–67 (50, N=16, n=53); D, 95–148 (119, N=16, n=53); E, 60–98 (77, N=16, n=53); F, 31–52 (43, N=16, n=53). Medial hook measurements (Fig. 14D): A', 48–93 (68, N=16, n=53); B', 93–145 (116, N=16, n=53); C', 38–62 (49, N=16, n=53); D', 95–157 (118, N=16, n=53); E', 57–107 (77, N=16, n=53); F, 36–52 (43, N=16, n=53).

Proglottids craspedote, laciniate (Fig. 19E). Cephalic peduncle with 2 dorsolateral and 2 ventrolateral pairs of laciniations; immature proglottids with 2 dorsolateral and 2 ventrolateral pairs and 1 central laciniation on dorsal and ventral surfaces (Fig. 19F), middle laciniations gradually disappearing toward mature proglottids; mature proglottids with 2 dorsolateral and 2 ventrolateral pairs of laciniations. Mature proglottids 576–3,323 (1,975, N=14, n=39) long, 506–1,573 (977, N=14, n=39) wide, becoming longer than wide with maturity. Testes 77–116 (93, N=13, n=36) in total number, 41–143 (85, N=13, n=37) long, 57–157 (100, N=13, n=37) wide, densely arranged, extend from near anterior margin of proglottid to anterior margin of ovary; postvaginal testes 26–43 (33, N=13, n=36) in number. Cirrus-sac spherical, 62–233 (160, N=13, n=35) long, 57–176 (116, N=13, n=35) wide, contains coiled cirrus, covered with small microtriches. Vas deferens medial, coiled lateral and anterior to cirrus-sac, enters the proximal end of cirrus-sac. Ovary posterior, 144–915 (438, N=12, n=39) long, 326–1,223 (708, N=12, n=39) wide, H-shaped in dorsoventral view; ovarian margins digitiform. Genital pores lateral, irregularly alternating, 62–81 (74, N=14, n=39)% from anterior margin of each proglottid. Vagina sinuous, arises from oötype, extends anteriorly along mid-line of proglottid, then laterally along the anterior margin of cirrus-sac, and opens in. common genital atrium next to cirrus. Vitellarium follicular, follicles arranged in two lateral fields consisting of multiple columns, interrupted by vagina and cirrus-sac on the poral side. Uterus median, occupies region from oötype to approximately anterior 1/5 of proglottid, ventral to the vagina.

Remarks

Calliobothrium shirozame was distinguished from the congeners by the number and form of laciniations. *Calliobothrium shirozame* has four posterior triangular laciniations in cephalic peduncle, six in immature proglottids and four in mature proglottids whereas *Ca. australis* and *Ca. verticillatum* have four posterior triangular laciniations in cephalic peduncle, six in early immature proglottids, eight in late immature proglottids, and four in mature proglottids (Euzet, 1959; Ivanov &

Brooks, 2002) while *Ca. creeveyae* and *Ca. tylotocephalum* have two posterior triangular laciniations in cephalic peduncle and all proglottids (Alexander, 1963; Butler, 1987).

All *Calliobothrium* species are oioxenous species. Two triakid sharks of the genus *Mustelus*, *Mu. griseus* and *Mu. manazo*, are sympatrically distributed in Japanese waters (Ebert et al., 2013), but *Calliobothrium* species except this new species have been reported only from *Mu. manazo* (Yoshida, 1917; Yamaguti, 1952; Yamaguchi et al., 2000). In this investigation, *Calliobothrium shirozame* was only found in *Mu. griseus*. Yamaguchi et al. (2000) also found no specimen of this new species from *Mu. manazo* in their surveys on parasites of *Mustelus* species in the coastal seas of Japan and Taiwan.

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4. Discussion

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Chapter II

Identification of phyllobothriidean larvae and their development

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General discussion

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Conclusion

The primary objective of this study was to revise the taxonomy of Phyllobothriidea genera based on their molecular phylogeny. According to the molecular analyses, Phyllobothriidea is composed of 17 genera, three of which are newly described. Considerable morphological variation was observed in each genus. The form of the bothridium has traditionally been used as the primary characteristic for the classification of phyllobothriidean genera, but this did not reflect the molecular phylogeny.

Based on these new systematics, the Phyllobothriidea fauna of the coastal seas of Japan were summarized. Phyllobothriidea from Japan are composed of 41 species belonging to 15 genera, which included 14 new species, and 12 species and five genera new to Japan. This suggests that the phyllobothriidean fauna of the coastal seas of Japan is rich in species diversity.

The second objective of this study was to identify plerocercoid larvae using molecular techniques for better understanding of the life cycle of Phyllobothriidea. Seven species of phyllobothriidean plerocercoids were found in teleosts and cephalopods. Four of these were identified as *Pelichnibothrium montaukensis*, *Pe*. cf. *montaukensis*, *Scyphophyllidium carcharhinus*, and *Vertebraeovicestus dobukasube* based on lsrDNA and mtDNA COI, and their intermediate host species were found to be *Alepisaurus ferox*, *Todarodes pacificus* and *Berryteuthis magister*, *Coryphaena hippurus*, and *Lycodes nakamurae*, respectively. The remaining three species were not identified. These Phyllobothriidea larvae were categorized into three morphological types based on the present observations and information from previous reports.

The evolution of Phyllobothriidea has resulted not only from co-speciation, but more importantly also from host switching events. Such events can readily occur between closely related hosts and also results in high host specificity at the genus level. Furthermore, host switching events may have caused the observed morphological diversification, resulting in phyllobothriidean morphology not reflecting their phylogeny.

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Table 1 Families of Tetraphyllidea in major taxonomical works before Caira et al. (2014). Circles denote that the family was included in Tetraphyllidea in each paper. Serendipidae was most recently a family of Tetraphyllidea, no comprehensive taxonomical works of tetraphyllidean families exist since the establishment of this family.

Family	Braun (1900)	Meggitt (1924)	Southwell (1925)	Fuhrmann (1931)	Joyeux & Baer (1936)	Hyman (1951)	Wardle & McLeod (1952)	Euzet (1959)	Yamaguti (1959)	Joyeux & Baer (1961)	Schmidt (1986)	Euzet (1994)
Ichthyotaeniidae Ariola, 1899	x	x			x							
Onchobothriidae Braun, 1900	x	x	x	x	x	x	x	x	x	x	x	x
Phyllobothriidae Braun, 1900	x	x	x	x	x	x	x	x	x	x	x	x
Lecanicephalidae Braun, 1900	x	x		x				x		x		
Monticelliidae La Rue, 1911				x								
Proteocephalidae La Rue, 1911				x								
Polypocephalidae Miggitt, 1924		x										
Cephalobothriidae Pintner, 1928				x	x			x		x		
Discocephalidae Pintner, 1928				x								
Disculicipitidae Joyeux & Baer, 1935					x			x		x		x
Gastrolecithidae Euzet, 1955								x		x		
Phoreiobothriidae Baer & Euzet 1955								x		x		
Prosobothriidae Baer & Euzet, 1955								x		x		x
Maccallumiellidae Yamaguti, 1959									x			
Triloculariidae Yamaguti, 1959									x		x	
Dioecotaeniidae Schmidt, 1969												x
Litobothriidae Dailey, 1969												x
Cathetocephalidae Dailey & Overstreet, 1973											x	x
Chimaerocestidae Williams & Bray, 1984												x
Serendipidae Brooks & Barriga, 1995												

Table 2 Phyllobothriidean species reported in coastal seas of Japan.

Species	Host species	Location	Reference
Phyllobothrium			
Phyllobothrium lactuca	*Mustelus manazo*	Hamajima (Mie Pref.)	Yoshida (1917)
		Sea of Japan	Yamaguti (1952)
Phyllobothrium serratum	*Triacis scyllium*	Hamajima (Mie Pref.)	Yamaguti (1952)
Phyllobothrium sp.	*Isurus glaucus*	Pacific Ocean	Yamaguti (1934)
Phyllobothrium sp.	*Mustelus manazo*	Coatal seas of Japan	Yamaguchi et al. (2000)
incertae sedis			
Phyllobothrium biacetabulatum	*Rhinobatus schlegeli*	Inland sea (Okayama Pref.)	Yamaguti (1960)
Phyllobothrium dasybati	*Dasrbatus akajei*	Pacific coast	Yamaguti (1934)
Phyllobothrium marginatum	*Squtina japonica*	Toyama Bay	Yamaguti (1934)
Phyllobothrium loculatum	*Heterodontus zebra*	East China Sea	Yamaguti (1952)
Phyllobothrium squali	*Squalus sucklii*	Onahama (Fukusima Pref.)	Yamaguti (1952)
Orygmatobothrium			
Orygmatobothrium musteli	*Mustelus manazo*	Hamajima (Mie Pref.)	Yamaguti (1952)
		Pacific	Yamaguti (1952)
		Sea of Japan	Yamaguti (1952)
species inquirenda			
Orygmatobothrium velaentum	*Mustelus manazo*	Hiroshima	Yoshida (1917)
Orygmatobothrium sp.	*Mustelus manazo*	Coatal seas of Japan	Yamaguchi et al. (2000)
Paraorygmatobothrium			
Paraorygmatobothrium angustum	*Triacis scyllium*	Misaki (Kanagawa Pref.)	Yoshida (1917)
Paraorygmatobothrium filiforme	*Alopias vulpinus*	Pacific Ocean	Yamaguti (1934)
Paraorygmatobothrium tiacis	*Triacis scyllium*	Pacific Ocean	Yamaguti (1952)
Paraorygmatobothrium prionacis	*Prionace glauca*	Pacific Ocean	Yamaguti (1934)
Marsupiobothrium			
Marsupiobothrium alopias	*Alopias vulpinus*	Pacific Ocean	Yamaguti (1934)

Table 3 Genera reported in Phyllobothriidae so far and their status (Ruhnke, 2011; Ruhnke & Workman, 2013). Genera included in Phyllobothriidea in Caira et al. (2014) are shown in bold face.

Order	Family	*Genus*
Tetraphyllidea		
	Phyllobothriidae	***Phyllobothrium*** **van Beneden, 1849**
		Alexandercestus Ruhnke & Workman, 2013
		Bibursibothrium McKenzie & Caira, 1998
		Calyptrobothrium **Monticelli, 1893**
		Cardiobothrium McKenzie & Caira, 1998
		Clistobothrium Dailey & Vogelbein, 1990
		Crossobothrium Linton, 1889
		Marsupiobothrium **Yamaguti, 1952**
		Doliobothrium Malek, Caira & Ruhnke, 2010
		Flexibothrium McKenzie & Caira, 1998
		Monorygma Diesing, 1863
		Nandocestus **Reyda, 2008**
		Orectolobicestus **Ruhnke, Caira & Carpenter, 2006**
		Orygmatobothrium **Diesing, 1863**
		Paraorygmatobothrium **Ruhnke, 1994**
		Ruhnkecestus **Caira & Durkin, 2006**
		Scyphophyllidium **Woodl&, 1927**
		Thysanocephalum **Linton, 1889**
		nomina dubia
		Aocobothrium Mola, 1907
		Dittocephalus Parona, 1887
		Hoaleshwaria Shinde & Chincholikar, 1975
		Phanobothrium Mola, 1907
		Shindeobothrium Shinde & Chincholikar, 1975
		nomen ad interim
		Phyllobothrideum Olsson, 1866
		inquirenda
		Bilocularia Obersteiner, 1914
		Biporophyllaeus Subramaniam, 1939
		Cyatocotyle Mola, 1908
		Kowsalyabothrium Muralidhar, Shinde & Jadhav, 1987
		Maccallumiella Yamaguti, 1959
		Mastacembellophyllaeus Shinde & Chincholikar, 1977
		Pillersium Southwell, 1927
		Pithophorus Southwell, 1925
		Polipobothrium Mola, 1908
	Serendipidae	*Duplicibothrium* Williams & Campbell, 1978
		Glyphobothrium Williams & Campbell, 1977
		inquirenda
		Myliobatibothrium Shinde & Mohekar, 1983
		Tiarabothrium Shipley & Hornell, 1906

Table 3 continued.

Order	Family	*Genus*
	incertae sedis	*Anindobothrium* Marques, Brooks & Lasso, 2001
		Anthobothrium van Beneden, 1850
		Carpobothrium Shipley & Hornell, 1906
		Caulobothrium Baer, 1948
		Caulopatera Cutmore, Bennett & Cribb, 2010
		Ceratobothrium Monticelli, 1892
		***Chimaerocestos* Williams & Bray, 1984**
		Dinobothrium van Beneden, 1889
		syn. *Diplobothrium* van Beneden, 1889
		syn. *Reesium* Euzet, 1955
		Gastrolecithus Yamaguti, 1952
		Guidus Ivanov, 2006
		Mixophyllobothrium Shinde & Chincholikar, 1980
		Myzocephalus Shipley & Hornell, 1906
		Myzophyllobothrium Shipley & Hornell, 1906
		Pelichnibothrium Monticelli, 1889
		syn. *Prionacestus* Mete & Euzet, 1996
		Rhoptrobothrium Shipley & Hornell, 1906
		Trilocularia Olsson, 1867
		syn. *Urogonoporus* Lühe, 1902
		Zyxibothrium Hayden & Campbell, 1981
Rhinebothriidea		
		Anthocephalum Linton, 1890
		Biotobothrium Tan, Zhou & Yang, 2009
		Clydonobothrium Euzet, 1959
		Echeneibothrium van Beneden, 1850
		Escherbothrium Berman & Brooks, 1994
		Notomegarhynchus Ivanov & Campbell, 2002
		Pararhinebothroides Zamparo, Brooks & Barriga, 1999
		Pentaloculum Alexander, 1963
		Phormobothrium Alexander, 1963
		Pseudanthobothrium Baer, 1956
		Rhabdotobothrium Euzet, 1953
		Rhinebothrium Linton, 1890
		Rhinebothroides Mayes, Brooks & Thorson, 1981
		Rhodobothrium Linton, 1889
		syn. *Inermiphyllidium* Riser, 1955
		syn. *Sphaerobothrium* Euzet, 1959
		syn. *Proboscidosaccus* Gallien, 1949
		Scalithrium Ball, Neifar, & Euzet, 2003
		Spongiobothrium Linton, 1889
		Tritaphros Lönnberg, 1889
		inquirenda
		Shindeiobothrium Jadhav, Shinde & Deshmukh, 1981

Table 4 Sampling data. See Fig. 1 for positions of the stations.

Station	Locality	Depth	Fishing gear	Remarks
1	off Erimo, Hokkaido Prefecture	-	set net	Bought from Onsenichiba Inc.
2	off Ooma, Aomori Prefecture	ca. 200 m	long line	Bought from Tamukaisyoten Inc.
3	off Sado Island, Niigata Prefecture	-	set net	Collected by Kamo-Suisan Set Nets Cooperative
4	off Ibaraki, Ibaraki Prefecture	ca. 200 m	crab cage	Collected using R/V Soyo-Maru of the Fisheries Research
5	Ooarai, Ibaraki Prefecture	-	-	A whale stranded on the beach
6	off Toyama, Toyama Prefecture	-	set net	Tapeworms specimens were provided by Tokyo Medical and Dental University.
7	off Kanaya, Chiba Prefecture	ca. 160–500 m	gill net	Collected using F/S Tyogoro-Maru of Kanaya Fishing Port
8	off Miura, Kanagawa Prefecture	ca. 160–500 m	gill net	Collected using F/S Marukin-Maru of Nagai Fishing Port
9	off Chigasaki, Kanagawa Prefecture	ca. 1–10 m	dragnet	Collected by Tokuami Inc.
10	off Izu-Ooshima Island, Tokyo Metropolitan	ca. 200 m	long-line	
11	off Akazawa, Shizuoka Prefecture	ca. 25 m	set net	Collected by Akazawa Gyogyou Inc.
12	off Shimoda, Shizuoka Prefecture	-	angling	
13	off Shimoda, Shizuoka Prefecture	ca. 30 m	long line	Collected using T/S Suzaki II of the Nihon University
14	off Toshima Island, Tokyo Metropolitan	ca. 30 m	long line	Collected using T/S Suzaki II of the Nihon University
15	off Yui, Shizuoka Prefecture	-	set net	
16	off Heda, Shizuoka Prefecture	ca. 140-690 m	bottom trawl	Collected using F/S Shoujin-Maru of Heda Fishing Port
17	off Irouzaki, Shizuoka Prefecture	ca. 30 m	long line	Collected using T/S Suzaki II of the Nihon University
18	off Obama, Fukui Prefecture	-	set net	
19	off Maizuru, Kyoto Prefecture	-	-	Bought from Mizushima-Suisan Inc.
20	off Oki Islands, Shimane Prefecture	ca. 200–400 m	otter trawl	Collected using T/S Tansyu-Maru of the Hyogo Prefectural Kasumi Fishery High School
21	off Kochi, Kochi Prefectere	ca. 55–70 m	beam trawl	Collected by Kochi Prefectural Fisheries Experimental Station
22	off Mimase, kochi Prefecture	-	trawl	Landed at Mimase Fishing Port
23	off Tosasaga, Kochi Prefecture	-	trawl	Landed at Tosasaga Fishing Port
24	off Iburi and Kubotsu, Kochi Prefecture	ca. 25 m	set net	Collected by Iburi Triangular Set Nets Cooperative
25	off Kubotsu, Kochi Prefecture	ca. 25 m	set net	Collected by Kubotsu Triangular Set Nets Cooperative

Table 4 continued.

