Cestode fauna of murid and cricetid rodents in Hokkaido, Japan, with assignment of DNA barcodes

Mizuki Sasaki1,3,4, Jason Lee Anders2,3, and Minoru Nakao1

1 Department of Parasitology, Asahikawa Medical University, Asahikawa, Hokkaido 078-8510, Japan
E-mail: mizuki_sasaki@asahikawa-med.ac.jp
2 Graduate School of Environmental Science, Hokkaido University, Sapporo, Hokkaido 060-0810, Japan
3 Equally contributed
4 Corresponding author

(Received 15 September 2020; Accepted 22 June 2021)

The cestode fauna of murid and cricetid rodents in Hokkaido, the northernmost island of Japan, was evaluated based on our parasite collection and a review of the literature. Adult and larval cestodes collected from Apodemus speciosus (Temminck, 1844), and Rattus norvegicus (Berkenhout, 1769) in Hokkaido were identified by both morphological and molecular diagnoses. A total of 10 species from 5 families were confirmed in our collection. Arostrilepis tenuicirrosa Makarikov, Gulyaev, and Kontrimavičius, 2011, Paranoelocephala kalelai Tenora, Hauksalmi, and Henttonen, 1985, and Taenia crassiceps (Zeder, 1800) were recorded for the first time from Hokkaido. A comprehensive look at both the present and previous studies revealed that the cestode fauna of rodents in Japan consists of at least 30 species from 6 families. Among them, 23 species occur in Hokkaido. The species composition is strongly affected by the nearby Eurasian continent, suggesting parasite migrations with rodent hosts over land bridges between Hokkaido and Sakhalin and between Hokkaido and Honshu, the main island of Japan. A DNA barcoding system using sequences of nuclear 28S rDNA and mitochondrial cox1 allowed us to identify cestodes at species and genus levels, even in different developmental stages. The integration of morphological and molecular diagnoses is essential in cestode taxonomy to establish a common ground for biogeographical studies worldwide. The standardization of DNA barcoding is particularly of critical importance.

Key Words: Cestode fauna, rodent hosts, Hokkaido, DNA barcoding.

Introduction

The Japanese archipelago is divided into the following three biogeographic regions based on the distribution of terrestrial mammals (Fig. 1): 1) Hokkaido and adjacent small islands, 2) Honshu, Shikoku, Kyushu and adjacent small islands, and 3) the Ryukyu Islands (also known as the Nansei Islands). Hokkaido is the northernmost island of Japan separated from Honshu by the Tsugaru strait, which acts as a zoogeographical boundary known as “Blakiston’s Line”. The fauna of Hokkaido is similar to that of the nearby northeastern Eurasian Continent, whereas the faunas of the other Japanese islands include elements of both the Palearctic and Oriental zoogeographic regions (Dobson 1994; Millien-Parra and Jaeger 2001). Thus, the terrestrial fauna of Japan is a typical example of insular biogeography on a continental shelf (Motokawa 2017).

Rodents of the families Muridae and Cricetidae in Japan are composed of 21 species (Ohdachi et al. 2015; Motokawa 2016), and the following nine species are distributed in Hokkaido: Myodes rufocanus (Sundevall, 1846), Myodes rex (Imaizumi, 1971), Myodes rutilus (Pallas, 1779), Apodemus speciosus (Temminck, 1844), Apodemus argenteus (Temminck, 1844), Rattus norvegicus (Berkenhout, 1769), Rattus rattus (Linnaeus, 1758), and Mus musculus Linnaeus, 1758. Among them, My. rufocanus, My. rutilus, and Ap. peninsularis prevail throughout northeastern Eurasia (Ohdachi et al. 2015; Knitlová and Horáček 2017). A phylogenetic study of the mitochondrial DNA (mtDNA) showed that populations of Ap. speciosus and Ap. argenteus in Hokkaido are different from those on the other Japanese islands (Suzuki et al. 2004). The synanthropic species, Ra. norvegicus, Ra. rattus, and Mu. musculus, are cosmopolitan (Khlyap et al. 2012).

The murid and cricetid rodents in Hokkaido serve as definitive hosts for cestodes of the families Hymenolepididae, Anoplocephalidae, Davaineidae, and Catenotaeniidae. It is most likely that the cestode fauna originated from the adjacent part of the Eurasian continent because most of the rodent hosts were introduced into Hokkaido in the middle to late Pleistocene (Asakawa 1989; Dobson 1994; Sato 2017). Land bridges connecting Hokkaido to the adjacent landmasses lead to the introduction of rodents; their migration routes were southward via Sakhalin and northward via Honshu (Fig. 1). Basic data on the molecular phylogenetics of rodent cestodes in Hokkaido is needed to elucidate their evolution and introduction process. However, the previous taxonomy of rodent cestodes in Hokkaido was based only on morphological characteristics (Ishimoto 1974; Asakawa et al. 1983; Asakawa and Ohbayashi 1986; Iwaki et al. 1994b, c; Tenora et al. 1999; Furuse et al. 2014), resulting in the difficulty of comparison among geographically separated lineages of each species.
Congeners of parasitic platyhelminths show low morphological variability. Molecular phylogenetic analyses accelerate the finding of cryptic species among them (Vilas et al. 2005) and lead to taxonomic revisions (Olson et al. 2003). In general, mitochondrial DNA (mtDNA) is more suitable than nuclear DNA for reconstructing phylogenetic relationships among closely related species because of the rapid sequence evolution (Brown et al. 1979). A mitochondrial gene for cytochrome c oxidase subunit 1 (cox1) has been used as a general marker for DNA barcoding in a wide array of animal species (Savolainen et al. 2005). Also in cestodes, the cox1-based DNA barcoding system is useful for the identification of species, the discovery of cryptic species, and the evaluation of species validity (Haukisalmi et al. 2004; Nakao et al. 2013; Lavikainen et al. 2016). In addition, the DNA barcoding is highly effective in demonstrating an identity between larval and adult stages of the same species (Savolainen et al. 2005).

The life cycle of rodent cestodes was first disclosed in the human-infecting species, Hymenolepis diminuta (Rudolphi, 1819) and Rodentolepis nana (Bilhartz, 1851), which use coleopterans as their intermediate hosts (Andreassen et al. 1999; Thompson 2015). However, the intermediate hosts of most rodent cestodes remain to be determined. Moreover, rodents themselves become intermediate hosts for members of the families Taeniidae and Paruterinidae, whose definitive hosts are carnivorous mammals and birds, respectively (Ishimoto 1974; Yagi et al. 1986; Georgiev et al. 2006; Nakao et al. 2013). From the evolutionary and ecological points of view, the connection of cestode developmental stages between definitive and intermediate hosts should be clarified by DNA barcoding. In the modern taxonomy of cestodes, it is requisite to establish a database including integrated information on morphological features, host records, localities, and DNA sequences. However, there is little molecular data on cestodes from wildlife animals in Japan.

In this report, the cestode fauna of murid and cricetid rodents in Hokkaido was evaluated based mainly on our parasite collections. The objectives of this study are: 1) to briefly record the morphology of rodent tapeworms, 2) to determine their DNA barcode sequences, 3) to consider phylogenetic relationships in members of every family examined, 4) to identify valid species and synonyms, and 5) to compile records of rodent tapeworms from Hokkaido and neighboring areas through literature search. The integration of the present and previous taxonomies, together with the assignment of DNA barcodes, must be of great help for future studies on the evolution and phylogeography of cestodes in Japan and its neighboring regions.

Materials and Methods

As part of master and doctoral theses of one of the authors (J. L. Anders), rodent parasites were collected from Ap. speciosus and My. rufocanus in Asahikawa, Biei, Obihiro, and Otofuke (Fig. 1) during the period from 2016 to 2019. Protocols of the field survey and the results of parasitic nematodes were previously published (Anders et al. 2019). Additional samples were obtained from My. rufocanus and Ra. norvegicus in Nayoro and Kushiro (Fig. 1) during the period of 2018 and 2019. A total of 41 cestode isolates (36 adults and 5 larvae) were analyzed in this study. The adult and larval cestodes were kept in 10% neural-buffered formalin or 70% ethanol for morphological and molecular analyses. A laboratory strain of Hymenolepis pseudodiminuta Te-nora, Asakawa, and Kamiya, 1994, which was maintained in Hamamatsu University School of Medicine (Ishii et al. 1994).
Table 1. Rodent cestodes found in this study, with their accession numbers of voucher specimens and DNA barcodes.

| Species                  | Stages | Hosts (localities in Hokkaido) | Isolate numbers | Vouchers | Accession numbers of DNA databases (bases in length) |
|--------------------------|--------|---------------------------------|-----------------|----------|--------------------------------------------------|
| *Hymenolepis* sp. 1     | Adult  | As (Asahikawa)                  | 18AK285, 19AK270| MPM21634 | LC535237–75 (798)                                 |
| *Hymenolepis* sp. 2     | Adult  | As (Otofuke) Mruf (Otofuke)     | JAI73, JAI75, JA220, JA244, H2B | LC535235 | LC535274–75 (798)                                 |
| *Anastrangia* sp.        | Adult  | Mruf (Asahikawa, Biei)          | 19AK170, 19AK439, 19AK454, 19AK459 | MPM21636 | LC535246–89 (798)                                 |
| *Microsomacanthus* sp.   | Adult  | As (Asahikawa, Obihiro)         | 19AK212, JA313, Para09, Para15, Para18, Para19 | MPM21635 | LC535276–81 (798)                                 |
| *Paranoplocephala kaeleli* | Adult  | Mruf (Asahikawa)                | 19AK378, 19AK412, 19AK419, 19AK436, 19AK454-2, 19AK454-3 | MPM21637 | LC535262–67 (810)                                 |
| *Catenotaenia* sp.       | Adult  | Mruf (Asahikawa, Nayoro, Otofuke, Obihiro) | 18AK131, JA212, JA317, AMU, O36 | MPM21638 | LC535243–85 (792)                                 |
| *Raillietina* sp.        | Adult  | As (Asahikawa, Otofuke)         | 19AK89, JA304, Para33, Para36, Para38, Para42, Para44, Para45 | MPM21639 | LC535254–61 (813)                                 |
| *Taenia crassiceps*      | Larva  | Mruf (Asahikawa)                | 19AK309         |         | LC535292 (923)                                    |
| *Hydatigera taeniaeformis*| Larva  | Mruf (Asahikawa) Ra (Nayoro, Kushiro) | 18AK309         |         | LC535290–91 (930)                                 |
| *Echinococcus multilocularis* | Larva  | Mruf (Asahikawa, Otofuke)       |                 |         |                                                  |

* Abbreviations of host rodents are as follows: As, Apodemus speciosus; Mruf, Myodes rufocanus; Ra, Rattus norvegicus. b The collection numbers of Meguro Parasitological Museum (Tokyo, Japan) are shown. c The following PCR primers were used: XZ-1 (Auwera et al. 1994) and 1500R (Snyder and Tkach 2001). d The following PCR primers were used: JB3 (Bowles and McManus 1993) and CO1-R trema (Miura et al. 2005). e The following PCR primers were used: COX-F and COX-R (Haukisalmi et al. 2005). f The following PCR primers were used: HYM01 and HYM08 (Makarikov et al. 2013).
Scolices and proglottids of adult tapeworms were stained with Heidenhain’s iron hematoxylin, dehydrated in a graded ethanol series, cleared in creosote, and finally mounted with Canada balsam. To observe the rostellar hooks of strobilocercus larvae, the tissue of their scolex was lysed in Tris-HCl buffer (10 mM, pH 8.0) containing 0.1% SDS and proteinase K (200 µg/mL). A calibrated optical microscope with a digital camera (Axio Imager, Zeiss, Germany) was used to observe the specimens. Object sizes were measured via their digital images using the accessory software (AxioVision, Zeiss, Germany). The specimens used for the morphological observation have been deposited as vouchers in Meguro Parasitological Museum, Tokyo, Japan (Table 1).

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Object sizes were measured via their digital images using the accessory software (AxioVision, Zeiss, Germany). The specimens used for the morphological observation have been deposited as vouchers in Meguro Parasitological Museum, Tokyo, Japan (Table 1).

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Hot-start Ex Taq® DNA polymerase (TaKaRa, Japan) was used for PCR with the manufacturer-supplied reaction buffer. Two genes were amplified using the primer set of XZ-1 (5′-ACC CGC TGA AYT TAA GCA TAT-3′) (Auwera et al. 1994) and 1500R (5′-GCT ATC ATC TTC AGGCAA ACT TCG-3′) (Nakao and Kato 2003) and cryopreserved in Asahikawa Medical University, was added to the analyses.

Scolices and proglottids of adult tapeworms were stained with Heidenhain’s iron hematoxylin, dehydrated in a graded ethanol series, cleared in creosote, and finally mounted with Canada balsam. To observe the rostellar hooks of strobilocercus larvae, the tissue of their scolex was lysed in Tris-HCl buffer (10 mM, pH 8.0) containing 0.1% SDS and proteinase K (200 µg/mL). A calibrated optical microscope with a digital camera (Axio Imager, Zeiss, Germany) was used to observe the specimens. Object sizes were measured via their digital images using the accessory software (AxioVision, Zeiss, Germany). The specimens used for the morphological observation have been deposited as vouchers in Meguro Parasitological Museum, Tokyo, Japan (Table 1).

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Hot-start Ex Taq® DNA polymerase (TaKaRa, Japan) was used for PCR with the manufacturer-supplied reaction buffer. Two genes were amplified using the primer set of XZ-1 (5′-ACC CGC TGA AYT TAA GCA TAT-3′) (Auwera et al. 1994) and 1500R (5′-GCT ATC ATC TTC AGGCAA ACT TCG-3′) (Nakao and Kato 2003) and cryopreserved in Asahikawa Medical University, was added to the analyses.

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Hot-start Ex Taq® DNA polymerase (TaKaRa, Japan) was used for PCR with the manufacturer-supplied reaction buffer. Two genes were amplified using the primer set of XZ-1 (5′-ACC CGC TGA AYT TAA GCA TAT-3′) (Auwera et al. 1994) and 1500R (5′-GCT ATC ATC TTC AGGCAA ACT TCG-3′) (Nakao and Kato 2003) and cryopreserved in Asahikawa Medical University, was added to the analyses.

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Hot-start Ex Taq® DNA polymerase (TaKaRa, Japan) was used for PCR with the manufacturer-supplied reaction buffer. Two genes were amplified using the primer set of XZ-1 (5′-ACC CGC TGA AYT TAA GCA TAT-3′) (Auwera et al. 1994) and 1500R (5′-GCT ATC ATC TTC AGGCAA ACT TCG-3′) (Nakao and Kato 2003) and cryopreserved in Asahikawa Medical University, was added to the analyses.

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Hot-start Ex Taq® DNA polymerase (TaKaRa, Japan) was used for PCR with the manufacturer-supplied reaction buffer. Two genes were amplified using the primer set of XZ-1 (5′-ACC CGC TGA AYT TAA GCA TAT-3′) (Auwera et al. 1994) and 1500R (5′-GCT ATC ATC TTC AGGCAA ACT TCG-3′) (Nakao and Kato 2003) and cryopreserved in Asahikawa Medical University, was added to the analyses.

DNA templates for PCR were prepared from pieces of ethanol-fixed adult tapeworms or larval metacestodes by a modified method described previously (Miura et al. 2017). Approximately 25 mg of the tissue were suspended in a total volume of 50 µL containing proteinase K (200 µg/mL) and 5% Chelex 100 resin (Bio-Rad, USA), and incubated at 56°C for 3 hours. After inactivating the enzyme at 95°C for 5 minutes, one µL of the supernatant was used as the template. Hot-start Ex Taq® DNA polymerase (TaKaRa, Japan) was used for PCR with the manufacturer-supplied reaction buffer. Two genes were amplified using the primer set of XZ-1 (5′-ACC CGC TGA AYT TAA GCA TAT-3′) (Auwera et al. 1994) and 1500R (5′-GCT ATC ATC TTC AGGCAA ACT TCG-3′) (Nakao and Kato 2003) and cryopreserved in Asahikawa Medical University, was added to the analyses.
MEGA X (Kumar et al. 2018) was used for genetic analyses. Phylogenetic trees of nuclear 28S rDNA and mitochondrial genes were inferred by using the maximum likelihood (ML) method under best-fit nucleotide substitution models. The robustness of the trees was tested by bootstrapping with 500 replicates. When illustrating the resultant trees, an outgroup taxon used was removed to save space. The values of pairwise divergence among nucleotide sequences of cox1 were computed under p-distance model for the assessment of intraspecific genetic variations. In particular, the cox1-based DNA barcoding was employed to identify metacestode larvae of the family Taeniidae. Nucleotide sequences determined in this study have been deposited into DDBJ/ENA/GenBank databases (Table 1).

A survey of literature on rodent cestodes in Japan and neighboring countries was conducted using several internet databases (PubMed, Scopus, and Google Scholar). The digital archives of parasitic helminths in Japan published by Meguro Parasitological Museum (https://kiseichu-archives.blogspot.com/p/mpm-archives-e.html) were also utilized. Based on the bibliographies of relevant articles, related publications were further identified.

Results and Discussion

A total of 10 species of cestodes were found from murid and cricetid rodents in this study (Table 1). Of these, seven were at the adult stage of Hymenolepididae, Anoplocephalidae, Catenotaeniidae, and Davaineidae, and three were at the larval stage of Taeniidae. The family-level identification of the adult tapeworms was strongly supported by a phylogenetic analysis using nuclear 28S rDNA sequences (Fig. 2). The brief description of morphology was made for each species. All morphometric measurements are given in mm.

Family Hymenolepididae Ariola, 1899
Genus Hymenolepis Weinland, 1858

1. Hymenolepis sp. 1

The adult tapeworms of Hymenolepis sp. 1 (the isolate numbers 18AK285 and 19AK270) were found from Ap. spe- ciosus in Asahikawa. The following description was made based on one specimen (Fig. 3A, B): Scolex 0.43 wide. Rostellum unarmed. Rostellar sac, 0.10 long by 0.08 wide. Suck- ers circular, four in number, 0.11–0.14 in diameter. Neck region not discernible. Mature proglottids much shorter in length than width, 0.26 long by 1.9 wide. Genital pore uni- lateral. Cirrus sac 0.22–0.29 long. Cirrus 0.03–0.04 long.
Testes spherical, three in number in each mature proglottid, almost of equal size, 0.097–0.12 in diameter, arranged in straight line. Ovary lobed, 0.19 long by 0.60 wide. Vitelline gland lobed, 0.018–0.027 long by 0.065–0.10 wide.