Station	Locality	Depth	Fishing gear	Remarks
26	off Tosazhimizu, Kochi Prefecture	-	long line	Collected by Tosashimizu Fisheries Cooperative
27	Minamisatsuma, Kagoshima Prefecture	-	-	A whale stranded on the beach
28	off Yomotan, Okinawa Prefecture	ca. 25 m	set net	Collected by Yomitan Fisheries Cooperative
29	off Yaeyama Islands, Okinawa, Prefecture	-	long line	Collected by Yaeyama Fisheries Cooperative
30	off Ogasawara Islands, Tokyo Metropolitan	-	hock and line	Using by F/B Aippara II or from land
31	off Ogasawara Islands, Tokyo Metropolitan	-	long line	Collected by R/V Koyo of the Tokyo Metropolitan Islands Area Research and Development Center of Agriculture

Table 5 List of the examined host specimens of elasmobranchs, teleosts and cetaceans. N means the number of host specimens and the number of measured specimens is shown in parentheses if all specimens were not measured. Length was measured by total length except some batoideans of Dasyatidae, Gymnuridae, and Myliobatidae by disk length (marked by asterisks). Weight is shown by gram for small specimens (indicated by g).

Host species	N	Length (mm)	Weight (kg)
		Range	Range
Elasmobranchii			
Galeomorphii			
Heterodontidae			
Heterodontus japonicus	19	326 – 1031	0.3 – 5.3
Orectolobidae			
Orectolobus japonicus	1	1071	10.2
Ginglymostomatidae			
Nebrius ferrugineus	1	2960	141.0
Mitsukurinidae			
Mitsukurina owstoni	8	1050 – 3600	1.7 – 167.0
Odontaspididae			
Odontaspis ferox	1	no data	no data
Megachasmidae			
Megachasma pelagios	1	4460	677.0
Lamnidae			
Carcharodon carcharias	1	4070	no data
Isurus oxyrinchus	3 (1)	1500	26.1
Scyliorhinidae			
Apristurus macrorhynchys	17	360 – 672	97 – 786 g
Cephaloscyllium umbratile	60	213 – 1022	0.03 – 8.6
Galeus eastmani	6	342 – 699	0.09 – 1.3
Galeus nipponensis	18	375 – 699	0.1 – 1.5
Parmaturus pilosus	1	622	860 g
Scyliorhinus torazame	17	390 – 489	194 – 490 g
Proscylliidae			
Proscyllium habereri	3	572 – 704	0.4 – 1.0
Triakidae			
Mustelus manazo	69	300 – 935	0.03 – 2.8
Mustelus griseus	20	460 – 880	0.3 – 2.9
Triakis scyllium	12	245 – 992	0.2 – 3.6
Hemitriakis japonica	6	750 – 954	1.3 – 4.1

Table 5 continued.

Host species	N	Length (mm) Range	Weight (kg) Range
Carcharhinidae			
Carcharhinus albimarginatus	4	1380 – 1560	18.0 – 25.0
Carcharhinus brevipinna	23	700 – 1020	1.3 – 5.5
Carcharhinus dussumieri	4	556 – 730	1.0 – 2.1
Carcharhinus galapagensis	9	790 – 1910	2.7 – 36.1
Carcharhinus leucas	1	2650	147.0
Carcharhinus longimanus	1	1730	32.0
Carcharhinus limbatus	2	1430 – 2090	1.1 – 1.5
Carcharhinus plumbeus	4	1120 – 1420	8.0 – 15.0
Galeocerdo cuvier	6	1130 – 2990	5.4 – 158.0
Loxodon macrorhinus	2	710 – 950	1.0 – 3.0
Prionace glauca	3	2080 – 2690	8.3 – 29.0
Triaenodon obesus	2	1265 – 1320	10.7 – 17.8
Sphyrnidae			
Sphyrna zygaena	5	933 – 1775	4.0 – 24.5
Squalomorphi			
Chlamydoselachidae			
Chlamydoselachus anguineus	18	1005 – 1485	1.7 – 6.7
Hexanchidae			
Heptranchias perlo	30	682 – 1150	0.9 – 5.9
Hexanchus griseus	1	4020	505.5
Echinorhinidae			
Echinorhinus cookei	1	no data	no data
Dalatiidae			
Dalatias licha	52	281 – 1542	0.14 – 29.1
Etmopteridae			
Etmopterus brachyurus	9	241 – 467	39 – 400 g
Etmopterus lucifer	19	284 – 430	70 – 274 g
Etmopterus molleri	17	202 – 385	20 – 179 g
Etmopterus pusillus	16	168 – 288	12 – 82 g
Etmopterus unicolor	1	520	606 g
Centrophoridae			
Deania calcea	46	315 – 1170	0.09 – 8.0
Deania hystricosa	34	324 – 1230	0.12 – 10.4
Centrophorus squamosus	7	461 – 1270	0.42 – 13.0
Centrophorus tessellatus	1	618	1.0
Centrophorus sp. 1	1	1220	12.7
Centrophorus sp. 2	1	895	3.7
Squalidae			
Cirrhigaleus barbifer	1	796	4.3
Squalus acanthias	10	745 – 840	1.6 – 2.2
Squalus brevirostris	69	510 – 880	0.6 – 3.6
Squalus japonicus	18	323 – 690	0.1 – 1.4
Squalus mitsukurii	72	348 – 1090	0.2 – 8.4

Table 5 continued.

Host species	N	Length (mm)	Weight (kg)
		Range	Range
Squatinidae			
Squatina japonica	5	588 – 840	1.7 – 6.0
Squatina nebulosa	3	484 – 1490	1.0 – 23.1
Pristiophoridae			
Pristiophorus japonicus	1	1010	1.3
Batoidea			
Rhynchobatidae			
Rhynchobatus djiddensis	1	2410	8.4
Rhinobatidae			
Rhinobatos schlegelii	16	753 – 955	1.1 – 3.4
Rhinobatos hynnicephalus	1	660	1.1
Platyrhinidae			
Platyrhina tangi	3	145 – 537	0.02 – 1.1
Narcinidae			
Narke japonica	18	104 – 351	20 – 750 g
Torpedinidae			
Torpedo tokionis	2	530 – 629	2.3 – 4.0
Arhynchobatidae			
Bathyraja smirnovi	6	517 – 1030	1.0 – 9.8
Rajiidae			
Amblyraja badia	1	922	6.5
Dipterus macrocauda	1	1075	7.6
Okamejei kenojei	2	360 – 373	200 – 460 g
Okamejei schmidti	1	473	550 g
Raja pulchra	17	648 – 885	0.5 – 6.2
Urolophidae			
Urolophus aurantiacus	3	275 – 362	220 – 534 g
Dasyatidae			
Dasyatis akajei	33	135 – 791*	0.07 – 23.3
Dasyatis izuensis	5	162 – 368*	0.2 – 3.0
Dasyatis matsubarai	2	376 – 380*	1.5 – 1.6
Taeniura meyeni	5 (3)	1180 – 1560	24.8 – 77.0
Pleroplatytrygon violacea	1	585*	6.0
Gymnuridae			
Gymnura japonica	7	324 – 1045*	0.3 – 10.0
Myliobatidae			
Myliobatis tobijei	25	220 – 405*	0.2 – 1.4
Neopterygii			
Alepisauridae			
Alepisaurus ferox	4	905 – 1050	840 – 1360
Salmonidae			
Oncorhynchus keta	1	630	2630
Mammalia			
Delphinidae			
Stenella coeruleoalba	3 (1)	2340	133

Table 6 List of the specimens of two Dataset for molecular phylogenic analyses. Systematic positions and scientific names of the specimens from GeneBank follow Caira et al. (2014). Type species are shown in bold face. Specimens marked by single asterisk are undescribed species reported by Caira et al. (2014), and specimens marked by double asterisks are unidentified species. Double quotation denotes species of undescribed genus reported by previous papers. Abbreviations of country names in locality: AUS; Australia, CAN; Canada, CHL; Chili, DNK; Denmark, GBR; United Kingdom, JAP; Japan, NZL; New Zealand, MEX; Mexico, MYS; Malaysia, PRY; Paraguay, PEL; Peru, ROU; Romania, SEN; Senegal, USA; U.S.A.

Specimens	Genotype	Host species	Locality	Accession Number		Dataset	
				ssrDNA	lsrDNA	1	2
Phyllobothriidea							
Phyllobothrium cf. *lactuca*		*Mustelus mento*	Puerto Montt, CHL	KF685770	KF685845	x	x
Phyllobothrium biacetabulatum		*Rhinobatos schlegelii*	off Chigasaki, JAP	This study	This study	x	
Phyllobothrium delphini		*Stenella coeruleoalba*	Minami-satsuma, JAP	This study	This study	x	x
Phyllobothrium hoshizame n. sp.		*Mustelus manazo*	off Kanaya, JAP	This study	This study	x	x
Phyllobothrium serratum		*Triakis scyllium*	off Shimoda, JAP	This study	This study	x	x
Phyllobothrium squali	1	*Squalus japonicus*	off Kanaya, JAP	This study	This study	x	
	2	*Squalus mitsukurii*	off Kanaya, JAP	This study	This study	x	x
	3	*Squalus japonicus*	off Mimase, JAP	This study	This study	x	
	4	*Squalus mitsukurii*	off Kanaya, JAP	This study	This study	x	
	5	*Squalus acanthias*	Rhode Island, USA	KF685897	KF685846	x	
Calyptrobothrium sp. *		*Torpedo nobiliana*	Rhode Island, USA	KF685754	KF685848	x	x
Calyptrobothrium sp. 1**		*Torpedo tokionis*	off Heda, JAP	This study	This study	x	x
Chimaerocestos sp. 1*		*Rhinochimaera pacifica*	Chatham Rise, NZL	KF685758	KF685827	x	x
Chimaerocestos sp. 2*		*Rhinochimaera pacifica*	Chatham Rise, NZL	KF685882	KF685850	x	x
Marsupiobothrium gobelinus		*Mitsukurina owstoni*	off Kanaya, JAP	This study	This study	x	x
Marsupiobothrium sp.**		*Alopias pelagicus*	Santa Rosalia, MEX	KF685771	KF685821	x	x
Nandocestus guariticus		*Paratrygon aiereba*	Mouth of Rio Shilve, PER	KF685888	KF685817	x	x
Orectolobicestus tyleri		*Chiloscyllium punctatum*	Mukah, Borneo, MYS	KF685890	KF685819	x	x
Orectolobicestus randyi		*Chiloscyllium hasseltii*	Mukah, Borneo, MYS	KF685767	KF685820	x	x
Orygmatobothrium musteli	1	*Mustelus manazo*	off Heda, JAP	This study	This study	x	x
	2	*Mustelus griseus*	off Chigasaki, JAP	This study	This study	x	
Orygmatobothrium cf. *musteli* 1		*Mustelus mustelus*	Soumbédioune, SEN	KF685768	KF685815	x	
Orygmatobothrium cf. *musteli* 2		*Mustelus mustelus*	Ouakam, SEN	KF685891	KF685816	x	x

Table 6 continued.

Specimens	Genotype	Host species	Locality	Accession Number		Dataset	
				ssrDNA	lsrDNA	1	2
Paraorygmatobothrium prionacis		*Prionace glauca*	Montauk, New York, USA	KF685892	KF685818	x	x
		Prionace glauca	off Tosashimizu, JAP	This study	This study	x	
Paraorygmatobothrium exiguum		*Alopias vulpinus*	Montauk, New York, USA	KF685769	KF685822	x	x
Paraorygmatobothrium paulum		*Galeocerdo cuvier*	off Iburi, JAP	This study	This study	x	x
Paraorygmatobothrium triacis		*Triakis scyllium*	off Shimoda, JAP	This study	This study	x	x
Paraorygmatobothrium sp. 1		*Carcharhinus plumbeus*	off Yaeyama, JAP	This study	This study	x	x
		Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	This study	x	
Paraorygmatobothrium sp. 2		*Hemitriakis japanica*	off Shimoda, JAP	This study	This study	x	x
Paraorygmatobothrium sp. 3		*Triaenodon obesus*	off Ogasawara Is., JAP	This study	This study	x	x
		Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	This study	x	
Paraorygmatobothrium sp. 4		*Carcharhinus brevipinna*	off Iburi, JAP	This study	This study	x	x
Paraorygmatobothrium sp. 5		*Carcharhinus limbatus*	off Yaeyama, JAP	This study	This study	x	x
Paraorygmatobothrium sp. 6		*Triaenodon obesus*	off Ogasawara Is., JAP	This study	This study	x	x
Paraorygmatobothrium sp. 7		*Carcharhinus longimanus*	off Yaeyama, JAP	This study	This study	x	x
Paraorygmatobothrium sp. 8		*Carcharhinus limbatus*	off Yaeyama, JAP	This study	This study	x	x
		Carcharhinus leucas	off Yaeyama, JAP	This study	This study	x	
		Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	This study	x	
Paraorygmatobothrium sp. 9		*Carcharhinus dussumieri*	off Tosasaga, JAP	This study	This study	x	x
Paraorygmatobothrium sp. 10		*Carcharhinus brevipinna*	off Iburi, JAP	This study	This study	x	x
		Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	This study	x	
Ruhnkecestus latipi		*Scoliodon macrorhynchus*	Mukah, Borneo, MYS	KF685900	KF685853	x	x
Scyphophyllidium cf. *giganteum*		*Galeorhinus galeus*	Chatham Rise, NZL	KF685901	KF685854	x	x
Thysanocephalum thysanocephalum		*Galeocerdo cuvier*	off Yaeyama, JAP	This study	This study	x	x
Thysanocephalum crispum		*Galeocerdo cuvier*	off Iburi, JAP	KF685902	KF685823	x	
***Vertebraeovicestus dobukasube* n. sp.**		*Bathyraja smirnovi*	off Oki Is., JAP	This study	This study	x	x
"Phyllobothriidea gen. sp."*		*Sphyrna lewini*	Straits of Florida, USA	KF685889	KF685814	x	x

Table 6 continued.