The genus *Hymenolepis* sensu stricto is characterized by a rudimentary unarmed rostellum and other defined morphological traits (Haukisalmi et al. 2010a; Makarikov and Tkach 2013; Nkouawa et al. 2016). The following four species of *Hymenolepis* have been found from *Apodemus* mice in Eurasia: *Hym. diminuta*, *Hym. Hibernia* Montgomery, Montgomery, and Dunn, 1987, *Hym. pseudodiminuta*, and *Hymenolepis apodemi* Makarikov and Tkach, 2013 (Montgomery et al. 1987; Asakawa 1989; Tenora et al. 1994; Makarikov and Tkach 2013). A lengthy cirrus of mature proglottids (0.060–0.076 mm in length) is distinctive of *Hym. apodemi* (Makarikov and Tkach 2013). Although *Hym. diminuta* and *Hym. hibernia* are quite similar to each other, the latter has a lateral bulge of each proglottid extending backward over adjacent proglottids (Montgomery et al. 1987).

The present phylogenetic trees of 28S rDNA and cox1 showed that our isolates from Hokkaido and the isolate of *Hym. pseudodiminuta* from Honshu (Ishih et al. 2003) might be classified as *Hym. hibernia* (Figs 2, 4). The values of pairwise divergence of cox1 sequences among 14 isolates of *Hymenolepis* sp. 1 from Hokkaido, *Hym. pseudodiminuta* from Honshu, and *Hym. hibernia* from Korea, Europe, Turkey ranged from 0.048 to 0 (mean = 0.030). The maximum value was reduced to 0.029, when excluded the Turkish isolates.

*Hymenolepis pseudodiminuta* was discovered from *Ap. argenteus* in Honshu and Shikoku and from *Ap. speciosus* in Honshu, Kyushu and Hokkaido (Tenora et al. 1994; Furuse et al. 2014). *Hymenolepis pseudodiminuta* is morphologically very similar to *Hym. hibernia*. The difference of host geographic range between the two species was considered to be important for their classification (Tenora et al. 1994). Our molecular analysis demonstrated the identity between *Hymenolepis* sp. 1 and both *Hym. pseudodiminuta* and *Hym. hibernia*, suggesting that *Hymenolepis* sp. 1 and *Hym. pseudodiminuta* might be proposed to be a junior synonym of *Hym. hibernia*. However, we here refrain from proposing a synonymization of them because further morphological and ecological evaluations of these species are needed.

2. *Hymenolepis* sp. 2

The adult tapeworms of *Hymenolepis* sp. 2 (nos. JA173,
JA175, JA220, JA244, and H22B) were found from *Ap. speciosus* and *My. rufocanus* in Otofuke. The specimens were unsuitable for morphological diagnosis. The phylogenetic trees of 28S rDNA and *cox*1 confirmed that this unknown species belongs to *Hymenolepis* (Figs 2, 4). The *cox*1 sequences of the five isolates were completely identical to one another. Further sample collections are needed to clarify whether this unknown species is *Hym. apodemi* or another new cryptic species.

**Family Hymenolepididae** Ariola, 1899

**Genus Arostrilepis** Mas-Coma and Tenora, 1997

3. *Arostrilepis tenuicirrosa* Makarikov, Gulyaev, and Kontrimavichus, 2011

The adult tapeworms of *Arostrilepis tenuicirrosa* (nos. 19AK170, 19AK439, 19AK454, and 19AK459) were found from *My. rufocanus* in Asahikawa and Biei. This is the first record from Japan. The following description was made based on three specimens (Fig. 3C–E): Scolex unarmed, 0.36–0.38 in maximum width, distinctly wider than neck. Suckers oval, four in number, 0.21–0.24 long by 0.11–0.18 wide. Rostellum absent. Mature proglottids shorter in length than width, 0.23–0.28 long by 0.95–1.20 wide. Testes pear-shaped, three in number, almost equal-sized, 0.11–0.15 long by 0.14–0.21 wide, arranged in nearly a right-angled triangle. Poral testis separated from antiporal testes by female gonads. Cirrus sac 0.17–0.22 long by 0.027–0.038 wide. Cirrus 0.09–0.10 long by 0.017–0.022 wide, armed with spines. Genital pore opens on middle of lateral proglottid margin. Ovary irregularly lobed, 0.27–0.48 wide. Vitellarium lobed, postovarian, 0.14–0.19 wide. Gravid proglottids trapezoidal, transversely elongated, 0.51 long by 1.8–2.2 in maximum width. Uterus labyrinthine, occupying entire space of gravid proglottids.

Members of the genus *Arostrilepis* are widely distributed in the Holarctic region, mainly using voles as definitive hosts. *Arostrilepis horrida* (Linstow, 1901) was once considered to be a morphologically hypervariable and geographically widespread species (Makarikov et al. 2011; Galbreath et al. 2013; Makarikov and Hoberg 2016). However, a recent molecular phylogenetic analysis using mitochondrial *cytb* sequences has revealed some cryptic species within the assemblage of the so-called “A. horrida” (Makarikov and
There are now eight species of *Arostrilepis* from the Palearctic region (Makarikov and Kontrimavichus 2011; Makarikov et al. 2011, 2013): *A. horrida* sensu stricto, *A. tenuicirrosa*, *A. beringiensis* (Kontrimavichus and Smirnova, 1991), *A. microtis* Gulyaev and Chechulin, 1997, *A. macrocirrosa* Makarikov, Gulyaev, and Kontrimavichus, 2011, *A. intermedia* Makarikov and Kontrimavichus, 2011, *A. janickii* Makarikov and Kontrimavichus, 2011, and *A. janickii* Makarikov, Galbreath, and Hoberg, 2013. Morphological differential points of these species are limited to the form and size of the cirrus, and other characters may vary and overlap among all species (Makarikov et al. 2011).

All the specimens of *Arostrilepis* obtained in this study were subjected to DNA sequencing of mitochondrial *cox1* and *cytb*. The values of pairwise divergence ranged at very low levels from 0.009 to 0.003 in both *cox1* and *cytb*, confirming the involvement of a single species. A phylogenetic tree of *cytb* showed that our samples should be classified as *A. tenuicirrosa* (Fig. 5).

Voles of *Myodes* spp., widely distributed from Europe to Russia as the definitive host for *A. tenuicirrosa* (Galbreath et al. 2013). The present study expands the distribution range to Hokkaido. There are also records of *Arostrilepis horrida* sensu lato from *Eothenomys smithii* (Thomas, 1905) and *Eothenomys andersonii* (Thomas, 1905) in Honshu (Asakawa et al. 2002). Further specimens of *Arostrilepis* from Honshu and their DNA sequences are required to better understand the phylogeography and taxonomy of this group in Japan.

The adult tapeworms of *Microsomacanthus* sp. (nos. 19AK212, JA313, Para09, Para15, Para18, and Para19) were found from *Ap. speciosus* in Asahikawa and Obihiro. The following description was made based on one specimen (Fig. 3F–H): Whole body tiny, without gravid proglottids, 16 long by 1.2 in maximum width. Scolex 0.25 in maximum width. Rostellum 0.18 long, armed with 10 hooks, 0.022–0.025 in length. Suckers circular, four in number, 0.09–0.10 in diameter. Mature proglottids much longer in width, 0.028 in length by 0.49 in width. Genital pore unilateral. Testes oval to pyriform, three in number, situated triangularly, 0.13–0.15 long by 0.49–0.55 wide. Ovary amorphous, 0.13–0.15 long by 0.25–0.28 wide, positioned in center of proglottid. Small vitellarium unlobed, postovarian.

All the six isolates of *Microsomacanthus* sp. were subjected to DNA sequencing of *cox1*. The resultant sequences were highly homogeneous (mean pairwise divergence = 0.004). A BLAST homology search could not detect any sequences similar to them. In the case of 28S rDNA, the unknown species showed 99.6% similarity (1360 out of 1365 nucleotides identical) to *Microsomacanthus crenatus* (Goeze, 1782) from *Apodemus sylvaticus* (Linnaeus, 1758) in Croatia (database accession no. GU166246). Haukisalmi et al. (2010a) treated this isolate (*M. crenatus* in DNA databases) as “*Hymenolepis* muris-sylvatici.” A 28S rDNA-based phy-
logenetic tree supports that the unknown species belongs to *Microsomacanthus* (see the isolate JA313 in Fig. 2). It is highly probable that “*Hymenolepis* muris-sylvatici” or *Microsomacanthus murissylvatici* (Rudolphi, 1819) is identical to *M. crenatus* (Czaplinski and Vaucher 1994; Tenora 2004).

Most members of *Microsomacanthus* exclusively use birds as definitive hosts (Yamaguti 1959; Czaplinski and Vaucher 1994). However, *M. crenatus* have been recorded exceptionally from *Apodemus* mice in Europe (Prokopič 1967; Behnke et al. 1999; Tenora 2004; Klimpel et al. 2007). Such a distant host-switching suggests a possibility that the rodent-related species belong to another genus. The confirmation of this hypothesis is challenging, because the present DNA databases lack the 28S rDNA and *cox*1 sequences of *Microsomacanthus* from birds.

Our specimen is morphologically similar to *M. murissylvatici*, particularly in the sizes of strobila, scolex and suckers, when compared with the data of previous reports (Baer 1931; Prokopič 1967). A preliminary phylogeny of 28S rDNA (Haukisalmi et al. 2010a) suggests that “*Hymenolepis* muris-sylvatici” is sister to *Rodentolepis evaginata* (Barker and Andrews, 1915). Molecular phylogenetic assessments and subsequent taxonomic revisions are required for the rodent-related species of *Microsomacanthus*.

Family *Anoplocephalidae* Cholodkovsky, 1902
Genus *Paranoplocephala* Lühe, 1910
5. *Paranoplocephala kalelai*

( Tenora, Haukisalmi, and Henttonen, 1985)

The adult tapeworms of *Paranoplocephala kalelai* (nos. 19AK378, 19AK412, 19AK419, 19AK436, 19AK454-2, and 19AK454-3) were found from *Myodes rufocanus* in Asahikawa. This is the first record from Japan. The following description was made based on one specimen (Fig. 6A–C): Scolex distinctly wider than neck, 0.59 in maximum width. Rostellum absent. Suckers protruding, crateriform, four in number, 0.28–0.29 in diameter. Mature proglottids shorter in length than width, 0.40–0.45 long by 0.74–0.78 wide. Genital pore located on posterior half of lateral margin. Testes spherical, 26–30 in number, 0.04–0.06 in diameter. Cirrus sac 0.13–0.15 long by 0.07–0.08 wide. Seminal receptacle pyriform or ovoid, 0.13–0.15 long by 0.17–0.19 wide. Ovary irregularly lobed, 0.40–0.48 in diameter. Vitellarium asymmetrically bilobed, 0.19–0.22 long by 0.07–0.10 wide. Gravid proglottids longer in length than width, 1.09–1.29 long by 0.82–0.93 wide. Uterus labyrinthine, occupying entire field of proglottid.

A phylogenetic tree of *cox*1 showed that *P. kalelai*, *Paranoplocephala omphalodes* (Hermann, 1783) sensu stricto, *Paranoplocephala macrocephala* (Douthitt, 1915), and

![Fig. 7. A maximum-likelihood phylogenetic tree of the genus Paranoplocephala. The tree was made with mitochondrial *cox*1 sequences (546 nucleotide sites) under the substitutional model GTR+G+I. The isolates of this study (19AK378, 19AK412, 19AK419, 19AK436, 19AK454-2, and 19AK454-3) are shown in bold face. The DNA accession number of each taxon is shown in parenthesis. *Hymenolepis diminuta* (accession no. AF314223) was used as an outgroup taxon.](image-url)
Paranoplocephala jarrelli (Haukisalmi, Henttonen, and Hardman, 2006) are distinguishable from one another, and that our isolates from Hokkaido should be classified as P. kalelai (Fig. 7). The tree reconfirmed that the Fennoscandian isolates of P. kalelai could be divided into two clades named as Narvik and Kilpisjärvi (Haukisalmi et al. 2004). The Hokkaido isolates of P. kalelai showed a sister relationship to the Narvik clade. The values of pairwise divergence between the Narvik and Kilpisjärvi clades and between the Hokkaido and Narvik clades were 0.034 and 0.015, respectively. The sequencing of 28S rDNA supports the species identification (see the isolate 19AK378 in Fig. 2).

Members of the genus Paranoplocephala Lühe, 1910 are widely distributed in the Holarctic region (Haukisalmi et al. 2014). Currently, the species complex of P. omphalodes sensu lato has been divided into several species (Haukisalmi and Henttonen 2003; Haukisalmi et al. 2004, 2007; Vlasenko et al. 2019). Most species of Paranoplocephala parasitize Microtus voles, whereas P. kalelai is specific to Myodes voles in Fennoscandia (Tenora et al. 1985; Haukisalmi et al. 2004, 2007). Our data suggest that P. kalelai is distributed widely from Fennoscandia to the Far East, along with the geographic expansion of Myodes voles.

Apodemus mice in Hokkaido also serve as definitive hosts for several species of anoplocephalid tapeworms (Ishimoto 1974; Rausch 1976; Asakawa and Ohbayashi 1986; Iwaki et al. 1994b). Those were identified as P. omphalodes, Paranoplocephala Blanchardi (Moniez, 1891), Anoplocephaloides baeri Rausch, 1976, and Andrya apodemi Iwaki, Tenora, Abe, Oku, and Kamiya, 1994. Tenora et al. (1999) erected the genus Hokkaidocephala for anoplocephalid tapeworms from Apodemus mice in Hokkaido. Haukisalmi et al. (2008) examined the generic status and regarded Hokkaidocephala apodemi (=And. apodemi) and Hokkaidocephala baeri (=Ano. baeri) as valid species due to their unique uterine structure and development.

Moreover, unidentified species of Anoplocephalidae were recorded from Eo. smithii and Microtus montebelli (Milne-Edwards, 1872) in Honshu and Shikoku islands (Asakawa et al. 1992c).

Family Catenotaeniidae Spasskii, 1950
Genus Catenotaenia Janicki, 1904

The adult tapeworms of Catenotaenia sp. (nos. 18AK131, JA212, JA317, AMU, and O36) were found from My. rufocanus in Asahikawa, Nayoro, Otofuke, and Obihiro. The 28S rDNA sequence of the isolate JA317 has already been reported (Haukisalmi et al. 2017). The following description was made based on one specimen (Fig. 6D–F): Scolex unarmed, 0.23 in maximum width. Suckers spherical, four in number, 0.11–0.13 in diameter. Mature proglottids much longer in length than width, 1.30–1.50 long by 0.85–0.95 wide. Genital pore positioned on anterior margin. Testes mini-spherical, 0.42–0.60 in diameter, 80–96 in number, assembled in a cluster behind female glands. Ovary lobed, asymmetrical, widely occupies anterior space of proglottid. Vitellarium lobed, positioned posterior to genital pore. Gravid proglottids much longer in length than width, 1.30–1.50 long by 0.85–0.10 wide. Genital pore positioned on anterior half of lateral margin. Testes mini-spherical, 0.42–0.60 in diameter, 80–96 in number, assembled in a cluster behind female glands. Ovary lobed, asymmetrical, widely occupies anterior space of proglottid. Vitellarium lobed, positioned posterior to genital pore. Gravid proglottids widest in middle, 2.83–2.96 long by 0.82–0.95 wide. Uterine branches 34–52 in number.
tical to one another (mean pairwise divergence = 0.011). A BLAST homology search could not detect any sequences similar to them. In contrast, the 28S rDNA sequences of related species (Haukisalmi et al. 2017) allowed us to construct a phylogenetic tree. The resultant tree (Fig. 8) clearly showed that our isolates (AMU, JA212, and JA317) are distinct from *Catenotaenia henttoneni* Haukisalmi and Tenora, 1993, *C. microti* Haukisalmi, Hardman, and Henttonen, 2010, *C. cricetuli* Haukisalmi, Hardman, and Henttonen, 2010, *C. apodemi* Haukisalmi, Hardman, and Henttonen, 2010, and *C. kirgizica* (Tokobaev, 1959).

Members of *Catenotaenia* are known as parasites of voles (Haukisalmi et al. 2010b). In Japan, *Catenotaenia pusilla* (Goeze, 1782) was reported from *My. rufocanus*, *My. rutilus*, and *Mu. musculus* in Hokkaido and Honshu (Yamaguti 1935; Asakawa et al. 1983), while *Catenotaenia gracilae* Asakawa, Tenora, Kamiya, Harada, and Borkovcova, 1992 was described from *Eo. andersoni* and *Eo. smithii* in Honshu (Asakawa et al. 1992b). In addition, unidentified species of *Catenotaenia* have been recorded from *Ap. argenteus, My. rufocanus, My. rutilus, Eo. smithii, and Mt. montebelli*, without their detailed morphological information (Asakawa and Ohbayashi 1986; Asakawa and Tomonari 1988; Asakawa 1989; Asakawa et al. 1992b; Asakawa 1993; Ito and Itagaki 2003). The morphological classification of *Catenotaenia* is usually based on the number of uterine branches and the shape of proglottids. However, the diagnosis is challenging because the scolex lacks a rostellum and hooks, and other organs are generally uniform (Asakawa et al. 1992b; Haukisalmi et al. 2010b). *Catenotaenia* sp. found in this study is similar to *C. pusilla* and *C. gracilae* from the views of the size and shape of proglottids and the amount of anterior free space in mature proglottids. However, *Catenotaenia* sp. has a greater number of uterine branches (34–52) than those of *C. pusilla* (9–17), and a fewer number of testes (80–96) than those of *C. gracilae* (about 150). The present morphological and molecular information is still insufficient for the description of a new species.

**Family Davaineidae** Braun, 1900  
Genus *Raillietina* Fuhrmann, 1920  
7. *Raillietina* sp.

The adult tapeworms of *Raillietina* sp. (nos. 18AK99, JA304, Para33, Para36, Para38, Para42, Para44, and Para45) were found from *Ap. speciosus* in Asahikawa and Otófu. The following description was made based on one specimen (Fig. 6G, H): Scolex 0.38 wide. Neck absent. Suckers oval, four in number, 0.12–0.14 long by 0.12–0.13 wide, with numerous hooks on the inside of the sucker. Rostellum 0.72 long by 0.08 wide, armed with about 80 tiny hooks, 0.014–0.016 in length. Proglottids trapezoidal. Mature proglottids much shorter in length than width, 0.13–0.15 long by 1.1–1.2 wide. Genital pore unilateral, opened on anterior half of lateral margin. Testes oval, 0.28–0.35 long by 0.33–0.39 wide, divided into two groups by female gonad. Number of testes 26–29, less in the side of genital pore. Ovary lobed, 0.08–1.10 long by 0.14–0.18 wide. Vitellarium lobed, post-
All the isolates of *Raillietina* sp. were subjected to DNA sequencing of *cox1*. The result sequences were completely identical to one another, and not matched by any known sequences in DNA databases. In contrast, the 28S rDNA sequence of *Raillietina* sp. showed 99.9% similarity (1554 out of 1555 nucleotides identical) to that of *Raillietina coreensis* Honda, 1939 (the database accession number KP171525, published only in databases). This species was first described from *Apodemus agrarius* (Pallas, 1771) in Korea (Honda 1939), and subsequently found from *Apodemus* mice in Hokkaido (Iwaki et al. 1994c) and the northern part of Honshu (Asakawa et al. 1997; Ito and Itagaki 2003). The *cox1* sequence of *R. coreensis* from Korea (the type locality) is necessary for the species-level identification of *Raillietina* sp. in Hokkaido.