Specimens	Genotype	Host species	Locality	Accession Number		Dataset	
				ssrDNA	lsrDNA	1	2
Tetraphyllidea							
Anthobothrium caseyi		*Prionace glauca*	Montauk, New York, USA	KF685879	KF685805	x	
		Prionace glauca	off Tosashimizu, JAP	This study	This study	x	
Anthobothrium sp. 1 *		*Carcharhinus tilstoni*	Wessel Is., AUS	KF685752	KF685806	x	
Anthobothrium sp. 2		*Carcharhinus brevipinna*	off Iburi, JAP	This study	This study	x	
Anthobothrium sp. 3		*Carcharhinus plumbeus*	off Yaeyama, JAP	This study	This study	x	
Anthobothrium sp. 4		*Carcharhinus brevipinna*	off Iburi, JAP	This study	This study	x	
Anthobothrium sp. 5		*Carcharhinus dussumieri*	off Tosasaga, JAP	This study	This study	x	
Alexandercestus oomejirozame n. sp.		*Carcharhinus leucas*	off Yaeyama, JAP	This study	This study	x	x
Balanobothrium sp.*		*Stegostoma fasciatum*	Mukah, Borneo, MYS	KF685880	KF685802	x	x
Bilocularia hyperapolytica		*Dalatias licha*	off Kanaya, JAP	This study	This study	x	x
Calliobothrium cf. *verticillatum*		*Mustelus canis*	Old Lyme, USA	KF685753	KF685812	x	x
Calliobothrium shirozame n. sp.		*Mustelus griseus*	off Shimoda, JAP	This study	This study	x	x
Ceratobothrium xanthocephalum		*Isurus oxyrinchus*	Montauk, New York, USA	KF685756	KF685849	x	x
Ceratobothrium sp. 1		*Carcharodon carcharias*	off Iburi, JAP	This study	This study	x	x
Clistobothrium carcharodoni		*Carcharodon carcharias*	off Iburi, JAP	This study	This study	x	x
Clistobothrium montaukensis	1	*Isurus oxyrinchus*	Montauk, New York, USA	EF095259	AF286996	x	
	2	*Isurus oxyrinchus*	off Toshima I., JAP	This study	This study	x	x
Clistobothrium tumidum		*Carcharodon carcharias*	off Iburi, JAP	This study	This study	x	x
Crossobothrium laciniatum		*Hexanchus griseus*	Puerto Montt, CHL	KF685883	KF685824	x	x
Crossobothrium campanulatum		*Hexanchus griseus*	off Sado I., JAP	This study	This study	x	x
Crossobothrium dohrnii		*Heptranchias perlo*	off Kanaya, JAP	This study	This study	x	x
Crossobothrium cf. *dohrnii*		*Heptranchias perlo*	Gulf of Mexico	KF685759	KF685847	x	
Megalonchos shawae		*Hemipristis elongata*	Wessel Is., AUS	KF685764	KF685807	x	
Monorygma chamydoselachii		*Chlamydoselachus anguineus*	off Kanaya, JAP	This study	This study	x	x
Monorygma grimaldii		*Stenella coeruleoalba*	Minami-satsuma, JAP	This study	This study	x	x

Table 6 continued.

Specimens	Genotype	Host species	Locality	Accession Number		Dataset	
				ssrDNA	lsrDNA	1	2
Monorygma megacotyle	1	*Cephaloscyllium umbratile*	off Heda, JAP	This study	This study	x	
	2	*Cephaloscyllium umbratile*	off Heda, JAP	This study	This study	x	
	3	*Galeus nipponensis*	off Kanaya, JAP	This study	This study	x	
	4	*Cephaloscyllium umbratile*	off Kanaya, JAP	This study	This study	x	
Pachybothrium hutsoni		*Nebrius ferrugineus*	Weipa, AUS	EF095260	EF095246	x	x
Pedibothrium mounseyi		*Nebrius ferrugineus*	Weipa, AUS	KF685893	KF685803	x	x
Pelichnibothrium speciosum		*Prionace glauca*	off Iburi, JAP	This study	This study	x	
		Alepisaurus ferox	off Toshima I., JAP	This study	This study	x	x
Pelichnibothrium caudatum		*Oncorhynchus keta*	off Erimo, JAP	This study	This study	x	x
Symcallio violae		*Mustelus canis*	Old Lyme, USA	KF685881	KF685813	x	x
Trilocularia gracilis		*Squalus acanthias*	Rhode I., USA	KF685776	KF685855	x	x
Yorkeria hilli		*Chiloscyllium punctatum*	Cairns, AUS	KF685903	KF685798	x	
***Rosebothrium ootenjikuzame* n. sp.**		*Nebrius ferrugineus*	off Yaeyama, JAP	This study	This study	x	x
Onchoproteocephalidea							
Acanthobothrium parviuncinatum		*Urobatis maculatus*	Bahia de Los Angeles, MEX	EF095264	EF095250	x	x
Acanthobothrium santarosaliense		*Heterodontus mexicanus*	Santa Rosalia, MEX	KF685751	KF685834	x	x
Peltidocotyle rugosa		*Pseduoplatystoma fasciatum*	Rio Paraguay, PRY	AF286937	AF286989	x	x
Phoreiobothrium lewinense		*Sphyrna lewini*	Straits of Florida, USA	KF685896	KF685830	x	x
Platybothrium auriculatum		*Prionace glauca*	Montauk, New York, USA	KF685898	KF685837	x	x
Platybothrium jondoeorum		*Negaprion acutidens*	Darwin, AUS	KF685772	KF685829	x	x
Potamotrygonocestus cf. *fitzgeraldae*		*Potamotrygon castexi*	Madre de Dios River, PEL	KF685773	KF685832	x	x
Prosobothrium armigerum		*Prionace glauca*	Montauk, New York, USA	KF685899	KF685828	x	x
Proteocephalus macrocephalus		*Anguilla anguilla*	River Thames, GBR	EF095261	EF095247	x	x
Proteocephalus perplexus		*Amia calva*	Hay Bay, CAN	KF685873	KF685833	x	x
Triloculatum andersonorum		*Negaprion acutidens*	Weipa, AUS	KF685895	KF685831	x	x
Uncibilocularis okei		*Pastinachus atrus*	Dundee Beach, AUS	KF685777	KF685835	x	x
Onchoproteocephalidea gen. sp.*		*Pristis clavata*	Darwin, AUS	KF685765	KF685836	x	x

Table 6 continued.

Specimens	Genotype	Host species	Locality	Accession Number		Dataset	
				ssrDNA	lsrDNA	1	2
Cathetocephalidea							
Cathetocephalus thatcheri		*Carcharhinus leucas*	Gulf of Mexico, USA	KF685884	KF685838	x	x
Rhinebothriidea							
Anthocephalum cf. *centrurum*		*Dasyatis centroura*	Mbour, SEN	FJ177099	FJ177059	x	
Rhinebothrium megacanthophallus		*Himantura polylepis*	Kinabatangan River, MSY	AF286962	FJ177080	x	
Rhodobothrium paucitesticulare		*Rhinoptera bonasus*	Davis, USA	FJ177100	FJ177060	x	
Nippoteaniidea							
Nippotaenia chaenogobii		*Chaenogobius urotaenia*	Lake Taupo, NZL	AF286933	AF286987	x	
Tetrabothriidea							
Tetrabothrius erostris		*Larus argentatus*	Danube Delta, ROU	AF286950	AJ287581	x	
Cyclophyllidea							
Hymenolepis diminuta		*Rattus norvegicus*	Univ. Copenhagen, DNK	AY157181	AF286983	x	
Lecanicephalidea							
Adelobothrium cf. *aetiobatidis*		*Aetobatus ocellatus*	Darwin, AUS	EF095257	EF095249	x	x
Paraberrapex manifestus		*Squatina californica*	Santa Rosalia, MEX	KF685868	KF685781	x	x
Litobothriidea							
Litobothrium amplifica		*Alopias pelagicus*	Santa Rosalia, MEX	KF685906	KF685843	x	
Litobothrium nickoli		*Alopias pelagicus*	Santa Rosalia, MEX	KF685907	KF685844	x	

Table 7 PCR and sequence primers of complete ssrDNA and partial lsrDNA. F means forward primer and R means reverse primer.

Primer names	Direction	Sequence	Reference
ssrDNA			
PCR primers			
WormA	**F**	GCG AAT GGC TCA TTA AAT CAG	Waeschenbach et al. (2007)
WormB	**R**	CTT GTT ACG ACT TTT ACT TCC	Waeschenbach et al. (2007)
Sequence primers			
300F	**F**	AGG GTT CGA TTC CGG AG	Waeschenbach et al. (2007)
300R	**R**	TCA GGC TCC CTC TCC GGA	Waeschenbach et al. (2007)
930F	**F**	GCA TGG AAT AAT GGA ATA GG	Waeschenbach et al. (2007)
1200F	**F**	CAG GTC TGT GAT GCC C	Waeschenbach et al. (2007)
1200R	**R**	GGG CAT CAC AGA CCT G	Waeschenbach et al. (2007)
1270F	**F**	ACT TAA AGG AAT TGA CGG	Waeschenbach et al. (2007)
1270R	**R**	CCG TCA ATT CCT TTA AGT	Waeschenbach et al. (2007)
18S-A27	**R**	CCA TAC AAA CGT CCC CGC CTG	Olson & Caira (1999)
lsrDNA			
PCR primers			
LSU5	**F**	TAG GTC GAC CCG CTG AAY TTA AGC A	Waeschenbach et al. (2007)
1500R	**R**	GCT ATC CTG AGG GAA ACT TCG	Waeschenbach et al. (2007)
Sequence primers			
300F	**F**	CAA GTA CCG TGA GGG AAA GTT G	Waeschenbach et al. (2007)
ECD2	**R**	CTT GGT CCG TGT TTC AAG ACG GG	Waeschenbach et al. (2007)
1200R	**R**	GCA TAG TTC ACC ATC TTT CGG	Waeschenbach et al. (2007)

Table 8 Sequence data of ssrDNA and lsrDNA of *Pelichnibothrium*, *Clistobothrium* and its related species. Only variable sites are shown, and numbers indicates the positions. Question marks mean missing sites. Completely identical sequences are indicated by gray markers.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 9 Sequence data of ssrDNA and lsrDNA of *Crossobothrium*and its related species. Only variable sites are shown, and numbers indicates the positions. Hyphen mean gaps.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 10 Sequence data of ssrDNA and lsrDNA of *Orygmatobothrium musteli* and its related species. Only variable sites are shown, and numbers indicates the positions.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 11 Sequence data of ssrDNA and lsrDNA of *Phyllobothrium squali*, *Monorygma megacotyla* and its related species. Only variable sites are shown, and numbers indicates the positions. Question marks mean missing sites. Completely identical sequences are indicated by gray markers.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 12 Sequence data of ssrDNA and lsrDNA of *Paraorygmatobothrium* and its related species. Only variable sites are shown, and numbers indicates the positions. Question marks mean missing sites, hyphen showed gaps. Completely identical sequences are indicated by gray markers.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 12 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 12 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 12 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 12 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 12 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 13 Comparison of statistical inference at each order. Order names were used revised orders in this study. UFBoot, ultrafast bootstrap; BPP, bayesian posterior probabilities; SH aLRT, SH-like interpretation of aLRT statistic. UFBoot ≥95, BPP ≥0.98, SH aLRT ≥80.0 are shown in bold face. Hyphens indicate branches which were not observed in each analysis.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 14 Morphological differences in the scolex among the revised genera of Phyllobothriidae. Degree means the degree of crumpling for the crumple type of bothridium. Asterisks mean the egg morphology was observed only for a part of the species of each genus. Old genera were also shown for *Pelichnibothrium* and *Scyphophyllidium* which included other synonymous old genera.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 14 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 15 New species and new combinations in this study. Abbreviations of the orders: Phy, Phyllobothriidea; Tet, Tetraphyllidea; Rhi, Rhinebothriidea.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 16 Sequence data of ssrDNA and lsrDNA of *Phyllobothrium* and its related species. Only variable sites are shown. Gray markers show the same sequence.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 17 Difference in measurements of *Pe. speciousm* between two different host species. Length and width were shown μm unit, large measurements were shown mm unit. L; length, MW; maxium width, W; width.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 18 Interspecific variations of *Sc. carcharhinus*. L; length, MW; maxium width, W; width.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 19 Interspecific variations of *Sc. insulaeum*. L; length, MW; maxium width, W; width.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 20 Interspecific variations of *Sc.maritimum*. L; length, MW; maxium width, W; width.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 21 Interspecific variations of *Sc.ogasawaraensis*. L; length, MW; maxium width, W; width.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 22 Interspecific variations of *Ya. megacotyla* . L; length, MW; maxium width, W; widtl

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 22 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 23 Phyllobothriidean fauna in the coastal seas of Japan. Single asterisks mean species of new to Japan, double asterisks mean new host records.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 23 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 23 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 23 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 23 continued.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 24 List of examined host specimens for investigation of larvae of Phyllobothriidea and its related orders. N means the number of examined host specimens and the number of measured host specimens is shown in parentheses if all specimens were not measured, and n means the number of larvae used in molecular analyses/ the total number of collected larvae.

Host species	Station	N	Total Length (mm)	Weight (g)	n	Specimen ID
			Min – Max	Min – Max		
Mollusca						
Cephalopoda						
Enoploteuthidae						
Watasenia scintillans	St. 6	1	no data	no data	1/1	Larva 14
Gonatidae						
Berryteuthis magister	St. 20	6	235 – 361	133 – 315	4/97	Larva 11–13, Larva 27
Octopodidae						
Octopus vulgaris	St. 20	1	374	315		
Ommastrephidae						
Todarodes pacificus	St. 20	6 (4)	331 – 375	40 – 271	1/7	Larva 26
Sepiolidae						
Rossia pacifica	St. 20	6	163 – 252	35 – 110		
Gastropoda						
Buccininae						
Buccinum striatissimum	St. 20	3	138 – 166	156 – 221		
Arthropoda						
Malacostraca						
Crangonidae						
Argis dentata	St. 20	6	134 – 160	20 – 30		
Hippolytidae						
Lebbeus groenlandicus	St. 20	6	118 – 154	25 – 44		
Chordata						
Elasmobranchii						
Arhynchobatidae						
Bathyraja smirnovi	St. 20	Examined by investigation of Chapter I			2/2	Larva 15, 16

Table 24 continued.

Host species	Station	N	Total Length (mm) Min – Max	Weight (g) Min – Max	n	Specimen ID
Actinopterygii						
Acanthuridae						
Zebrasoma flavescens	St. 30	1	80	13		
Alepisauridae						
Alepisaurus ferox	St. 14	Examined by investigation of Chapter I			2/258	Larva 24, 25
Argentinidae						
Glossanodon semifasciatus	St. 20	5	202 – 229	40 – 66		
Balistidae						
Sufflamen fraenatum	St. 30	2(1)	340	840		
Xanthichthys mento	St. 30	1	no data	no data		
Bramidae						
Taractichthys steindachneri	St. 31	1	712	no data	2/3	Larva 30, 31
Carangidae						
Carangoides orthogrammus	St. 30	3	375 – 580	700 – 3060		
Caranx lugubris	St. 30	2	530 – 550	1990 – 3030		
Seriola rivoliana	St. 30	1	640 – 1000	2700 – 10800		
Trachurus japonicus	St. 19	2	280	230 – 250	1/16	Larva 5
Coryphaenidae						
Coryphaena hippurus	St. 19	1	880	4000	2/32	Larva 4, 34
Chaetodontidae						
Chaetodon daedalma	St. 30	1	175	160		
Cyclopteridae						
Aptocyclus ventricosus	St. 20	2	no data	184 – 246	2/38	Larva 20, 21
Eumicrotremus asperrimus	St. 20	4 (3)	77 – 102	67 – 81	1/31	Larva 22
Gadidae						
Gadus macrocephalus	St. 20	2	324 – 614	162 – 2000	1/10	Larva 17
Holocentridae						
Neoniphon sammara	St. 30	1	150	46		
Sargocentron ittodai	St. 30	2	130 – 140	40 – 51		

Table 24 continued.

Host species	Station	N	Total Length (mm)	Weight (g)	n	Specimen ID
			Min – Max	Min – Max		
Kyphosidae						
Girella leonina	St. 30	1	590	3470		
Kyphosus pacificus	St. 30	1	430	1580		
Labridae						
Bodianus perditio	St. 30	2	190 – 380	130 – 750		
Coris aygula	St. 30	1	500	1990	1/1	Larva 10
Thalassoma lutescens	St. 30	4	170 – 230	53 – 150	1/1	Larva 9
Liparidae						
Careproctus trachysoma	St. 20	6	141 – 320	27 – 410	1/1	Larva 19
Lutjanidae						
Gnathodentex aureolineatus	St. 30	2	215 – 220	160 – 200		
Gymnocranius euanus	St. 30	11	270 – 475	400 – 2175		
Gymnocranius griseus	St. 30	2	325 – 345	620 – 710		
Lethrinus rubrioperculatus	St. 30	12 (11)	300 – 430	390 – 1000		
Lutjanus kasmira	St. 30	3	220 – 300	170 – 430		
Lutjanus stellatus	St. 30	1	585	3330		
Paracaesio xanthura	St. 30	3	220 – 390	160 – 560		
Pristipomoides argyrogrammicus	St. 30	1	350	620		
Pristipomoides filamentosus	St. 30	1	535	1930		
Pristipomoides zonatus	St. 30	3	365 – 420	770 – 1110		
Monacanthidae						
Aluterus scriptus	St. 30	1	475	550		
Sufflamen bursa	St. 30	1	210	230		
Mullidae						
Mulloidichthys vanicolensis	St. 30	2	240 – 260	160 – 210		
Parupeneus multifasciatus	St. 30	3	225 – 265	180 – 220		
Parupeneus pleurostigma	St. 30	5	210 – 305	120 – 310		

Table 24 continued.