**Family Taeniidae** Ludwig, 1886  
Genus *Taenia* Linnaeus, 1758  
8. *Taenia crassiceps* (Zeder, 1800)

The larval cysticerci of *Taenia crassiceps* were found from the subcutaneous tissue of *My. rufocanus* in Asahikawa (Fig. 9A). This is the first record from Hokkaido. More than 50 proliferating cysticerci were recovered from one vole. The morphometric feature of the cysticercus is as follows: Whole body 1.0–2.3 mm in maximum diameter. Scolex armed with 34 hooks. Large hooks 0.173–0.175 long (n=10), 17 in number. Small hooks 0.133–0.136 long (n=10), 17 in number. The *cox1* sequence of the cysticercus (no. 19AK309) showed 99.8% similarity (939 out of 941 nucleotides identical) to that of *T. crassiceps* from North America (database accession no. AF216699) (Le et al. 2000).

This species is widely distributed in the northern hemisphere (Deplazes et al. 2019). The larval cysticerci were already found from *Ap. speciosus* and *Mi. montebelli* in Honshu (Sato and Kamiya 1989; Uchida et al. 1990, 2001; Ishama et al. 2000). Canid carnivores serve as the definitive hosts (Freeman 1962), and the cysticerci multiply in the subcutaneous tissue and body cavity of wide-ranging mammalian intermediate hosts including humans (Delvalle 1989; Miyaji et al. 1990; Deplazes et al. 2019). In Hokkaido, the main definitive host is still unclear.

**Family Taeniidae** Ludwig, 1886  
Genus *Hydatigera* Lamarck, 1816  
9. *Hydatigera taeniaeformis* (Batsch, 1786)

The bladder cysts of *Hydatigera taeniaeformis*, each containing a strobilocercus larva, were found from the liver of *My. rufocanus* in Asahikawa and *Ra. norvegicus* in Nayoro and Kushiro (Fig. 9B). The morphometric feature of the strobilocercus is as follows: Whole body 3.6–5.4 long by 2.8–3.6 wide (n=3). Scolex armed with 36 hooks. Large hooks 0.444–0.450 long (n=10), 19 in number. Small hooks 0.268–0.271 long (n=10), 19 in number. The *cox1* sequences of the strobilocerci (nos. Ces05 and O22) showed 99.2% similarity (923 out of 930 nucleotides identical) to that of *Hy. taeniaeformis* from China (accession no. FJ597547) (Liu et al. 2011).

The former *Hy. taeniaeformis* sensu lato is a cryptic species complex, including *Hy. taeniaeformis* and *Hydatigera kaniyai* Iwaki, 2016 (Galimberti et al. 2012; Jia et al. 2012; Nakao et al. 2013; Lavikainen et al. 2016). Both species prevail in Hokkaido, using domestic cats and rodents as definitive and intermediate hosts, respectively (Iwaki et al. 1993; Asakawa and Fukumoto 1997; Okamoto et al. 2007). In general, the host specificity of both species is strict in selecting intermediate hosts, namely, murids (e.g., *R. norvegicus*) for *Hy. taeniaeformis* and cricetids (e.g., *My. rufocanus*) for *Hy. kaniyai* (Nonaka et al. 1994; Iwaki et al. 1994a; Lavikainen et al. 2016). However, in this study, fully developed strobilocerci of *Hy. taeniaeformis* were found from cricetids.

In Japan, the adult tapeworms of *Hy. taeniaeformis* sensu lato have been found from the following carnivores: the cat, *Felis catus* Linnaeus, 1758; the dog *Canis lupus familiaris* Linnaeus, 1758; the Tushima leopard cat, *Prionailurus bengalensis euptilurus* (Elliot, 1871); the raccoon, *Procyon lotor* (Linnaeus, 1758) (Oiishi and Kume 1973; Yagisawa 1978; Uga et al. 1983; Matoba et al. 2003; Yasuda et al. 2005). A special attention should be paid to the raccoon, an invasive species from North America, because it is now increasing in number in Hokkaido (Ikedo et al. 2004). Both *Hy. taeniaeformis* and *Hy. kaniyai* are also alien species probably due to the anthropogenic movement of domestic cats or commensal rodents into Japan (Lavikainen et al. 2016).

**Family Taeniidae** Ludwig, 1886  
Genus *Echinococcus* Rudolphi, 1801  
10. *Echinococcus multilocularis* Leuckart, 1863

The lesions of alveolar hydatid containing numerous pro-toscolecites were found from the liver, lungs, and abdominal cavity of *My. rufocanus* in Asahikawa and Otofuke (Fig. 9C). The appearance of the lesions completely agreed with that of *Echinococcus multilocularis* (Houin et al. 1982; Miller et al. 2016). Although the two isolates of *E. multilocularis* were obtained in this study, we did not perform any detailed analysis because the morphological feature and genetic uniformity of *E. multilocularis* have already been well examined in Hokkaido (Yagi et al. 1986; Iwaki et al. 1993; Nakao et al. 2003; Okamoto et al. 2007).

This species is well known to cause human alveolar echino-coccosis, which is one of the most important zoonoses in the Holarctic region. A small number of the human cases occur every year in Hokkaido (Takahashi et al. 2005; National Institute of Infectious Diseases 2019; Kamiyama 2020). The red fox, *Vulpes vulpes* Linnaeus, 1758, is the main definitive host of *E. multilocularis* (Romig et al. 2017; Tsukada et al. 2000). It seems that *E. multilocularis* has been recently introduced into Hokkaido from the Kurile islands by migrant foxes on drift ice or the anthropogenic movement of foxes and rapidly spread throughout Hokkaido (Yamashita 1956). A lower genetic divergence among the parasite population in Hokkaido supports this hypothesis (Nakao...
Table 2. A comprehensive record of cestodes found from murid and cricetid rodents in Japan.

| Families                | Species                                   | Stages | Hosts | Localities | References                                      |
|-------------------------|-------------------------------------------|--------|-------|------------|-------------------------------------------------|
| Hymenolepididae         | *Arostrilepis horrida sensu lato*         | Adult  | Mruf, Ea, Es | HK, H       | Asakawa 1993; Asakawa et al. 2002               |
|                         | *Arostrilepis tenacirostra*               | Adult  | Mruf  | HK         | This study                                      |
|                         | *Coronacanthus apodemii*                  | Adult  | Aa, As | HK, H       | Yamaguti 1954; Ishimoto 1974; Asakawa and Obhayashi 1986 |
|                         | *Hymenolepis diminuta*                   | Adult  | Aa, As, Rn, Rr, Mmu | H   | Hamajima 1963; Hori and Kusui 1972; Ito and Itagaki 2003 |
|                         | *Hymenolepis pseudominuta*               | Adult  | Aa, As | HK, H       | Tenora et al. 1994; Pirurse et al. 2014         |
|                         | *Hymenolepis spp.*                       | Adult  | As, Mmu | HK         | Asakawa 1989; this study                        |
|                         | Rodentolepis nana*                       | Adult  | Mmu, Rn | H, R        | Hamajima 1963; Kamiya et al. 1968; Hori and Kusui 1972; Uga et al. 1983 |
|                         | Microsomacanthus sp.                     | Adult  | As     | H           | This study                                      |
|                         | *Hymenolepididae* gen. spp.*             | Adult  | Aa, As | HK, H       | Asakawa et al. 1992a; Sakata et al. 2003        |
|                         | *Anoplocephaloides dentatoides*          | Adult  | Mruf  | HK Sato et al. 1993 |
|                         | *Anoplocephaloides* spp.                 | Adult  | Aa, As, Mruf, Es | HK, H       | Asakawa et al. 1983; Asakawa and Obhayashi 1986; Asakawa 1989 |
|                         | *Hokkaidocepha* alapodemii*              | Adult  | Aa     | HK          | Ishikawa et al. 1994a; Haikisalmi et al. 2008   |
|                         | *Hokkaidocepha* laeri*                   | Adult  | Aa, As | HK          | Asakawa and Obhayashi 1986; Haikisalmi et al. 2008 |
|                         | *Panpostodocha* blancundii*              | Adult  | Aa, As | HK          | Asakawa and Obhayashi 1986                      |
|                         | *Panpostodocha* omphalodes*              | Adult  | Aa, As | HK          | Iwagui 1974                                    |
|                         | *Panpostodocha* kalida*                  | Adult  | Mmu    | HK This study |
|                         | *Panpostodocha* spp.*                    | Adult  | Es, Mmu | H          | Asakawa 1989; Asakawa et al. 1992c               |
|                         | *Catenotaenia pustilla*                  | Adult  | Mmu, Mmu | HK, H       | Yamaguti 1935; Asakawa et al. 1983               |
|                         | *Catenotaenia gracilis*                  | Adult  | Ea     | H           | Asakawa et al. 1992b                           |
|                         | *Catenotaenia* spp.*                     | Adult  | Aa, Mruf, Mrut, Es, Mmu | HK, H       | This study; Asakawa and Tonomori 1988; Asakawa 1989; Ito and Itagaki 2003 |
| Davaineidae             | *Radlletina corenseis*                   | Adult  | Aa, As | H           | Ishikawa et al. 1994c; Asakawa et al. 1997; Ito and Itagaki 2003 |
|                         | *Radlletina cedabensis*                  | Adult  | Ms, Rr | R           | Kamiya and Kanda 1977                          |
|                         | *Radlletina* spp.*                       | Adult  | Aa, Ms | HK, R       | Kamiya and Machida 1977; Asakawa 1989; this study |
| Taeniidae               | *Echinococcus multilocularis*            | Larva  | Aa, As, Mruf, Mrut, Rr | HK       | Yagi et al. 1986; Asakawa 1989; Ishikawa et al. 1993; Fukumoto et al. 2017; this study |
|                         | *Hydatigera kamya*                      | Larva  | Mruf | HK Lakivainen et al. 2016 |
|                         | *Hydatigera taeniiformis*               | Larva  | Aa, As, Mruf, Mrut, Mmu, Rr, Rr | HK, R       | Kamiya and Machida, 1977; Asakawa and Fukumoto 1997; Banzai et al. 2018; this study |
|                         | *Taenia crassiceps*                     | Larva  | Aa, Mruf, Mmu | HK         | Uchida et al. 1990; Iitaka et al. 2000; this study |
|                         | *Taenia* polyacantha*                   | Larva  | Aa     | H, HK (?)   | Iitaka et al. 2000                            |
|                         | *Taenia* spp.*                          | Larva  | Aa, Mruf | HK         | Ishihito 1974; Asakawa et al. 1983; Yagi et al. 1986 |
| Paruterinidae           | *Cladotaenia* sp.*                      | Larva  | Aa, As, Mruf, Mrut, Mmu | HK       | Ishihito 1974; Yagi et al. 1986; Kugi 1987; Asakawa et al. 1991; Ito and Itagaki 2003 |

---

* Asterisks indicate the followings: single asterisk, a common species between Hokkaido and the Russian Far East; double asterisk, a common species between Hokkaido and Honshu; triple asterisk, a common species among Hokkaido, Honshu, and the Russian Far East. The geographic ranges of unidentified species are excluded.  
** Abbreviations of host rodents are as follows: Aa, *Apodemus argenteus*; As, *Apodemus speciosus*; Mruf, *Myodes rufocanus*; Mrut, *Myodes rutilus*; Ea, *Eothenomys andersonii*; Es, *Eothenomys smithii*; Mmu, *Microtus montebelli*; Mmm, *Mus musculus*; Rn, *Rattus norvegicus*; Rr, *Rattus rattus*.  
# Localities of the Japanese Archipelago are shown with the following three biogeographic regions of Japan: HK, Hokkaido; H, Honshu, Shikoku, Kyushu and adjacent small islands; R, Ryukyu Islands.
et al. 2003; Okamoto et al. 2007). Red foxes are colonizing urban areas because they can adapt to the artificial environment (Tsukada et al. 2000; Uraguchi et al. 2009). One of the present isolates was obtained from an urban park in Asahikawa.

**Conclusion.** Our collections and literature search revealed that the cestode fauna of murid and cricetid rodents in Japan consists of at least 30 species from 6 families (Table 2). Among them, 23 species occur in Hokkaido. The species composition is strongly affected by the nearby Eurasian continent. It is most likely that the diverse cestode fauna is caused by rodent migrations over land bridges between Hokkaido and Sakhalin and between Hokkaido and Honshu during the late Pleistocene. The recent anthropogenic introduction of host animals seems to be responsible for the distribution of *T. crassiceps*, *Hyd. taeniaeformis*, *Hyd. kamiyai*, and *E. multilocularis*. This report contains the first records of *A. tenuicirrosa*, *P. kaelinii*, and *T. crassiceps* from Hokkaido. The former two species correspond to the first records in Japan. Several cestodes are still waiting to be further investigated and placed into suitable taxonomic positions by an integrated approach of molecular phylogeny, morphology, and ecology.

In this study, nuclear and mitochondrial DNA barcodes were generated for some cestodes from rodents in Hokkaido (Table 1). The DNA barcoding system has a great potential to revise existing classification systems and to accelerate the discovery of cryptic species. In order to expand its potential, it is necessary to enhance DNA databases with reliable data from cestode taxonomists across the world. Moreover, it is most important to standardize DNA markers for the taxonomy of cestodes. In previous studies on rodent cestodes, various regions of nuclear and mitochondrial DNA were used as DNA markers for phylogenetic analyses (Haukisalmi et al. 2004; Haukisalmi et al. 2010b; Makarikov et al. 2013). The use of the markers, however, lacks consistency. We especially recommend the primer set, JB3 and CO1-R trema (Miura et al. 2005), because it enables the amplification of cox1 sequences (approximately 800 bases in length) from most platyhelminths. The sequencing of mitochondrial cox1 and nuclear 28S rDNA is a minimum requirement for the species and genus level identification of cestodes.

**Acknowledgements**

We are grateful to Hikaru Tsuno (Hokkoku Museum, Nayoro) and Shigeharu Terui (Environment Grasp Promotion network-PEG, NPO, Kushiro) for supplying rodent samples. Members of Koizumi lab. for field-based ecology (Graduate School of Environmental Science, Hokkaido University) assisted us in collecting rodents. Thanks are also due to Hirotaka Katakishi (Azabu University) for supporting the field work and supplying cestode samples and to Akira Ito (Asahikawa Medical University) for providing a laboratory strain of *Hym. pseudodiminuta*.

**References**

Anders, J. L., Nakao, M., Uchida, K., Ayer, C. G., Asakawa, M., and Koizumi, I. 2019. Comparison of the intestinal helminth community of the large Japanese field mouse (*Apodemus speciosus*) between urban, rural, and natural sites in Hokkaido, Japan. Parasitology International 70: 51–57.

Andreassen, J., Bennet-Jenkins, E. M., and Bryant, C. 1999. Immunology and biochemistry of *Hymenolepis diminuta*. Advances in Parasitology 42: 223–275.

Ariola, V. 1899. Il gen. *Scyphocephalus* Rigg. E proposta di una nuova classificazione dei cestodi. Atti della Società Ligustica di Scienze Naturali e Geografiche, Genova 10: 160–167.

Asakawa, M. 1989. Helminth fauna of the Japanese Microtidae and Muridae. Mammalian Science 29: 17–35. [In Japanese]

Asakawa, M. 1993. Parasitic helminths obtained from rodents on Nemuro peninsula and Notsu-saki, Hokkaido, Japan. Memoirs of the National Science Museum, Tokyo 26: 75–82. [In Japanese]

Asakawa, M. and Fukushima, S. 1997. A report on abnormal metacestode of *Taenia taeniaeformis* obtained from Norway rat, *Rattus norvegicus*, in Ebusu-shi, Hokkaido, Japan. Journal of the College of Dairying. Natural science 21: 171–172. [In Japanese]

Asakawa, M., Mori, A., and Motokawa, M. 1997. Parasitic helminths of Japanese wood mouse, *Apodemus argentus* (Muridae: Rodentia), collected on Kinkazan Island, Miyagi Pref., Japan. Journal of the College of Dairying. Natural science 22: 147–150. [In Japanese]

Asakawa, M. and Ohbayashi, M. 1986. Genus *Heligmosomoides* Hall, 1916 (*Heligmososomidae*: Nematoda) from the Japanese wood mouse, *Apodemus* spp. I. A taxonomical study on four taxon of the genus *Heligmososomoides* from three species of the Japanese *Apodemus* spp. Journal of the College of Dairying. Natural science 11: 317–331. [In Japanese]

Asakawa, M., Tamura, T., Fukushima, S., and Ohbayashi, M. 1992a. Parasitic helminths of small mammals in a sandbank of Lake Saroma, Hokkaido, Japan. Journal of the College of Dairying. Natural Science 17: 9–16. [In Japanese]

Asakawa, M., Tenora, F., Kamiya, M., Harada, M., and Borkovcova, M. 1992b. Taxonomical study on the genus *Catenotaenia* Jankic, 1904 (Cestoda) from voles in Japan. Bulletin of the Biogeographical Society of Japan 47: 73–76. [In Japanese]

Asakawa, M., Tenora, F., and Koubkova, B. 2002. *Arostrilepis horrida* (Linstow, 1901) (Cestoda, Hymenolepididae) from *Eothenomys* spp. (Rodentia) in Japan. Biogeography 4: 51–55.

Asakawa, M., Tenora, F., Fukushima, S., Kano, K., and Tomonari, T. 1992c. Faunal and zoogeographical study on the parasitic helminths of voles and field mice in Shikoku, Japan. Bulletin of Tokushima Prefectural Museum 2: 51–75. [In Japanese]

Asakawa, M. and Tomonari, T. 1988. Study on the internal parasite fauna of the Japanese grass vole, *Microtus montebelli* Milne-Edwards. Bulletin of the Biogeographical Society of Japan 43: 19–23. [In Japanese]

Asakawa, M., Yamaguchi, S., Fujino, R., Ohbayashi, M., and Hasegawa, H. 1991. Study on the helminth fauna of the Japanese wood and field mice, *Apodemus* spp. on the Tsushima and Iki Islands. Bulletin of the Biogeographical Society of Japan 46: 59–68. [In Japanese]

Asakawa, M., Yokoyama, Y., Fukushima, S., and Ueda, A. 1983. A study of the internal parasites of *Clethrionomys rufocanus bedfordiae* (Thomas). Japanese Journal of Parasitology 32: 399–411.