Host species	Station	N	Total Length (mm) Min – Max	Weight (g) Min – Max	n	Specimen ID
Muraenesocidae						
Muraenesox cinereus	St. 19	1	514	no data		
Nemipteridae						
Pentapodus nagasakiensis	St. 30	1	160	60		
Pleuronectidae						
Glyptocephalus stelleri	St. 20	2	no data	no data		
Hippoglossoides dubius	St. 20	3	340 – 414	316 – 570	1/1	Larva 23
Hippoglossoides pinetorum	St. 20	2	281 – 431	159 – 625		
Pomacentridae						
Abudefduf sexfasciatus	St. 30	2	150 160	72 82		
Psychrolutidae						
Dasycottus setiger	St. 20	5 (4)	124 – 158	32 – 68	1/2	Larva 33
Malacocottus gibber	St. 20	3	208 – 272	207 – 530		
Salmonidae						
Oncorhynchus keta	St. 1	Examined by investigation of Chapter I			4/63	Larva 35–38
Sebastidae						
Sebastes owstoni	St. 20	4	172 – 283	52 – 190		
Serranidae						
Cephalopholis miniata	St. 30	2	305 – 355	400 – 670		
Cephalopholis urodeta	St. 30	1	240	220		
Epinephelus fasciatus	St. 30	8 (5)	245 – 315	190 – 410	3/24	Larva 6–8
Epinephelus merra	St. 30	2	148 – 170	35 – 67		
Epinephelus retouti	St. 30	4	335 – 375	620 – 850		
Epinephelus tauvina	St. 30	1	265	285		
Variola louti	St. 30	4(3)	320 – 750	320 – 5700	1/1	Larva 2
Scaridae						
Scarus ghobban	St. 30	1	205	160		

Table 24 continued.

Host species	Station	N	Total Length (mm) Min – Max	Weight (g) Min – Max	n	Specimen ID
Scombridae						
Scomber australasicus	St. 19	2	315 – 320	345 – 363	1/1	Larva 1
Siganidae						
Siganus fuscescens	St. 30	1	350	620		
Sparidae						
Pagrus major	St. 19	3	90 – 95	11 – 16		
Sphyraenidae						
Sphyraena pinguis	St. 19	2	135 – 150	9 – 15		
Tetraodontidae						
Lagocephalus lagocephalus	St. 30	2	360 – 365	500 – 570		
Lagocephalus spadiceus	St. 19	2	105 – 115	18 – 27		
Trichiuridae						
Trichiurus japonicus	St. 25	1	no data	no data	1/2	Larva 3
Trichodontidae						
Arctoscopus japonicus	St. 20	3	211 – 272	50 – 163	1/6	Larva 18
Xiphiidae						
Xiphias gladius	St. 31	1	1735	no data	2/104	Larva 28, 29
Zoarcidae						
Bothrocara hollandi	St. 20	6	244 – 294	53 – 89		
Lycodes nakamurai	St. 20	5 (3)	302 – 314	69 – 97	1/22	Larva 32
Lycodes tanakae	St. 20	3 (2)	475 – 784	1350 – 2250		
Lycodes toyamensis	St. 20	3	318 – 380	147 – 235		
Mammalia						
Delphinidae						
Stenella coeruleoalba	St. 25	Examined by investigation of Chapter I			4/7	Larva 39–42

Table 25 List of the specimens for molecular phylogenic analyses of larvae. Species names revised in this study are used. Larvae specimens which collected in this study were given the number to distinguish the individual, Larva 1-42 (see Table 24). Alphabet specific names of *Scyphophyllidium* are undescribed species reported by Jensen & Bullard (2010). Abbreviations of country names in the locality: AUS; Australia, GBR; United Kingdom, JAP; Japan, NZL; New Zealand, MYS; Malaysia, SEN; Senegal, USA; U.S.A.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Adult							
Phyllobothriidea							
Phyllobothrium cf. *lactuca*	*Mustelus mento*	Puerto Montt, CHL	KF685845	-	x		
Phyllobothrium hoshizame	*Mustelus manazo*	off Kanaya, JAP	This study	-	x		
Phyllobothrium serratum	*Triakis scyllium*	off Shimoda, JAP	This study	-	x		
Alexandercestus oomejirozame	*Carcharhinus leucas*	off Yaeyama, JAP	This study	-	x		
Alexandercestus gibsoni	*Negaprion acutidens*	Timor Sea, AUS	KC505623	-	x		
Bilocularia hyperapolytica	*Dalatias licha*	off Kanaya, JAP	This study	-	x		
Calliobothrium cf. *verticillatum*	*Mustelus canis*	Old Lyme, USA	KF685812	-	x		
Calliobothrium shirozame	*Mustelus griseus*	off Shimoda, JAP	This study	-	x		
Calyptrobothrium sp.	*Torpedo nobiliana*	Rhode Island, USA	KF685848	-	x		
Calyptrobothrium sp. 1	*Torpedo tokionis*	off Heda, JAP	This study	-	x		
Chimaerocestos sp. 1	*Rhinochimaera pacifica*	Chatham Rise, NZL	KF685827	-	x		
Chimaerocestos sp. 2	*Rhinochimaera pacifica*	Chatham Rise, NZL	KF685850	-	x		
Crossobothrium laciniatum	*Hexanchus griseus*	Puerto Montt, CHL	KF685824	-	x		
Crossobothrium campanulatum	*Hexanchus griseus*	off Sado I., JAP	This study	-	x		
Crossobothrium dohrnii	*Heptranchias perlo*	off Kanaya, JAP	This study	-	x		
Crossobothrium cf. *dohrnii*	*Heptranchias perlo*	Gulf of Mexico	KF685847	-	x		
Mitsukuricestus gobelinus	*Mitsukurina owstoni*	off Kanaya, JAP	This study	-	x		
Monorygma chamydoselachi	*Chlamydoselachus*	off Kanaya, JAP	This srudy	This srudy	x	x	x
Orygmatobothrium musteli	*Mustelus manazo*	off Heda, JAP	This study	-	x		
	Mustelus griseus	off Chigasaki, JAP	This study	-	x		
Orygmatobothrium cf. *musteli* 1	*Mustelus mustelus*	Soumbédioune, SEN	KF685815	-	x		
Orygmatobothrium cf. *musteli* 2	*Mustelus mustelus*	Ouakam, SEN	KF685816	-	x		

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Pelichnibothrium speciosum	*Prionace glauca*	off Iburi, JAP	This srudy	This srudy	x	x	x
	Prionace glauca	off Iburi, JAP	This srudy	This srudy		x	x
	Alepisaurus ferox	off Toshima I., JAP	This srudy	This srudy	x	x	x
	Alepisaurus ferox	off Toshima I., JAP	This srudy	This srudy		x	x
Pelichnibothrium carcharodoni	*Carcharodon carcharias*	Kaipara Harbour, NZL	HM856633	-	x	x	
	Carcharodon carcharias	off Iburi, JAP	This srudy	This srudy	x	x	x
	Carcharodon carcharias	off Iburi, JAP	This srudy	This srudy		x	x
Pelichnibothrium montaukensis	*Isurus oxyrinchus*	Montauk, New York, USA	AF286996	JQ268541	x	x	x
	Isurus oxyrinchus	off Toshima I., JAP	This srudy	This srudy	x	x	x
	Isurus oxyrinchus	off Toshima I., JAP	This srudy	This srudy		x	x
	Isurus oxyrinchus	off Ogasawara Is., JAP	This srudy	This srudy		x	x
	Isurus oxyrinchus	off Obama, JAP	This srudy	This srudy		x	x
Pelichnibothrium tumidum	*Carcharodon carcharias*	off Iburi, JAP	This srudy	This srudy	x	x	x
	Carcharodon carcharias	off Iburi, JAP	This srudy	This srudy		x	x
Pelichnibothrium cf. *montaukensis*	*Lamna nasus*	Falkland Is., GBR	JF436969	-	x	x	
Scyphophylodium bai	*Mustelus mustelus*	Ouakam Senegal, SEN	KC505625	-	x		
Scyphophyllidium carcharhinus	*Carcharhinus limbatus*	off Yaeyama, JAP	This study	This study	x		
	Carcharhinus leucas	off Yaeyama, JAP	This study	This study	x		
	Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	This study	x		
Scyphophyllidium eirakubuka	*Hemitriakis japanica*	off Shimoda, JAP	This study	This study	x		
Scyphophylodium exiguum	*Alopias vulpinus*	Montauk, New York, USA	KF685769	KF685822	x		
Scyphophylodium guariticus	*Paratrygon aiereba*	Mouth of Rio Shilve, PER	KF685888	KF685817	x		
Scyphophyllidium hanazame	*Carcharhinus brevipinna*	off Iburi, JAP	This study	This study	x		
Scyphophyllidium insulatum	*Carcharhinus plumbeus*	off Yaeyama, JAP	This study	This study	x		
	Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	This study	x		
Scyphophylodium janineae	*Hemigaleus australiensis*	Moreton Bay, AUS	HQ680627	-	x		
Scyphophylodium kirstenae	*Hemigaleus microstoma*	Mukah, Borneo, MYS	KC505626	-	x		
Scyphophyllidium latipi	*Scoliodon macrorhynchus*	Mukah, Borneo, MYS	KF685853	-	x		
Scyphophyllidium longiproglottius	*Carcharhinus limbatus*	off Yaeyama, JAP	This study	-	x		

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Scyphophyllidium maritimum	*Carcharhinus brevipinna*	off Iburi, JAP	This study	-	x		
	Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	-	x		
Scyphophyllidium nenuribuka	*Triaenodon obesus*	off Ogasawara Is., JAP	This study	-	x		
Scyphophyllidium ogasawaraensis	*Triaenodon obesus*	off Ogasawara Is., JAP	This study	-	x		
	Carcharhinus galapagensis	off Ogasawara Is., JAP	This study	-	x		
Scyphophylodium paulum	*Galeocerdo cuvier*	off Iburi, JAP	This study	-	x		
	Galeocerdo cuvier	Moreton Bay, AUS	HQ680630	-	x		
Scyphophylodium prionacis	*Prionace glauca*	Montauk, New York, USA	KF685818	-	x		
	Prionace glauca	off Tosashimizu, JAP	This study	-	x		
Scyphophylodium randyi	*Chiloscyllium hasseltii*	Mukah, Borneo, MYS	KF685820	-	x		
Scyphophyllidium sumitukizame	*Carcharhinus dussumieri*	off Tosasaga, JAP	This study	-	x		
Scyphophylodium triacis	*Triakis scyllium*	off Shimoda, JAP	This study	-	x		
Scyphophylodium taylori	*Hemigaleus australiensis*	Moreton Bay, AUS	HQ680633	-	x		
Scyphophylodium tyleri	*Chiloscyllium punctatum*	Mukah, Borneo, MYS	KF685819	-	x		
Scyphophyllidium yogore	*Carcharhinus longimanus*	off Yaeyama, JAP	This study	-	x		
Scyphophylodium sp. A	*Carcharhinus brevipinna*	Gulf of Mexico, USA	GQ470001	-	x		
Scyphophylodium sp. B	*Carcharhinus brevipinna*	Gulf of Mexico, USA	GQ470031	-	x		
	Carcharhinus isodon	Gulf of Mexico, USA	GQ470037	-	x		
	Carcharhinus limbatus	Gulf of Mexico, USA	GQ470034	-	x		
	Rhizoprionodon terraenovae	Gulf of Mexico, USA	GQ470033	-	x		
Scyphophylodium sp. C	*Rhizoprionodon terraenovae*	Gulf of Mexico, USA	GQ470020	-	x		
Scyphophylodium sp. D	*Carcharhinus brevipinna*	Gulf of Mexico, USA	GQ470011	-	x		
	Carcharhinus limbatus	Gulf of Mexico, USA	GQ470005	-	x		
	Rhizoprionodon terraenovae	Gulf of Mexico, USA	GQ470006	-	x		
Scyphophyllidium cf. *giganteum*	*Galeorhinus galeus*	Chatham Rise, NZL	KF685854	-	x		
Scyphophylodium sp.	*Alopias pelagicus*	Santa Rosalia, MEX	KF685821	-	x		
Symcallio violae	*Mustelus canis*	Old Lyme, USA	KF685813	-	x		
Thysanocephalum thysanocephalum	*Galeocerdo cuvier*	off Yaeyama, JAP	This study	-	x		
	Galeocerdo cuvier	off Iburi, JAP	KF685823	-	x		

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Trilocularia gracilis	*Squalus acanthias*	Rhode I., USA	KF685855	-	x		
Yamaguticestus squali	*Cephaloscyllium umbratile*	off Heda, JAP	This study	-	x		
	Cephaloscyllium umbratile	off Heda, JAP	This study	-	x		
	Cephaloscyllium umbratile	off Kanaya, JAP	This study	-	x		
	Galeus nipponensis	off Kanaya, JAP	This study	-	x		
	Squalus acanthias	Rhode Island, USA	KF685846	-	x		
	Squalus japonicus	off Kanaya, JAP	This study	-	x		
	Squalus japonicus	off Mimase, JAP	This study	-	x		
	Squalus mitsukurii	off Kanaya, JAP	This study	-	x		
	Squalus mitsukurii	off Kanaya, JAP	This study	-	x		
Vertebraeovicestus dobukasube	*Bathyraja smirnovi*	off Oki Is., JAP	This study	-	x		
"Phyllobothriidea gen. sp."	*Sphyrna lewini*	Straits of Florida, USA	KF685814	-	x		
Tetraphyllidea							
Anthobothrium caseyi	*Prionace glauca*	Montauk, New York, USA	KF685805	-	x		
	Prionace glauca	off Tosashimizu, JAP	This study	-	x		
Anthobothrium sp. 1	*Carcharhinus tilstoni*	Wessel Is., AUS	KF685806	-	x		
Anthobothrium sp. 2	*Carcharhinus brevipinna*	off Iburi, JAP	This study	-	x		
Anthobothrium sp. 3	*Carcharhinus plumbeus*	off Yaeyama, JAP	This study	-	x		
Anthobothrium sp. 4	*Carcharhinus brevipinna*	off Iburi, JAP	This study	-	x		
Anthobothrium sp. 5	*Carcharhinus dussumieri*	off Tosasaga, JAP	This study	-	x		
Balanobothrium sp.	*Stegostoma fasciatum*	Mukah, Borneo, MYS	KF685802	-	x		
Ceratobothrium xanthocephalum	*Isurus oxyrinchus*	Montauk, New York, USA	KF685849	-	x		
Ceratobothrium sp. 1	*Carcharodon carcharias*	off Iburi, JAP	This study	-	x		
Megalonchos shawae	*Hemipristis elongata*	Wessel Is., AUS	KF685807	-	x		
Pachybothrium hutsoni	*Nebrius ferrugineus*	Weipa, AUS	EF095246	-	x		
Pedibothrium mounseyi	*Nebrius ferrugineus*	Weipa, AUS	KF685803	-	x		
Yorkeria hilli	*Chiloscyllium punctatum*	Cairns, AUS	KF685798	-	x		
Rosebothrium ootenjikuzame	*Nebrius ferrugineus*	off Yaeyama, JAP	This study	-	x		