Auwera, G. van der, Chapelle, S., and Wachter, R. de. 1994. Structure and phylogeny of the oomycetes. FEBS Letters 338: 133–136.

Bae, J. G. 1931. Sur la position systématique du *Taenia muris-sylvatici*
Cestode fauna of rodents in Hokkaido

Rudolphi, 1819. Bulletin de la Société neuchâteloise des sciences naturelles 55: 35–39.

Banai, A., Tanikawa, T., Kimura, G., Sasaki, T., and Kawakami, Y. 2018. Parasitic helminths collected from the brown rat, *Rattus norvegicus*, in Chuo Ward, Tokyo, Japan. Medical Entomology and Zoology 69: 171–176. [In Japanese]

Batsch, A. J. G. K. 1786. *Naturegeschichte der Bandwurmgattung überhaupt und ihrer Arten insbesondere, nach den neuen Beobachtungen in einem systematischen Auszuge*. Johann Jacob Gebauer, Halle, 298 pp.

Behnke, J. M., Lewis, J. W., Mohd Zain, S. N., and Gilbert, F. S. 1999. Helminth infections in *Apodemus sylvaticus* in southern England: interactive effects of host age, sex and year on the prevalence and abundance of infections. Journal of Helminthology 73: 31–44.

Bowles, J., and McManus, D. P. 1993. Rapid discrimination of *Echinococcus* species and strains using a polymerase chain reaction-based RFLP method. Molecular and Biochemical Parasitology 57: 231–240.

Braun, M. 1900. Cestodes. Pp. 927–1731. in *Bronn, H. G. (Ed.)* *Brehm’s Naturgeschichte der Tiere in allgemeinem und systematischem Auszuge*. Verlagsgesellschaft, Leipzig.

Brown, W. M., George, M. Jr., and Wilson, A. C. 1979. Rapid evolution of animal mitochondrial DNA. Proceedings of the National Academy of Sciences, USA 76: 1967–1971.

Cholodkowsky, N. 1902. Contributions à la connaissance des Tenias des Mammifères. Bulletin de la Société neuchâteloise des sciences naturelles 55: 35–39.

Deplazes, P., Eichenberger, R. M., and Grimm, F. 2019. Wildlife-transmitted *Davainea* in the grey-sided vole *Myodes rufocanus* in northern Fennoscandia. Acta Parasitologica 52: 335–341.

Dobson, M. 1994. Patterns of distribution in Japanese land mammals. Mammal Review 24: 91–111.

Echinococcus multilocularis. *Infestation in a domestic cat and its impact in Japan*. Grobal Environmental Resource 12: 403–413.

Echino - coccus *hominis*. Helminth parasites of the mouse living in two different environments. Japanese Journal of Parasitology 12: 12–15. [In Japanese]

Fukumoto, S., Yamaida, S., Fushikida, M., Toyoda, S., Nishikawa, T., Hi - guchi, H., Ueno, H., Ueda, H., Sugiyama, H., and Morishima, Y. 2017 Natural larval *Echinococcus multilocularis* infection in a Nor - way rat, *Rattus norvegicus*, captured indoors in Hokkaido, Japan. Journal of Veterinary Medical Science 79: 1857–1860.

Fuhrmann, O. 1920. Considérations générales sur les Davainea. Festungen in einem systematischen Auszuge. Akademische Verlagsgesellschaft, Leipzig.

Furuse, A., Nagai, T., and Asakawa, M. 2014. Parasitic helminths of field mice, *Apodemus speciosus*, on Okushiri Island, Hokkaido, Japan, with a special reference to comparative study between 1990 and 2012. Journal of the College of Dairying. Natural Science 39: 37–39. [In Japanese]

Galbreath, K. E., Ragaliauskaitė, K., Kontrimavičius, L., Makarikov, A. A., and Hoberg, E. P. 2013. A widespread distribution for *Aorostri - lepis tenacirrostra* (Eucestoda: Hymenolepididae) in *Mus* voles (*Cricetidae: Arvicolinae*) from the Palearctic based on molecular and morphological evidence: historical and biogeographic implications. Acta Parasitologica 58: 441–452.

Galimberti, A., Romano, D. F., Genchi, M., Paoloni, D., Vercillo, F., Bizzarri, L., Sassera, D., Bandi, C., Genchi, C., Ragni, B., and Casiraghi, M. 2012. Integrative taxonomy at work: DNA barcoding of taenids harboured by wild and domestic cats. Molecular Ecology Resource 12: 403–413.

Haukisalmi, V., Asakawa, M., and Gubányi, A. 2008. The status of the genus *Hokkaidocephala* Tenora, Gulyaev & Kamiya, 1999 (Cesto - da: Anoplocephalidae), parasites of the endemic Japanese field mice (*Apodemus* spp.). Zootaxa 125: 62–68.

Haukisalmi, V., Hardman, L. M., Foronda, P., Felu, C., Laakkonen, J., Niemimaa, J., Lehtonen, J. T., and Henthonen, H. 2010a. Systematic relationships of hymenolepidid cestodes of rodents and shrews inferred from sequences of 28S ribosomal RNA. Zoologica Scripta 39: 631–641.

Haukisalmi, V., Hardman, L. M., and Henthonen, H. 2010b. *Taxonomic review of cestodes of the genus Catenotaenia* Janicki, 1904 in Eurasia and molecular phylogeny of the *Catenotaeniidae* (Cyclophy - lidae). Zootaxa 2489: 1–33.

Haukisalmi, V., Hardman, L. M., Hoberg, E. P., and Henthonen, H. 2014. Phylogenetic relationships and taxonomic revision of *Para - nophlocephala* Lühe, 1910 sensu lato (*Cestoda: Cyclophyllidea, Anop - locephalidae*). Zootaxa 3873: 371–415.

Haukisalmi, V., Hardman, L. M., Niemimaa, J., and Henthonen, H. 2007. *Taxonomy and genetic divergence of Paranophlocephala kulei* (Tenora, *Hokkaidocephalidae*). (Cestoda, Anoplocephalidae) in the grey-sided vole *Myodes rufocanus* in northern Fennoscandia. Acta Parasitologica 52: 335–341.

Haukisalmi, V. and Henthonen, H. 2003. What is *Paranophlocephala macrocephalopsis* (Douthitt, 1915) (*Cestoda: Anoplocephalidae*)? Systematic Parasitology 54: 53–69.

Haukisalmi, V., Ribas, A., Junker, K., Spickett, A., Matthee, S., Henthonen, H., Irjer, J., Halajian, A., Anders, J. L., and Nakao, M. 2017. Molecular systematics and evolutionary history of catenotaeniid cestodes (*Cyclophyllidae*). Zoologica Scripta 47: 221–230.

Haukisalmi, V., Wickström, L. M., Henthonen, H., Hantula, J., and Gubányi, A. 2004. Molecular and morphological evidence for multiple species within *Paranophlocephala omphalodes* (Cestoda, Anoplocephalidae) in *Microtus* voles (*Arvicolinae*). Zoologica Scripta 33: 277–290.

Honda, D. 1939. On a new cestode, *Raillietina (Raillietina) corensis* n. sp. from a field mouse, *Apodemus agrarius coreae* in Chosen. Journal of Chosen Medical Association 29: 229–233. [In Japanese]

Ikeda, T., Asano, M., Matoba, Y., and Abe, G. 2004. Present status of in - vasive alien raccoon and its impact in Japan. Grobal Environmental Research 8: 125–131.

Ishii, A., Sekijima, T., Asakawa, M., Tenora, F., and Uchikawa, R. 2003. *Hymenolepis pseudodiminuta* Tenora et al. 1994 from *Apodemus speciosus* and *H. diminuta*: a comparison of experimental infec -
tions in rats. Parasitology Research 89: 297–301.

Ishimoto, Y. 1974. Studies on helminths of voles in Hokkaido I. Taxonomic study. Japanese Journal of Veterinary Research 22: 1–12.

Ito, M. and Itagaki, T. 2003. Survey on wild rodents for endoparasites in Iwate Prefecture, Japan. Journal of Veterinary Medical Science 65: 1151–1153.

Iwaki, T., Hatakeyama, S., Nonaka, N., Miyai, S., Hokohata, Y., Okamoto, M., Ooi, H. K., Oku, Y., and Kamiya, M. 1993. Survey on larval 

Echinococcus multilocularis and other hepatic helminths in rodents and insectivores in Hokkaido, Japan, from 1985 to 1992. Japanese Journal of Parasitology 42: 502–506.

Iwaki, T., Nonaka, N., Okamoto, M., Oku, Y., and Kamiya, M. 1994a. Developmental and morphological characteristics of Taenia taeniiformis (Batsch, 1786) in Clethrionomys rafocanus bedfordiae and Rattus norvegicus from different geographical locations. Journal of Parasitology 80: 461–467.

Iwaki, T., Tenora, F., Abe, N., Oku, Y., and Kamiya, M. 1994b. Andrya apodemi n. sp. (Cestoda: Anoplocephalidae), a parasite of Apodemus argenteus (Rodentia: Muridae) from Hokkaido, Japan. Journal of the Helminthological Society of Washington 61: 215–218.