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Onchoproteocephalidea							
Acanthobothrium parviuncinatum	*Urobatis maculatus*	Bahia de Los Angeles, MEX	EF095250	-	x		
Acanthobothrium santarosaliense	*Heterodontus mexicanus*	Santa Rosalia, MEX	KF685834	-	x		
Peltidocotyle rugosa	*Pseduoplatystoma fasciatum*	Rio Paraguay, PRY	AF286989	-	x		
Phoreiobothrium lewinense	*Sphyrna lewini*	Straits of Florida, USA	KF685830	-	x		
Platybothrium auriculatum	*Prionace glauca*	Montauk, New York, USA	KF685837	-	x		
Platybothrium jondoeorum	*Negaprion acutidens*	Darwin, AUS	KF685829	-	x		
Potamotrygonocestus cf. *fitzgeraldae*	*Potamotrygon castexi*	Madre de Dios River, PEL	KF685832	-	x		
Prosobothrium armigerum	*Prionace glauca*	Montauk, New York, USA	KF685828	-	x		
Proteocephalus macrocephalus	*Anguilla anguilla*	River Thames, GBR	EF095247	-	x		
Proteocephalus perplexus	*Amia calva*	Hay Bay, CAN	KF685833	-	x		
Triloculatum andersonorum	*Negaprion acutidens*	Weipa, AUS	KF685831	-	x		
Uncibilocularis okei	*Pastinachus atrus*	Dundee Beach, AUS	KF685835	-	x		
Onchoproteocephalidea gen. sp.	*Pristis clavata*	Darwin, AUS	KF685836	-	x		
Cathetocephalidea							
Cathetocephalus thatcheri	*Carcharhinus leucas*	Gulf of Mexico, USA	KF685838	-	x		
Rhinebothriidea							
Anthocephalum biacetabulatum	*Rhinobatos schlegelii*	off Chigasaki, JAP	This study	-	x		
Anthocephalum cf. *centrurum*	*Dasyatis centroura*	Mbour, SEN	FJ177059	-	x		
Rhinebothrium megacanthophallus	*Himantura polylepis*	Kinabatangan River, MSY	FJ177080	-	x		
Rhodobothrium paucitesticulare	*Rhinoptera bonasus*	Davis, USA	FJ177060	-	x		
Lecanicephalidea							
Adelobothrium cf. *aetiobatidis*	*Aetobatus ocellatus*	Darwin, AUS	EF095249	-	x		
Paraberrapex manifestus	*Squatina californica*	Santa Rosalia, MEX	KF685781	-	x		
Litobothriidea							
Litobothrium amplifica	*Alopias pelagicus*	Santa Rosalia, MEX	KF685843	-	x		
Litobothrium nickoli	*Alopias pelagicus*	Santa Rosalia, MEX	KF685844	-	x		

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Plerocercoid							
Pelichnibothrium carcarodoni	*Grampus griseus*	Spain	GQ839587	-	x	x	
	Stenella coeruleoalba	Spain	GQ839588	-	x	x	
Pelichnibothrium caudatum -Larva 35	*Oncorhynchus keta*	off Erimo, JAP	This srudy	This srudy	x	x	x
-Larva 36	*Oncorhynchus keta*	off Erimo, JAP	This srudy	This srudy		x	x
-Larva 37	*Oncorhynchus keta*	off Erimo, JAP	This srudy	This srudy		x	x
-Larva 38	*Oncorhynchus keta*	off Erimo, JAP	This srudy	This srudy		x	x
Pelichnibothrium cf. *montaukensis*	*Doryteuthis gahi*	Falkland Is., GBR	AF382072	-	x	x	
	Regalecus glesne	Santa Catalina I., USA	KM272992	-	x	x	
Scyphophylodium sp. C	*Trichiurus lepturus*	Gulf of Mexico, USA	GQ470022	-	x		
Scyphophylodium sp. D	*Lobotes surinamensis*	Gulf of Mexico, USA	GQ470014	-	x		
	Paralichthys lethostigma	Gulf of Mexico, USA	GQ470008	-	x		
Plerocercoid -Larva 1	*Scomber australasicus*	off Maizuru, JAP	This srudy	-	x		
-Larva 2	*Variola louti*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 3	*Trichiurus japonicus*	off Kubotsu, JAP	This srudy	-	x		
-Larva 4	*Trachurus japonicus*	off Maizuru, JAP	This srudy	-	x		
-Larva 5	*Coryphaena hippurus*	off Maizuru, JAP	This srudy	-	x		
-Larva 6	*Epinephelus fasciatus*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 7	*Epinephelus fasciatus*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 8	*Epinephelus fasciatus*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 9	*Thalassoma lutescens*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 10	*Coris aygula*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 11	*Berryteuthis magister*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 12	*Berryteuthis magister*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 13	*Berryteuthis magister*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 14	*Watasenia scintillans*	off Toyama, JAP	This srudy	This srudy	x	x	x
-Larva 15	*Bathyraja smirnovi*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 16	*Bathyraja smirnovi*	off Oki Is., JAP	This srudy	This srudy	x	x	x

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Plerocercoid -Larva 17	*Gadus macrocephalus*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 18	*Arctoscopus japonicus*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 19	*Careproctus trachysomai*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 20	*Aptocyclus ventricosus*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 21	*Aptocyclus ventricosus*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 22	*Eumicrotremus asperrimus*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 23	*Hippoglossoides dubius*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 24	*Alepisaurus ferox*	off Toshima I., JAP	This srudy	This srudy	x	x	x
-Larva 25	*Alepisaurus ferox*	off Toshima I., JAP	This srudy	This srudy	x	x	x
-Larva 26	*Todarodes pacificus*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 27	*Berryteuthis magister*	off Oki Is., JAP	This srudy	This srudy	x	x	x
-Larva 28	*Xiphias gladius*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 29	*Xiphias gladius*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 30	*Taractichthys steindachneri*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 31	*Taractichthys steindachneri*	off Ogasawara Is., JAP	This srudy	-	x		
-Larva 32	*Lycodes nakamurae*	off Oki Is., JAP	This srudy	-	x		
-Larva 33	*Dasycottus setiger*	off Oki Is., JAP	This srudy	-	x		
-Larva 34	*Coryphaena hippurus*	off Maizuru, JAP	This srudy	-	x		
Plerocercoid	*Ariopsis felis*	Gulf of Mexico, USA	GQ470051	-	x		
	Cynoscion nebulosus	Gulf of Mexico, USA	GQ470049	-	x		
	Opsanus beta	Gulf of Mexico, USA	GQ470030	-	x		
	Stenella coeruleoalba	Spain	DQ839568	-	x	x	
	Grampus griseus	Spain	DQ839573	-	x	x	
	Tursiops truncatus	Spain	DQ839580	-	x	x	

Table 25 continued.

Specimens	Host species	Locality	Accession Number		Dataset		
			lsrDNA	COI	3	4	5
Merocercoid							
Pelichnibothrium delphini - Larva 39	*Stenella coeruleoalba*	Minami-satsuma, JAP	This srudy	This srudy	x	x	x
- Larva 40	*Stenella coeruleoalba*	Minami-satsuma, JAP	This srudy	This srudy		x	x
	Stenella coeruleoalba	Spain	AY741599	-	x	x	
	Grampus griseus	Spain	DQ839593	-	x	x	
	Tursiops truncatus	Spain	DQ839590	-	x	x	
Pelichnibothrium grimaldii - Larva 41	*Stenella coeruleoalba*	Minami-satsuma, JAP	This srudy	This srudy	x	x	x
- Larva 42	*Stenella coeruleoalba*	Minami-satsuma, JAP	This srudy	This srudy		x	x
	Stenella coeruleoalba	Spain	AY741591	-	x	x	
	Grampus griseus	Spain	DQ839585	-	x	x	
	Tursiops truncatus	Spain	DQ839582	-	x	x	

Table 26 Sequence data of lsrDNA of plerocercoid, merocercoid, and adult *Pelichnibothrium*. Only variable sites are shown, and numbers indicate the positions. Question marks mean missing sites.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

Table 27 List of phyllobothriidean species having multiple final host species. Abbreviations of host order names in order: Car; Carcharinidae, Etm; Etomopteridae, Hex; Hexanchidae, Odo; Odontaspididae, Tri; Triakidae, Scy; Scyliorhinidae, Squ; Squalidae.

本表については，5年以内に雑誌等で刊行予定のため，非公開.

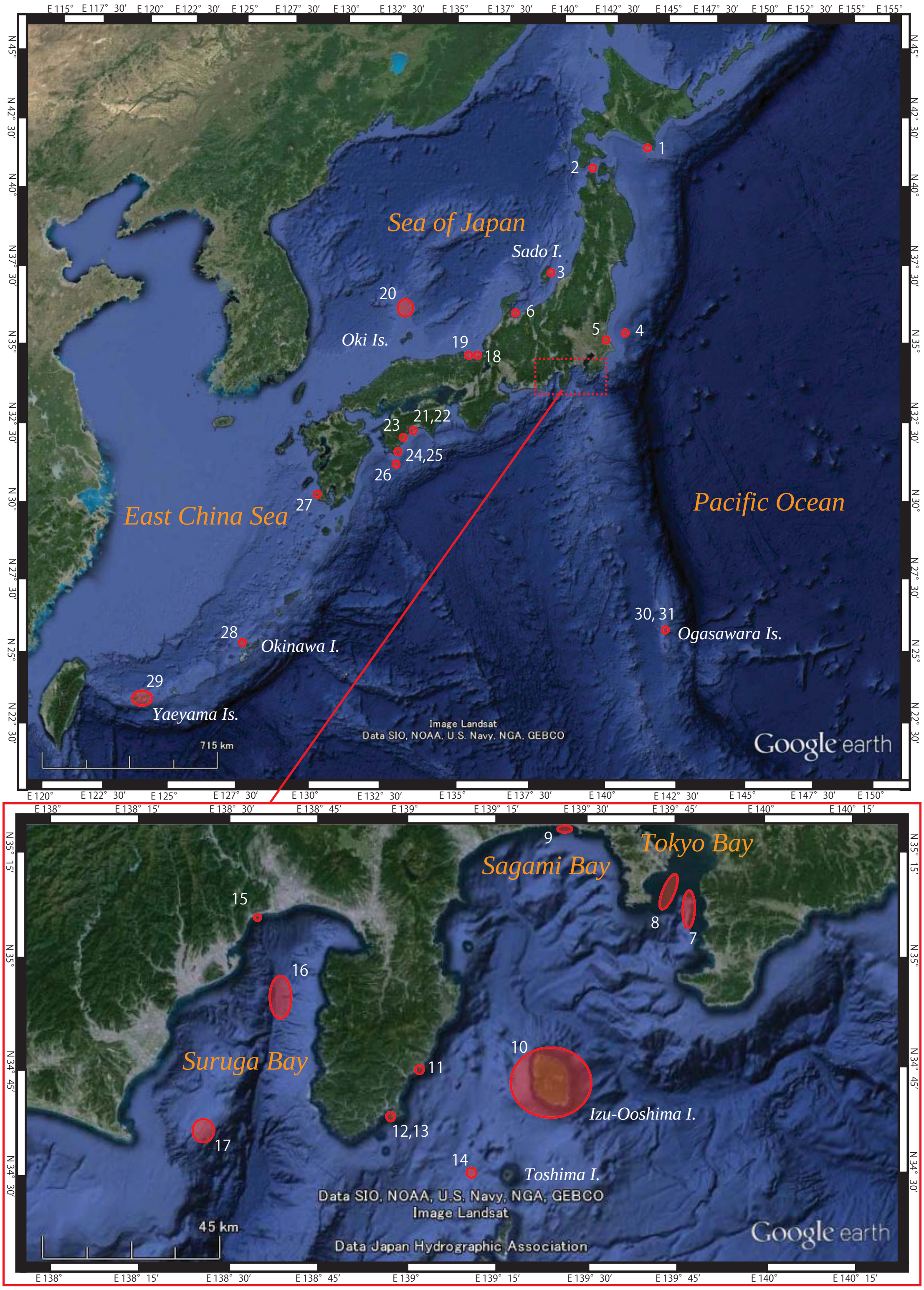

Fig. 1 Sampling locality. Circles show sampling locality, and numbers denote the station number in Table 4. See Table 4 for the detailed information on each station.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 2 Morphological terminology of Phyllobothriidea. **A**, Whole worm (*Scyphophyllidium brevipinnacis*), **B**, Scolex (*Pelichnibothrium speciosum*), **C**, Scolex (*Orygmatobothrium musteli*), **D**, Scolex (*Mitsukuricestus gobelinus*), **E**, Mature proglottid (*Sc. brevipinnacis*), **F**, Free proglottid (*Pe. speciosum*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 3 Maximum likelihood tree by Analysis 1 (Dataset 1, ssrDNA and lsrDNA). UFBootstrap and BPP are shown at each branch, and hyphens indicate branches which were not observed in the bayesian tree. Red arrowhead shows the node of the clade of revised order supported by SH aLRT ≥80 (see Table 8). Current scientific names are used and some of them were revised in this study (see Table 15). Sequences obtained in this study are shown in black color, and those collected from GenBank are in gray color. Open and solid circles near species names indicate the current order sensu Caira et al. (2014), Phyllobothriidea and Tetraphyllidea, respectively. Open boxes indicate the revised orders in this study (see Section 3.3). Polyphyletic genera are shown by dotted lines: A, *Phyllobothrium*; B, *Clistobothrium*; C, *Monorygma*; D, *Marsupiobothrium*; E, *Paraorygmatobothrium*.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 4 Maximum likelihood tree by Analysis 2 (Dataset 1, ssrDNA). See Fig. 3 for the explanations of symbols in the tree. Phyllobothriidea, Tetraphyllidea and Onchoproteocephalidea were polyphyletic in this analysis (connected by dotted lines).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 5 Maximum likelihood tree by Analysis 3 (Dataset 1, lsrDNA). See Fig. 3 for the explanations of symbols in the tree. Phyllobothriidea were polyphyletic in this analysis (connected by dotted lines).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 6 Maximum likelihood tree by Analysis 4 (Dataset 2, ssrDNA and lsrDNA). See Fig. 3 for the explanations of symbols in the tree.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 7 Maximum likelihood tree by Analysis 5 (Dataset 2, ssrDNA). See Fig. 3 for the explanations of symbols in the tree. Phyllobothriidea were polyphyletic in this analysis (connected by dotted lines).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 8 Maximum likelihood tree by Analysis 6 (Dataset 2, lsrDNA). See Fig. 3 for the explanations of symbols in the tree. Phyllobothriidea were polyphyletic in this analysis (connected by dotted lines).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 9 Phylogenetic consideration of the hook in Phyllobothriidea and related orders. Based on the tree of Analysis 1 (Fig. 3), robust nodes (UFBoot ≥95 or BPP ≥0.98) are shown by solid circles, and the other nodes are shown by open circles. Hooked taxa are shown in red color, and non-hooked taxa are shown in black. Open boxes show the revised orders (see Section 3.3).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 10 Phylogenetic consideration of the bothridium types in the revised Phyllobothriidea. Based on the tree of Analysis 1 (Fig. 3), robust nodes (UFBoot ≥95 or BPP ≥0.99) are shown by solid circles, and the other nodes are shown by open circles. Colors show bothridium types: black, flat; blue, crumple; pink, cup; green, divided; light green, loculate margin; purple, sac.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 11 Phylogenetic consideration of the types of bothridium base in the revised Phyllobothriidea. See Fig. 10 for the explanations of the tree. Stalked taxa are shown in red color, and sessile taxa are shown in black.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 12 Phylogenetic consideration of the laciniation in Phyllobothriidea. See Fig. 10 for the explanations of the tree. Laciniated taxa were shown by red color, and non-lacinated taxa shown by black.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 13 Phylogenetic consideration of the additional suckers and the reduced suckers in Phyllobothriidea. See Fig. 10 for the explanations of the tree. Colors show additional suckers: black, general; blue, apical sucker; yellow, central sucker; green, no sucker.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 14 Revision of the genera in the revised Phyllobothriidea. The phylogenetic tree was based on Analysis 1 (Fig. 3). Bars indicate the revised genera. Type species of the current genera are shown in bold face. Robust nodes (UFBoot ≥95 or BPP ≥0.98) are shown by solid circles and thick lines, and the other nodes are shown by open circles and thin lines.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 15 *Phyllobothrium hoshizame* n. sp. **A**, Scolex, **B**, Mature proglottid, No. *Mustelus manazo* 27 (Host: *Mustelus manazo*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 16 *Phyllobothrium serratum*. **A**, Scolex, No. *Triakis scyllium* 32 (Host: *Triakis scyllium*). **B**, Mature proglottid, **C**, Gravid proglottid, **D**, Eggs, MPM 22715, SY7159 (Host: *Triakis scyllium*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 17 *Alexandercestus oomejirozame* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Carcharhinus leucas* 10 (Host: *Carcharhinus leucas*). Overlapping vitelline follicles are not drawn on the left side of a broken line.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 18 *Bilocularia hyperapolytica*. **A**, Scolex, No. *Dalatias licha* 15 (Host: *Dalatias licha*). **B**, Free proglottid, **C**, Egg, No. *Dalatias licha* 16 (Host: *Dalatias licha*).

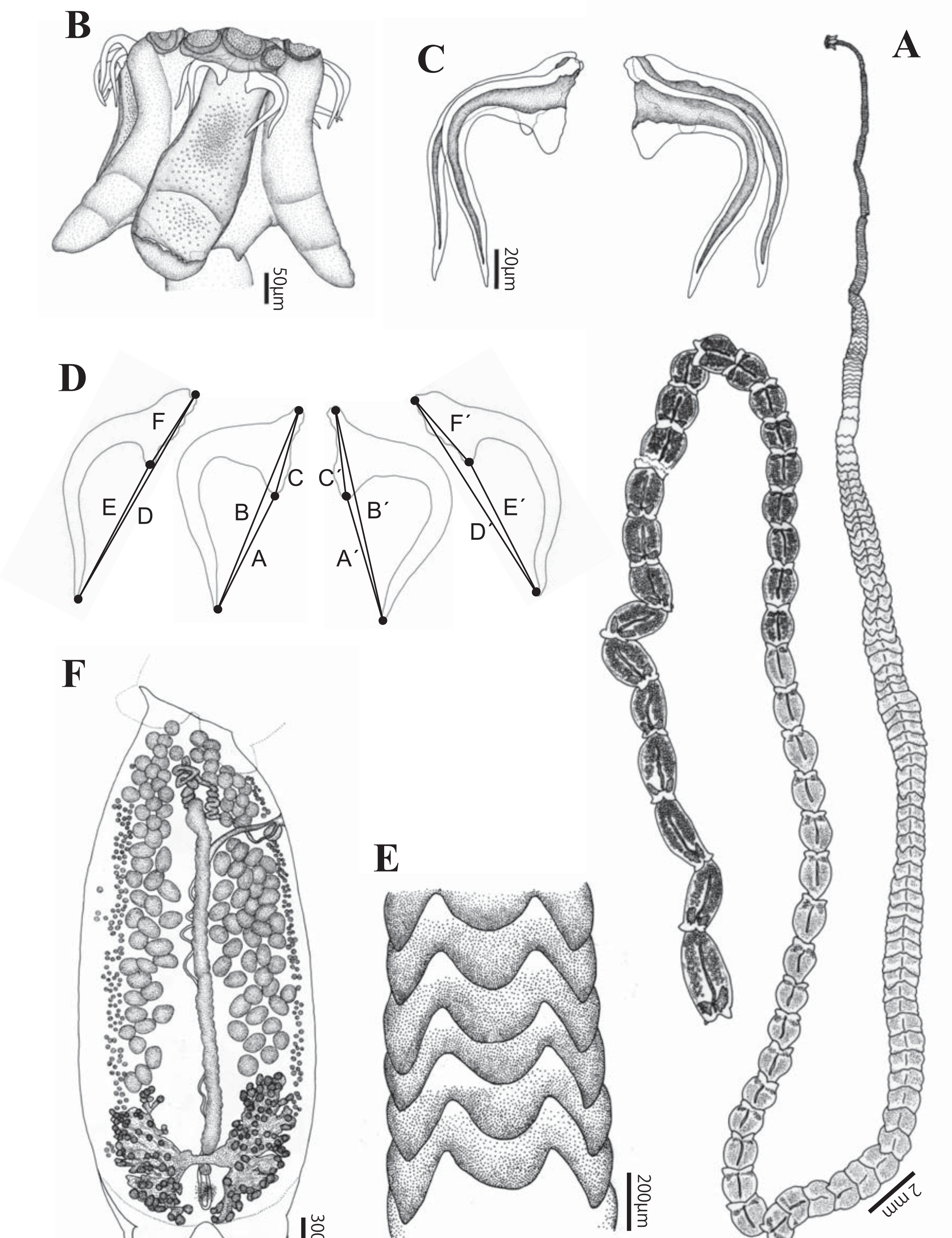

Fig. 19 *Calliobothrium shirozame* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Hook, **D**, Hook measurements, letters reflect those used in the description, **E**, Mature proglottid, **F**, Lacination, NSMT-Pl 6037 (Host: *Mustelus griseus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 20 *Calyptrobothrium* sp. Scolex, No. *Torpedo tokionis* 1 (Host: *Torpedo tokionis*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 21 *Crossobothrium campanulatum*. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, **D**, Egg, No. *Hexanchus griseus* 1 (Host: *Hexanchus griseus*). Overlapping vitelline follicles are not drawn on the right side of a broken line.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 22 *Crossobothrium dohrni*. **A**, Whole worm, No. *Heptranchias perlo* 23 (Host: *Heptranchias perlo*). **B**, Scolex, **B-1**, Scolex with opened bothridia, No. *Heptranchias perlo* 23 (Host: *Heptranchias perlo*). **B-2**, Scolex with closed bothridia, **C**, Mature proglottid, No. *Heptranchias perlo* 20 (Host: *Heptranchias perlo*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 23 *Mitsukuricestus gobelinus* n. comb. **A**, Whole worm, No. *Miysukurina owstoni* 4 (Host: *Miysukurina owstoni*). **B**, Scolex, No. *Miysukurina owstoni* 1 (Host: *Miysukurina owstoni*). **C**, Mature proglottid, No. *Miysukurina owstoni* 4 (Host: *Miysukurina owstoni*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 24 *Monorygma chlamydoselachi*. **A**, Whole worm, No. *Chlamydoselachus anguineus* 1 (Host: *Chlamydoselachus anguineus*). **B**, Scolex, No. *Chlamydoselachus anguineus* 9 (Host: *Chlamydoselachus anguineus*). **C**, Mature proglottid, No. *Chlamydoselachus anguineus* 10 (Host: *Chlamydoselachus anguineus*). **D**, Egg, No. *Chlamydoselachus anguineus* 1 (Host: *Chlamydoselachus anguineus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 25 *Orygmatobothrium musteli*. **A**, Whole worm, No. *Mustelus manazo* 8 (Host: *Mustelus manazo*). **B**, Scolex, **C**, Mature proglottid, No. *Mustelus griseus* 20 (Host: *Mustelus griseus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 26 *Pelichinibothrium speciosum.* **A**, Whole worm, No. *Prionace glauca* 29 (Host: *Prionace glauca*). **B**, Mature proglottid, MPM 23879, SY3102 (Host: *Prionace glauca*). **C**, Free proglottid, MPM 23879, SY5624 (Host: *Prionace glauca*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 27 *Pelichinibothrium speciosum*. **A**, Whole worm, **B**, Mature proglottid, No. *others* 365 (Host: *Alepisaurus ferox*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 28 *Pelichinibothrium carcharodoni* n. comb. **A**, Whole worm, No. *Carcharodon carcharias* 19 (Host: *Carcharodon carcharias*). **B**, Mature proglottid, No. *Carcharodon carcharias* 15 (Host: *Carcharodon carcharias*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 29 *Pelichnibothrium caudatum*. **A**, Plerocercoid, No. *others* 512 (Host: *Onchorhynchus keta*). **B**, Plerocercoid, **C**, Plerocercoid, No. *others* 61 (Host: *Berryteuthis magister*). **D**, Plerocercoid, No. *others* 101 (Host: *Gadus macrocephalus*), **E**, Plerocercoid, arrow showed site which caused initial proglottization, **F**, Proglottids, No. *others* 68 (Host: *Aptocyclus ventricosus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 30 *Pelichinibothrium delphni* n. comb. Merocercoid, No. *others* 629 (Host: *Stenella coeruleoalba*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 31 *Pelichinibothrium grimaldii* n. comb. **A**, Merocercoid, **B**, Scolex, No. *others* 633 (Host: *Stenella coeruleoalba*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 32 *Pelichinibothrium montaukensis* n. comb. **A**, Whole worm, No. *Isurus oxyrinchus* 18 (Host: *Isurus oxyrinchus*). **B**, Scolex, No. *Isurus oxyrinchus* 1 (Host: *Isurus oxyrinchus*). **C**, Mature proglotiid, No. *Isurus oxyrinchus* 18 (Host: *Isurus oxyrinchus*). Overlapping vitelline follicles are not drawn on the right side of a broken line. **D**, Juvenil worm, No. *Isurus oxyrinchus* 25 (Host: *Isurus oxyrinchus*). **E**, Plerocercoid, No. *others* 343 (Host: *Alepisaurus ferox*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 33 *Pelichinibothrium tumidum* n. comb. **A**, Whole worm, No. *Carcharodon carcharias* 12 (Host: *Carcharodon carcharias*). **B**, Scolex, No. *Carcharodon carcharias* 7 (Host: *Carcharodon carcharias*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 34 *Scyphophyllidium carcharhinus* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Carcharhinus limbatus* 14 (Host: *Carcharhinus limbatus*). **D**, Plerocercoid, No. *othres* 426 (Host: *Coryphaena hippurus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 35 *Scyphophyllidium eirakubuka* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Hemitriakis japanica* 64 (Host: *Hemitriakis japanica*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 36 *Scyphophyllidium hanazame* n. sp. **A**, Whole worm, *Carcharhinus brevipinna* 11 (Host: *Carcharhinus brevipinna*). **B**, Scolex, No. *Carcharhinus brevipinna* 74 (Host: *Carcharhinus brevipinna*). **C**, Mature proglottid, No. *Carcharhinus brevipinna* 11 (Host: *Carcharhinus brevipinna*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 37 *Scyphophyllidium insulaeum* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Carcharias galapagensis* 3 (Host: *Carcharias galapagensis*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 38 *Scyphophyllidium longiproglottidum* n. sp. **A**, Whole worm, **B**, Mature proglottid, No. *Carcharhinus limbatus* 6 (Host: *Carcharhinus limbatus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 39 *Scyphophyllidium maritimum* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Carcharhinus brevipinna* 78 (Host: *Carcharhinus brevipinna*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 40 *Scyphophyllidium nemuribuka* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Triaenodon obesus* 26 (Host: *Triaenodon obesus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 41 *Scyphophyllidium ogasawaraensis* n. sp. **A**, Whole worm, No. *Triaenodon obesus* 27 (Host: *Triaenodon obesus*). **B**, Scolex, **C**, Mature proglottid, No. *Triaenodon obesus* 6 (Host: *Triaenodon obesus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 42 *Scyphophyllidium paulum* n. com. **A**, Whole worm, No. *Galeocerdo cuvier* 7 (Host: *Galeocerdo cuvier*). **B**, Scolex, **C**, Mature proglottid, No. *Galeocerdo cuvier* 5 (Host: *Galeocerdo cuvier*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 43 *Scyphophyllidium prionacis* n. comb. **A**, Whole worm, No. *Prionace glauca* 24 (Host: *Prionace glauca*). **B**, Scolex, **C**, Mature proglottid, No. *Prionace glauca* 23 (Host: *Prionace glauca*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 44 *Scyphophyllidium sumitsukizame* n. sp. **A**, Whole worm, No. *Carcharhinus dussumieri* 14 (Host: *Carcharhinus dussumieri*). **B**, Scolex, No. *Carcharhinus dussumieri* 11 (Host: *Carcharhinus dussumieri*). **C**, Mature proglottid, No. *Carcharhinus dussumieri* 14 (Host: *Carcharhinus dussumieri*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 45 *Scyphophyllidium triacis* n. comb. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Triakis scyllium* 27 (Host: *Triakis scyllium*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 46 *Scyphophyllidium yogore* n. sp. **A**, Scolex, **B**, Mature proglottid, No. *Carcharhinus longimanus* 9 (Host: *Carcharhinus longimanus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 47 *Thysanocephalum thysanocephalum*. **A**, Whole worm, No. *Galeocerdo cuvier* 8 (Host: *Galeocerdo cuvier*). **B**, Scolex, No. *Galeocerdo cuvier* 1 (Host: *Galeocerdo cuvier*). **C**, Mature proglottid, No. *Galeocerdo cuvier* 8 (Host: *Galeocerdo cuvier*). Overlapping vitelline follicles are not drawn on the right side of a broken line. **D**, Egg, No. *Galeocerdo cuvier* 24 (Host: *Galeocerdo cuvier*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 48 *Vertebraeovicestus dobukasube* n. sp. **A**, Whole worm, No. *Bathyraja smirnovi* 11 (Host: *Bathyraja smirnovi*). **B**, Scolex, No. *Bathyraja smirnovi* 13 (Host: *Bathyraja smirnovi*). **C**, Mature proglottid, No. *Bathyraja smirnovi* 11 (Host: *Bathyraja smirnovi*). Overlapping vitelline follicles are not drawn on the left side of a broken line. **D**, Eggs, No. *Bathyraja smirnovi* 13 (Host: *Bathyraja smirnovi*). **E**, Plerocercoid, No. *others* 34 (Host: *Lycodes nakamurae*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 49 *Yamaguticestus squali* n. comb. **A**, Whole worm, No. *Squalus japonicus* 11 (Host: *Squalus japonicus*). **B**, Scolex, No. *Squalus japonicus* 62 (Host: *Squalus mitsukurii*). **C**, Mature proglottid, **D**, Free proglottid, No. *Squalus japonicus* 11 (Host: *Squalus japonicus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 50 *Yamaguticestus squali* n. comb. **A**, Whole worm, No. *Cephaloscyllium umbratile* 56 (Host: *Cephaloscyllium umbratile*). **B**, Scolex, No. *Cephaloscyllium umbratile* 19 (Host: *Cephaloscyllium umbratile*). **C**, Mature proglottid, No. *Cephaloscyllium umbratile* 11 (Host: *Cephaloscyllium umbratile*). **D**, Eggs, No. *Cephaloscyllium umbratile* 5 (Host: *Cephaloscyllium umbratile*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 51 *Rosebothrium ootenjikuzame* n. sp. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, **D**, Microtriches in cirrus, No. *Nebrius ferrugineus* 2 (Host: *Nebrius ferrugineus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 52 *Anthocephalum biacetabulatum* n. comb. **A**, Whole worm, **B**, Scolex, **C**, Mature proglottid, No. *Rhinobatos schlegelii* 31 (Host: *Rhinobatos schlegelii*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 53 Morphological terminology of larvae. Phyllobothriidean larvae, **A**, Plerocercoid of *Vertebraeovicestus dobukasube*; **B**, Plerocercoid of *Pelichnibothrium* cf. *montaukensis*; **C**, Merocercoid of *Pelichnibothrium delphini*. Tetraphyllidean larva, **D**, Plerocercoid of *Anthobothrium* sp. L3.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 54 Maximum likelihood tree using Dataset 3 (lsrDNA). Bootstrap values and BPP are shown at each branch, and hyphens indicate branches which were not observed in the Bayesian Inference tree. Larval sequences obtained in this study are shown in red color, adult sequences obtained in this study are shown in black color, and those collected from GenBank are in gray color. Open boxes indicate the revised orders. Solid bars indicate species which identified by this study. *Pelichnibothrium* clade is shown by dotted lines.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 55 Maximum likelihood tree of *Pelichnibothrium* clade using Dataset 4 (lsrDNA). See Fig. 54 for the explanations of trees and open box. Solid bars indicate clades of each species clades.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 56 Maximum likelihood tree of *Pelichnibothrium* clade using Dataset 5 (mtDNA COI). See Fig. 54 for the explanations of trees and open box. Solid bars indicate clades of each species clades.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 57 Plerocercoids. **A**. *Pelichnibothrium* cf. *montaukensis*, No. *others* 52 (Host: *Todarodes pacificus*). **B**. Phyllobothriidae gen. sp. L1, No. *others* 577 (Host: *Xiphias gladius*). **C**. Phyllobothriidae gen. sp. L2, No. *others* 99 (Host: *Dasycottus setiger*). **D**. *Anthobothrium* sp. L3, No. *others* 390 (Host: *Trichiurus japonicus*), **E**. *Anthobothrium* sp. L4, No. *others* 430 (Host: *Coryphaena hippurus*). **F**. *Anthobothrium* sp. L5, No. *others* 132 (Host: *Epinephelus fasciatus*). **G**. *Anthobothrium* sp. L5, No. *others* 553 (Host: *Coris aygula*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 58 Morphological variation of the scolex of plerocercoids of *Pelichnibothrium caudatum*. **A**, flatted bothridium, No. *others* 48 (Host: *Hippoglossoides dubius*). **B**, flatted bothridium, No. *others* 29 (Host: *Careproctus trachysoma*). **C**, slightly crumpled bothridium, No. *others* 22 (Host: *Aptocyclus ventricosus*).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 59 Invagination of scolex of *Pelichnibothrium caudatum*, No. *others* 527 (Host: *Onchorhynchus keta*). Pictures were arranged in time series from left to right. Drawings were given to show outlines of the body and organs for pictures of 0 sec and 30 sec.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 60 Life cycle of *Pelichnibothrium montaukensis*. Arrows show the flow of life cycle, black arrows show the free-living flows, red arrows show host transportation by food web. Squares show host, life stages in the square are a parasitic stage.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 61 Life cycle of *Pelichnibothrium* cf. *montaukensis*. The information was followed as Fig. 60.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 62 Life cycle of *Pelichnibothrium carcharodoni*. The information was followed as Fig. 60.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 63 Life cycle of *Pelichnibothrium speciosum*. The other information was followed as Fig. 60.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 64 Life cycle of *Scyphophyllidium carcharhinus*. The other information was followed as Fig. 60.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 65 Life cycle of *Vertebraeovicestus dobukasube*. The other information was followed as Fig. 60.

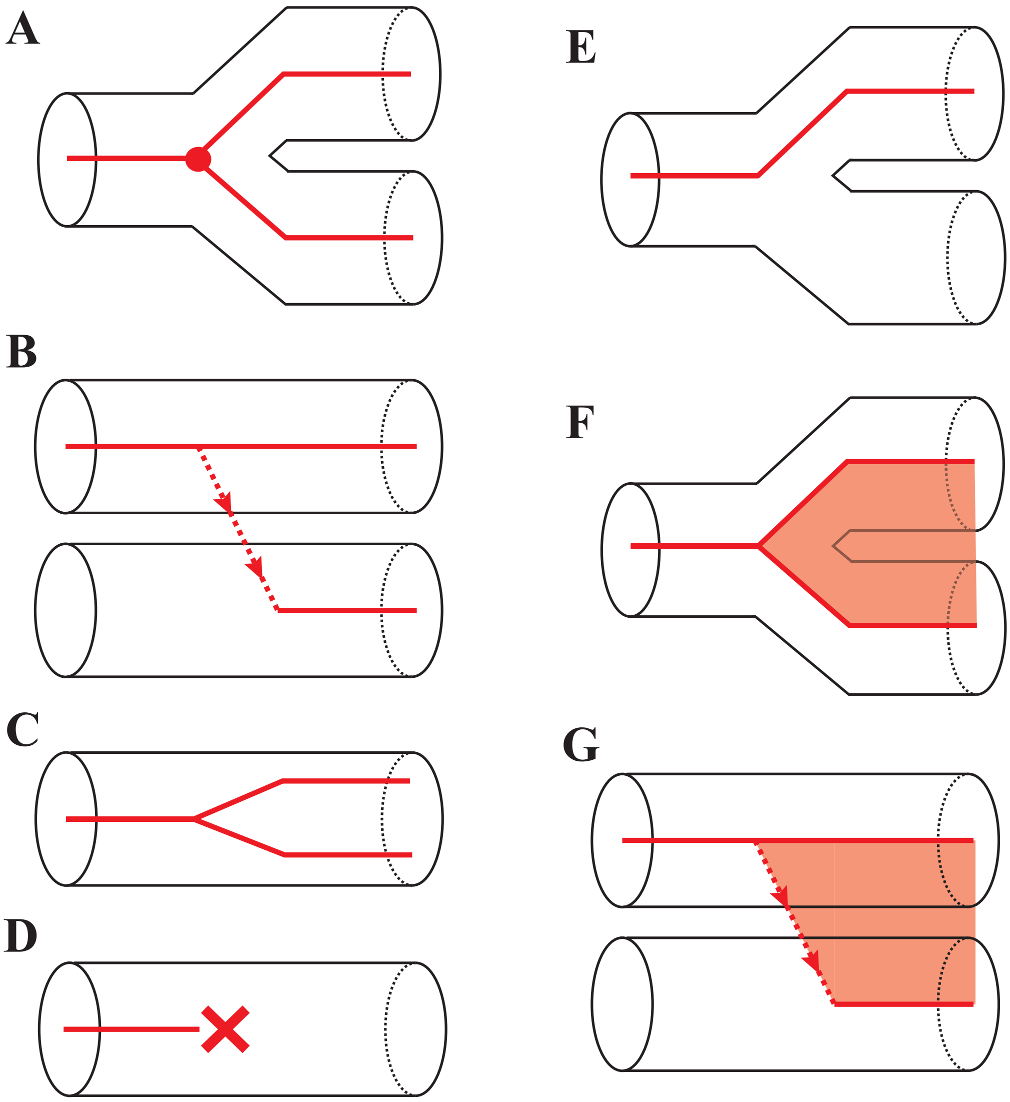

Fig. 66 Evolutionally processes. **A**. co-speciation, **B**. host switch, **C**. independent speciation, **D**. extinction, **E**. missing the boat, **F**. failure to speciation, **G**. host range expansion. Black tubes represent host lineages, red lines represent parasite lineages. A circle shows co-speciation, arrows and dotted lines show host switching, and a cross shows extinction. This figures were modified from Page (2003) and Clayton et al. (2003).

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 67 Relationship between phyllobothriidean lineages and their host elasmobranch lineages. The phylogenetic tree of phyllobothriideans was based on Fig. 14. The phylogenetic tree of elasmobranch families was based on Naylor et al. (2012). Single asterisks mean polyphyletic families, and double asterisks mean paraphyletic families. Lines show parasite-host associations, and their color shows subclasses of the host familes: black, Holocephali; blue, Galeomorphi; green, Batoidea; red, Squalomorphi.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 68 Relationship between *Pelichnibothrium* lineages and their host's lineages. Phylogenetic tree of *Pelichnibothrium* was based on Fig. 55. Phylogenetic tree of their host elasmobranchs was based on Naylor et al. (2012). Single asterisks mean polyphyletic families. Lines show parasite-host relationship.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 69 Estimation of co-evolutionary history between *Pelichnibothrium* and their host shark species. See Fig. 66 for the explanations of symbols and lines in the tree. Species in red show parasite, and species in black color show host.

本図については，5年以内に雑誌等で刊行予定のため，非公開.

Fig. 70 Relationship between *Alexandercestus*, *Scyphophyllidium* and *Thysanocephalum* lineages and their host elasmobranch lineages. The phylogenetic tree of the three genera was based on Fig. 14. The phylogenetic tree of elasmobranchs was based on Naylor et al. (2012). See Fig. 67 for the explanations of symbols in the tree. Red color Phyllobothriidean species in red color indicatespecies parasitic in multiple hosts. Lines show the relationship between phyllobothriidean and carcharhinid sharks.

Appendix History of systematics of the order Phyllobothriidea and Tetraphyllidea. The genera included in Phyllobothriidea in this study are shown in bold face.

Braum (1900)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrius, *Acanthobothrium*, ***Calliobothrium***, *Ceratobothrium*, *Cylindrophorus*, *Phoreiobothrium*, *Platybothrium*, *Prosthecobothriunm*, *Thysanocephalum*

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, ***Calyptrobothrium***, ***Crossobothrium***, *Dinobothrium*, *Diplobothrium*, *Echeneibothrium*, ***Monorygma***, ***Orygmatobothrium***, *Spongiobothrium*, ***Trilocularia***, *Tritaphros*

Family Lecanicephalidae

Discocephalum, *Lecanicephalum*, *Tylocephalum*

Family Ichthyoteaniidae

Ichthyotaenia, *Corallobothrium*, *Crepidobothrium*

Meggitt (1924)

Order Tetraphyllidea

Family Ichthyoteaniidae

Ichthyoteania, *Corallobothrim*, *Crepidobothrium*, *Gangesia*

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, *Balanobothrium*, ***Calliobothrium***, *Ceratobothrium*, *Cylindrophorus*, *Pedibothrium*, *Phyllobothroides* *Platybothrium*, *Prosthecobothrium*, ***Thysanocephalum***

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Aocobothrium*, ***Bilocularia***, ***Calyptobothrium***, *Carpobothrium*, *Dinobothrium*, *Diplobothrium*, *Echeneibothrium*, *Eniochobothrium*, *Hornellobothrium*, ***Monorygma***, *Myzocephalus*, *Myzophyllobothrium*, *Oriana*, ***Orygmatobothrium***, ***Pelichnibothrium***, *Peltidocotyle*, *Prosobothrium*, *Rhinebothrium*, *Rhoptrobothrium*, *Spongiobothrium*, *Tiarabothrium*, ***Trilocularia***, *Tritaphros*, *Zygobothrium*

Family Lecanicephalidae

Anthemobothrium, *Calycobothrium*, *Polypocephalus*

Family Polypocephalidae

Polypocephalus, *Anthemobothrium*, *Calycobothrium*

Southwell (1925)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, ***Calliobothrium***, *Ceratobothrium*, *Cylindrophorus*, *Uncibilocularis*, *Platybothrium*, *Pedibothrium*, *Tetracampos*, ***Thysanocephalum***

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Aocobothrium*, *Carpobothrium*, *Echeneibothrium*, *Myzophyllobothrium*, ***Orygmatobothrium***, *Pithophorus*

Fuhrmann (1931)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, *Balanobothrium*, ***Calliobothrium***, *Cylindrophorus*, *Pedibothrium*, *Platybothrium*, *Spiniloculus*, ***Thysanocephalum*** *Uncibilocularis*, *Yorkeria*

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, ***Bilocularia***, ***Calyptrobothrium***, *Carpobothrium*, *Ceratobothrium*, *Dinobothrium*, *Echeneibothrium*, *Myzophyllobothrium*, ***Orygmatobothrium***, ***Scyphophyllidium***, ***Trilocularia***, *Tritaphros*

Family Lecanicephalidae

Lecanicephalum, *Adelobothrium*, *Anthemobothrium*, *Polypocephalus*

Family Monticelliidae

Monticellia, *Goezeella*, *Ephedrocephalus*, *Marsypocephalus*, *Peltidocotyle*

Family Proteocephalidae

Proteocephalus, *Acanthoteania*, *Corallobotilrium*, *Crepidobothrium*, *Ophioteania*

Family Cephalobothriidae

Cephalobothrium, *Tylocephalum*, *Discobothrium*

Family Discocephalidae

Discocephalum

Joyeux & Baer (1936)

Order Tetraphyllidea

Family Onchobothiidae

Onchobothrium, *Acanthobothrium*, ***Calliobothrium***, *Cylindrophorus*

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Ceratobothrium*, *Dinobothrium*, *Echeneibothrium*, ***Orygmatobothrium***, *Prosobothrium*, ***Scyphophyllidium***

Family Ichthyotaeniidae

Ichthyotaenia, *Ophiotaenia*

Family Cephalobothriidae

Discobothrium

Family Disculicipitidae

Disculiceps

Hyman (1951)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, ***Calliobothrium***, ***Thysanocephalum***

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Carpobothrium*, *Dinobothrium*, *Echeneibothrium*, *Myzophyllobothrium*, ***Orygmatobothrium***, ***Trilocularia***

Wardle & McLeod (1952)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, ***Calliobothrium***, ***Thysanocephalum***

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Carpobothrium*, *Dinobothrium*, *Echeneibothrium*, *Mysophorus*, *Myzophyllobothrium*, ***Orygmatobothrium***, *Pithophorus*, ***Pelichnibothrium***, ***Scyphophyllidium***

Euzet (1959)

Order Tetraphyllidea

Superfamily Phyllobothrioidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, ***Calliobothrium***

Family Phyllobothriidae

Subfamily Phyllobothriinae

Phyllobothrium, *Anthobothrium*, ***Calyptrobothrium***, *Ceratobothrium*, ***Crossobothrium***, *Dinobothrium*, ***Monorygma***, ***Orygmatobothrium***, ***Scyphophyllidium***, *Sphaerobothrium*

Subfamily Echeneibothriinae

Echeneibothrium, *Clydonobothrium*, *Tritaphros*

Subfamily Rhinebothriinae

Rhinebothrium, *Caulobothrium*, *Rhabdotobothrium*

Subfamily Thysanocephalinae

Thysanocephalum

Superfamily Prosobothrioidea

Family Prosobothriidae

Subfamily Prosobothriinae

Prosobothrium

Subfamily Platybothriinae

Platybothrium

Family Phoreiobothriidae

Subfamily Phoreiobothriinae

Phoreiobothrium

Subfamily Reesiinae

Reesium, ***Trilocularia***

Family Gastrolecithidae

Gastrolecithus

Superfamily Lecanicephaloidea

Family Lecanicephalidae

Lecanicephalum, *Tetragonocephalum*

Family Disculicipitidae

Disculiceps

Family Cephalobothriidae

Cephalobothrium

Yamaguti (1959)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, ***Calliobothrium***, *Ceratobothrium*, *Cylindrophorus*, *Phoreiobothrium*, *Pinguicollum*, *Platybothrium*, *Spiniloculus*, ***Thysanocephalum***, *Uncibilocularis*, *Yorkeria*

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Aocobothrium*, *Carpobothrium*, *Cyatocotyle*, *Dinobothrium*, *Echeneibothrium*, *Gastrolecithus*, *Marsupiobothrium*, ***Monorygma***, ***Orygmatobothrium***, ***Pelichnibothrium***, *Pithophorus*, *Pseudanthobothrium*, *Reesium*, *Rhodobothrium*, ***Scyphophyllidium***

Family Maccallumiellidae

Maccallumiella

Family Trilocülariidae

Trilocularia

Joyeux & Baer (1961)

Order Tetraphyllidea

Superfamily Phyllobothrioidea

Family Onchobothriidae

Onchobothrium, *Acanthobothrium*, *Balanobothrium*, ***Calliobothrium***, *Pediobothrium*, *Pinguicollum*, *Spiniloculus*, *Uncibilocularis*, *Yorkeria*

Family Phyllobothriidae

Subfamily Phyllobothiinae

Phyllobothrium, *Anthobothrium*, ***Calyptrobothrium***, *Carpobothrium*, *Ceratobothrium*, ***Crossobothrium***, *Dinobothrium*, *Inermiphyllidium*, *Marsupiobothrium*, ***Monorygma***, ***Orygmatobothrium***, *Pillersium*, *Pithophorus*, *Polypobothrium*, ***Scyphophyllidium***, *Sphaerobothrium*, *Staurobothrium*

Subfamily Echeneibothriinae

Clydonobothrium, *Echeneibothrium*, *Pseudanthobothrium*, *Tritaphros*

Subfamily Rhinebothriinae

Caulobothrium, *Rhabdotobothrium*, *Rhinebothrium*, *Tiarabothrium*

Subfamily Thysanocephalinae

Myzocephalus, *Myzophyllobothrium*, *Rhoptrobothrium*, ***Thysanocephalum***

Superfamily Lecanicephaloidea

Family Lecanicephalidae

Anthemobothrium, *Calycobothrium*, *Lecanocephalum*, *Polypocephalus*

Family Cephalobothriidae

Adelobothrium, *Cephalobothrium*, *Hexacanalis*, *Tetragonocephalum*

Superfamily Prosobothrioidea

Family Disculicepitidae

Disculiceps

Family Gastrolecithidae

Gastrolecithus

Family Phoreiobothriidae

Subfamily Phoreiobothiinae

Phoreiobothrium

Subfamily Reesiinae

Reesium, ***Triloculraria***

Family Prosobothiidae

Subfamily Platybothriinae

Dicranobothrium, *Platybothrium*

Schmidt (1986)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothroides*, *Acanthobothrium*, ***Calliobothrium***, *Ceratobothrium*, *Cylindrophorus*, *Pachybothrium*, *Pedibothrium*, *Phoreiobothrium*, *Pinguicollum*, *Platybothrium*, *Pomatotrygonocestus*, *Spiniloculus*, ***Thysanocephalum***, *Uncibilocularis*, *Yorkeria*

Family Phyllobothriidae

Phyllobothrium, *Anthobothrium*, *Aocobothrium*, *Carpobothrium*, *Caulobothrium*, *Clydonobothrium*, *Cyatocotyle*, *Dinobothrium*, *Duplicibothrium*, *Echeneibothrium*, *Gastrolecithus*, *Glyphobothrium*, *Marsupiobothrium*, *Mixophyllobothrium*, ***Monorygma***, *Myzophyllobothrium*, ***Orygmatobothrium***, ***Pelichnibothrium***, *Phormobothrium*, *Pithophorus*, *Pseudanthobothrium*, *Rhabdotobothrium*, *Rhinebothrium*, *Rhinebothroides*, *Rhodobothrium*, *Reesium*, ***Scyphophyllidium***

Family Trilocularidae

Trilocularia, *Pentaloculum*, *Zyxibothrium*

Family Cathetocephalidae

Cathetocephalus

Euzet (1994)

Order Tetraphyllidea

Family Onchobothriidae

Onchobothrium, *Acanthobothroides*, *Acanthobothrium*, *Balanobothrium*, ***Calliobothrium***, *Dicranobothriun*, *Megalonchos*, *Pachybothrium*, *Pedibothrium*, *Phoreiobothrium*, *Platybothrium*, *Pomatotrygonocestus*, *Spiniloculus*, *Uncibilocularis*, *Yorkeria*

Family Phyllobothriidae

Subfamily Thysanocephalinae

Thysanocephalum, *Myzocephalus*, *Myzophyllobothrium*

Subfamily Echeneibothriinae

Pseudoanthobothrium, *Clydonobothrium*, *Phormbothrium*, *Tritaphros*, *Echeneibothrium*

Subfamily Phyllobothriinae

Phyllobothrium, *Anthobothrium*, *Calyptrobothrium*, *Carpobothrium*, *Ceratobothrium*, *Clistobothrium*, *Crossobothrium*, *Dinobothrium*, *Gastrolecithus*, *Marsupiobothrium*, ***Monorygma***, ***Orygmatobothrium***, *Pithophorus*, *Rhodobothrium*, ***Scyphophyllidium***

Subfamily Triloculariinae

Trilocularia, *Pentaloculum*, *Zyxibothrium*

Subfamily Rhinebothriinae

Rhinebothrium, *Caulobothrium*, *Duplicibothrium*, *Glyphobothrium*, *Rhabdotobothrium*, *Rhinebothroides*

Family Disculidpitidae

Disculiceps

Family Prosobothriidae

Prosohothrium

Family Dioecotaeniidae

Dioecotaenia

Family Litobothriidae

Litobothrium

Family Cathetocephalidae

Cathetocephalus

Family Chimaerocestidae

Chimaerocestos

Caira et al. (2014)

Order Phyllobothriidea

Family Phyllobothriidae

Phyllobothrium, ***Calyptrobothrium***, ***Chimaerocestos***, *Marsupiobothrium*, *Nandocestus*, *Orectolobicestus*, ***Orygmatobothrium***, *Paraorygmatobothrium*, *Ruhnkecestus*, ***Scyphophyllidium***, ***Thysanocephalum***

Order Tetraphyllidea

incertae sedis

Alexandercestus, *Anthobothrium*, *Balanobothrium*, *Bibursibothrium*, *Biloculuncus*, ***Calliobothrium***, *Caulobothrium*, *Carpobothrium*, *Cardiobothrium*, *Ceratobothrium*, ***Clistobothrium***, ***Crossobothrium***, *Dinobothrium*, *Dioecotaenia*, *Duplicibothrium*, *Erudituncus*, *Flexibothrium*, *Megalonchos*, *Myzocephalus*, *Myzophyllobothrium*, *Pachybothrium*, *Pedibothrium*, ***Pelichnibothrium***, *Rhoptrobothrium*, *Spiniloculus*, ***Trilocularia***, *Yorkeria*

This study

付録については，5年以内に雑誌等で刊行予定のため，非公開.

Appendix Table 1 Revised nominal species of Phyllobothriidea. Taxonomic status excepted species using in this study were given from Ruhnke (2011) and followed descriptions.

付録については，5年以内に雑誌等で刊行予定のため，非公開.

Appendix Table 1 continued.

付録については，5年以内に雑誌等で刊行予定のため，非公開.

Appendix Table 1 continued.

付録については，5年以内に雑誌等で刊行予定のため，非公開.

Appendix Table 1 continued.

付録については，5年以内に雑誌等で刊行予定のため，非公開.

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Appendix Fig. 1 Bayesan Inference tree of Analysis 7 (Dataset 1, ssrDNA+lsrDNA). BPP were showed upper orders clade. Current scientific names are used and some of them were revised in this study (see Table 15). Sequences obtained in this study are shown in black color, and those collected from GenBank are in gray color. Open boxes indicate the revised orders in this study (see Section 3.3 of Chapter I).

付録については，5年以内に雑誌等で刊行予定のため，非公開.

Appendix Fig. 2 Bayesan Inference tree of Analysis 8 (Dataset 1, ssrDNA). See Apendix Fig. 1 for the explanations of symbols in the tree. Phyllobothriidea, Tetraphyllidea and Onchoproteocephalidea were polyphyletic in this analysis (connected by dotted lines).

付録については，5年以内に雑誌等で刊行予定のため，非公開.

Appendix Fig. 3 Bayesan Inference tree of Analysis 9 (Dataset 1, lsrDNA). See Apendix Fig. 1 for the explanations of symbols in the tree. Phyllobothriidea were polyphyletic in this analysis (connected by dotted lines).

付録については，5年以内に雑誌等で刊行予定のため，非公開.

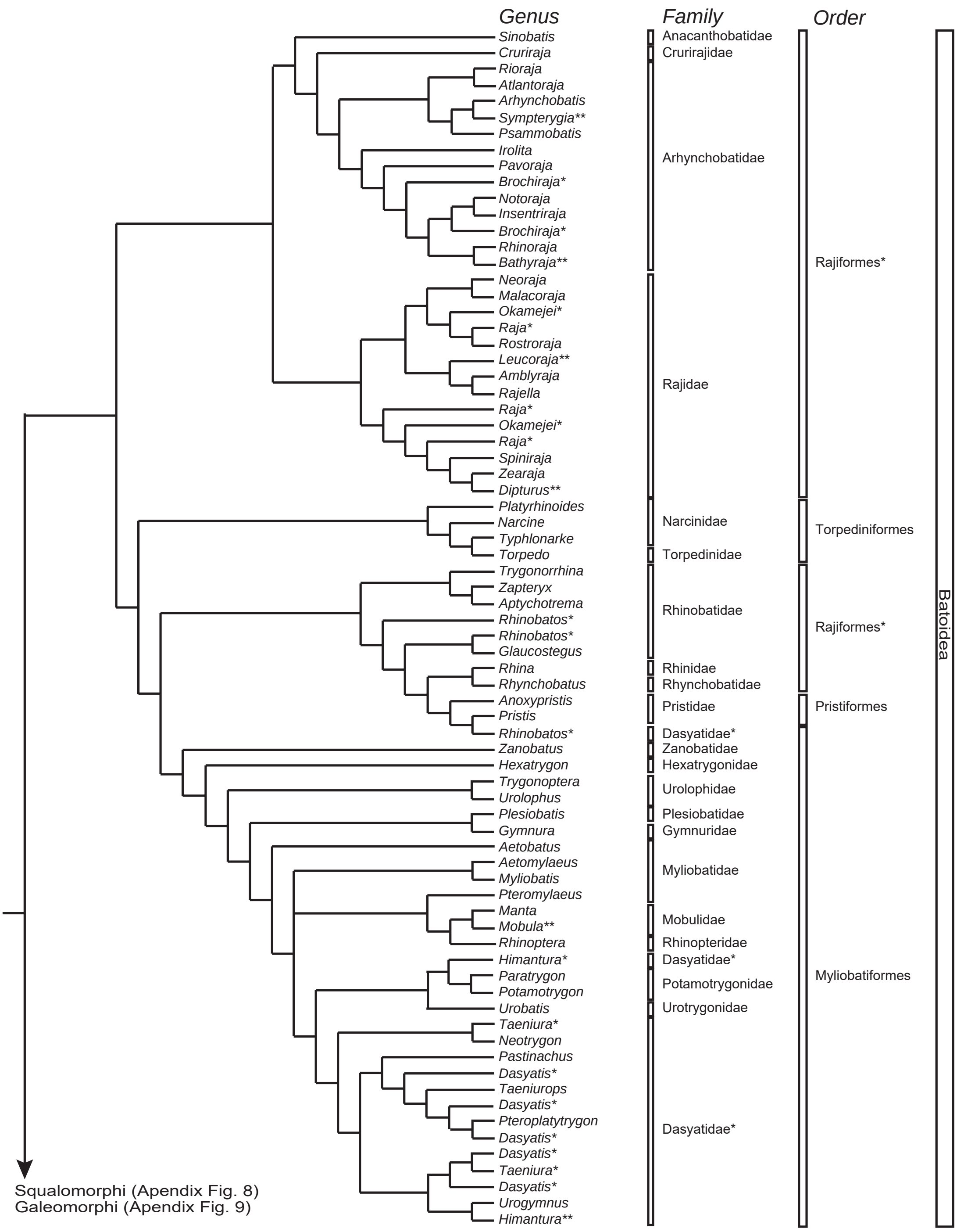
Appendix Fig. 4 Bayesan Inference tree of Analysis 10 (Dataset 2, ssrDNA and lsrDNA). See Apendix Fig. 1 for the explanations of symbols in the tree.

付録については，5年以内に雑誌等で刊行予定のため，非公開.

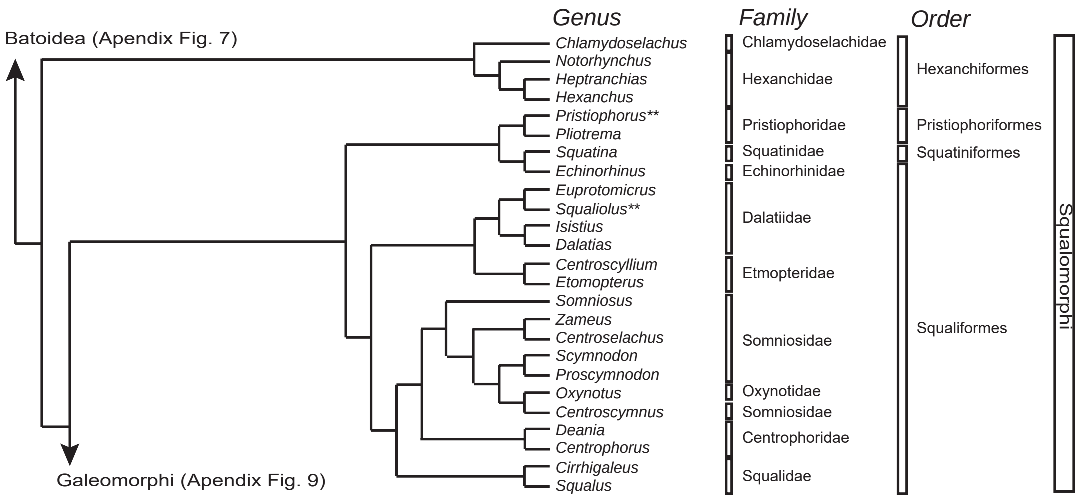
Appendix Fig. 5 Bayesan Inference tree of Analysis 11 (Dataset 2, ssrDNA). See Apendix Fig. 1 for the explanations of symbols in the tree. Phyllobothriidea were polyphyletic in this analysis (connected by dotted lines).

付録については，5年以内に雑誌等で刊行予定のため，非公開.

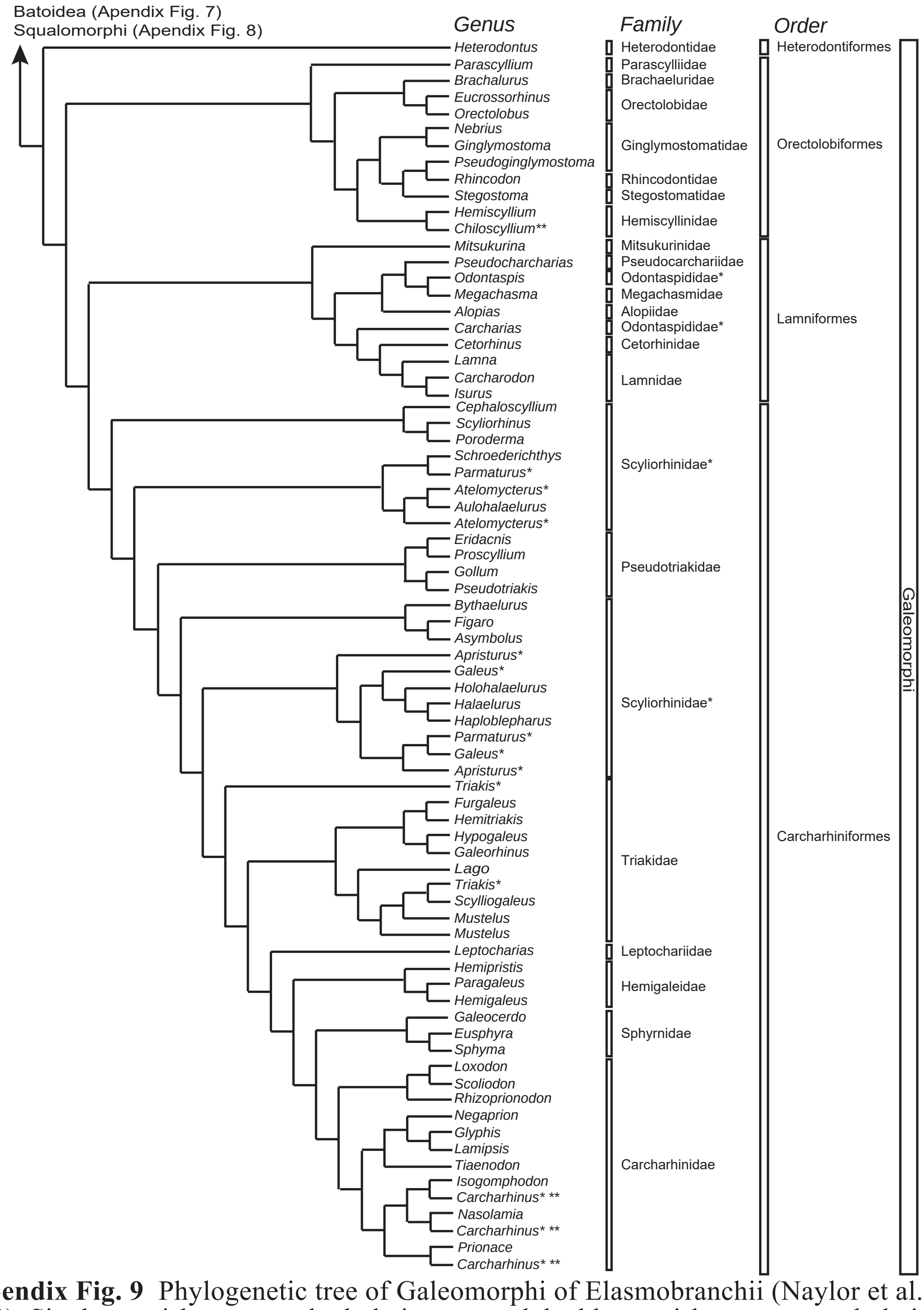
Appendix Fig. 6 Bayesan Inference tree of Analysis 12 (Dataset 2, lsrDNA). See Apendix Fig. 1 for the explanations of symbols in the tree. Phyllobothriidea were polyphyletic in this analysis (connected by dotted lines).



Appendix Fig. 7 Phylogenetic tree of Batoidea of Elasmobranchii (Naylor et al., 2012). Single asterisks mean polyphyletic taxa, and double asterisks mean paraphyletic taxa.



Appendix Fig. 8 Phylogenetic tree of Squalomorphi of Elasmobranchii (Naylor et al., 2012). Single asterisks mean polyphyletic taxa, and double asterisks mean paraphyletic taxa.



Appendix Fig. 9 Phylogenetic tree of Galeomorphi of Elasmobranchii (Naylor et al., 2012). Single asterisks mean polyphyletic taxa, and double asterisks mean paraphyletic taxa.