Iwaki, T., Tenora, F., and Kamiya, M. 1994c. New host and distribution record of Raillietina (Raillietina) corenisi (Cestoda) from Apodemus argenteus (Rodentia) in Japan. Journal of the Helminthological Society of Washington 61: 238–240.

Janicki, C. 1904. Zur Kenntnis einiger Saugetiercestodenten. Zoologischer Anzeiger 27, 770–782.

Jia, W., Yan, H., Lou, Z., Ni, X., Dyachenko, V., Li, H., and Littlewood, D. T. J. 2016. Cestode genera and genomes support a cryptic species of tapeworm within Taenia taeniaeformis. Acta Tropica 123: 238–240.

Kamiya, M., Chizei, H., and Sasa, M. 1968. A survey on helminth parasites of rats from Ishikawa Prefecture, Japan. Kugi, G. 1987. Studies on the Helminth Fauna of Vertebrates in Oita Prefecture. Part 1. Mammalian Helminths. Published by the author, 137 pp.

Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549.

Lamarck, J. B. 1816. Histoire Naturelle des Animaux sans Vertébres, Tome Troisieme. Verdière, Paris, 586 pp.

Lavikainen, A., Iwaki, T., Haukisalmi, V., Konyaev, S. V., Casiraghi, M., Dokuchaev, N. E., Galimberti, A., Halajian, A., Hen-tonen, H., Ichikawa-Seki, M., Itagaki, T., Krivopalov, A. V., Meri, S., Morand, N., Năreaho, A., Olsson, G. E., Ribas, A., Terefe, Y., and Nakao, M. 2016. Reappraisal of Hydatigera taeniiformis (Batsch, 1786) (Cestoda: Taeniidae) sensu lato with description of Hydatigera kamiyai n. sp. International Journal for Parasitology 46: 361–374.

Le, T. H., Blair, D., Agatsuma, T., Humair, P. F., Campbell, N. J., Iwagami, M., Littlewood, D. T. J., Peacock, B., Johnston, D. A., Bartley, J., Rollinson, D., Herniou, E. A., Zarlenz, D. S., and McManus, D. P. 2000. Phylogenies inferred from mitochondrial gene orders—A cautionary tale from the parasitic flatworms. Molecular Biology and Evolution 17: 1123–1125.

Leuckart, K. G. R. 1863. die menschlichen parasiten. Archives des Sciences Physiques et Naturelles 16: 243–245.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturrea, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Vol. I. Laurentii Salvii, Holmiae, pp. 824.

Liu, G., Lin, R., Li, M., Liu, W., Liu, Y., Yuan, Z., Song, H., Zhao, G., Zhang, K., and Zhu, X. 2010. The complete mitochondrial genomes of three cestode species of Taenia infecting animals and humans. Molecular Biology Reports 38: 2249–2256.

Lopez-Neyra, C. R. 1942. Division del género Hymenolepis Weinland (s.l) en otros mas naturales. Revista Ibérica Parasitología 2: 46–93.

Ludwig, H. 1886. Cestodes. Pp. 886–889. In: Leunis J. and Ludwig H. (Eds) Dr. Johannes Leunis Synopsis der thierkunde. Ein handbuch für höhere lehranstalten und für alle, welche sich wissenschaftlich mit der naturgeschichte der thiere beschäftigen wollen, Vol. II, Hahnsche buchhandlung. Hannover.

Lühe, M. 1910. Cestoden. Pp. 1–153. In: Brauer, A. (Ed.) Die Süsswasser fauna Deutschlands. Gustav Fischer, Jena.

Makarikov, A. A., Galbreath, K. E., and Hoberg, E. P. 2013. Parasite diversity in the Holarctic nexus: species of Arostrilepis (Eucestoda: Hymenolepididae) in voles and lemmings (Cricetidae: Arvicolidae) from greater Beringia. Zootaxa 3608: 401–439.

Makarikov, A. A., Gulyaev, V. D., and Kontrimavichus, V. L. 2011. A redescription of Arostrilepis horrida (Linstow, 1901) and descriptions of two new species from Palaeaeartic microtine rodents, Arostrilepis macrocirrosus sp. n. and A. tenuicirrosus sp. n. Cestoda: Hymenolepididae. Folia Parasitologica 58: 108–120.

Makarikov, A. A. and Hoberg, E. P. 2016. Broadening diversity in the Arostrilepis horrida complex: Arostrilepis kontrimavichusi n. sp. (Cyclophyllidea: Hymenolepididae) in the western red-backed vole Myodes californicus (Merriam) (Cricetidae: Arvicolinae) from temperate latitudes of the Pacific Northwest, North America. Systematic Parasitology 93: 467–477.

Makarikov, A. A. and Kontrimavichus, V. L. 2011. A redescription of Arostrilepis heringiensis (Kontrimavichus et Smirnova, 1991) and descriptions of two new species from Palaeaeartic microtine rodents, Arostrilepis intermedius sp. n. and A. janicki sp. n. (Cestoda: Hymenolepididae). Folia Parasitologica 58: 289–301.

Makarikov, A. A. and Tkach, V. V. 2013. Two new species of Hymenolepis (Cestoda: Hymenolepididae) from Spalacidae and Muridae (Rodentia) from eastern Palaeartic. Acta Parasitologica 58: 37–49.

Mas-Coma, S. and Tenora, F. 1997. Proposal of Arostrilepis n. gen. (Cestoda: Hymenolepididae). Research and Reviews in Parasitology 93: 103–121.

Matoba, Y., Asano, M., Yagi, K., and Asakawa, M. 2003. Detection of a taeniid species Taenia taeniaeformis from a feral raccoon Procyon lotor and its epidemiological significance. Mammal Study 28: 157–160.

Miller, A. L., Olsson, G. E., Walburg, M. R., Sollenberg, S., Skarin, M. L., Wahlström, H., and Höglund, J. 2016. First identifica-
tion of *Echinococcus multilocularis* in rodent intermediate hosts in Sweden. International Journal for Parasitology: Parasites and Wildlife 5: 56–63.

Millen-Parra, V. and Jaeger, J. J. 2001. Island biogeography of the Japanese terrestrial mammal assemblages: An example of a relic fauna. Journal of Biogeography 26: 959–972.

Miura, K., Higashiura, Y., and Maeto, K. 2017. Evaluation of easy, non-destructive methods of DNA extraction from minute insects. Applied Entomology and Zoology 52: 349–352.

Miura, O., Kuris, A. M., Torchin, M. E., Hechinger, R. F., Dunham, E. J., and Chiba, S. 2005. Molecular-genetic analyses reveal cryptic species of trematodes in the intertidal gastropod, *Batillaria cunningi* (Crose). International Journal for Parasitology 35: 793–801.

Miyaji, S., Oka, Y., Kamiya, M., Okamoto, M., Ohbayashi, M., Uchida, A., and Rausch, R. L. 1990. Growth of a Japanese isolate of *Taenia crassiceps* in intermediate and definitive hosts. Parasitology Research 76: 351–354.

Montgomery, S. S. J., Montgomery, W. I., and Dunn, T. S. 1987. Biochemical, physiological and morphological variation in unarmored hymenolepids (Eucestoda: Cyclophyllidae). Zoological Journal of the Linnean Society 91: 293–324.

Motokawa, M. 2017. “Land emergence” and “elevation shift” affect diversification: A new perspective toward understanding the high species diversity of terrestrial animals in Japan. Pp. 3–23. In: Motokawa, M. and Kajihara, H. (Eds) Species diversity of animals in Japan. Springer, Berlin.

Motokawa, M. 2016. *Mice and Rats in Japan: Their Diversity and Evolution*. University of Tokyo Press, Tokyo, 241 pp. [in Japanese]

Nakao, M., Lavikainen, A., Iwaki, T., Haukisalmi, V., Konyaev, S., Oka, Y., Okamoto, M., and Ito, A. 2013. Molecular phylogeny of the genus *Taenia* (Cestoda: Taeniidae): Proposals for the resurrection of *Hydatigera* Lamarck, 1816 and the creation of a new genus *Versteria*. International Journal for Parasitology 43: 427–437.

Nakao, M., Sako, Y., and Ito, A. 2003. Isolation of polymorphic microsatellite loci from the tapeworm *Echinococcus multilocularis*. Infection, Genetics and Evolution 3: 159–163.

National Institute of Infectious Diseases. 2019. *Echinococcosis in Japan, 1999–2018*. Infectious Agents Surveillance Report 40: 33–34.

Nkouawa, A., Haukisalmi, V., Li, T., Nakao, M., Lavikainen, A., Chen, X., Henttonen, H., and Ito, A. 2016. Cryptic diversity in hymenolepid tapeworms infecting humans. Parasitology International 120: 423–428.

Nokouta, A., Haukisalmi, V., Li, T., Nakao, M., Lavikainen, A., Chen, X., Henttonen, H., and Ito, A. 2016. Cryptic diversity in hymenolepid tapeworms infecting humans. Parasitology International 65: 83–86.

Nonaka, N., Iwaki, T., Okamoto, M., Ooi, H. K., Oka, Y., Ohbayashi, M., and Kamiya, M. 1994. Infectivities of four isolates of *Taenia taeniaeformis* to various rodents. Journal of Veterinary Medical Science 56: 565–567.

Ohdachi, S. D., Iwasa, Y., Matsuura, M. A., Fukui, D., and Saitoh, T. 2015. *The Wild Mammals of Japan, Second edition*. Shoukadoh Tokai-sha, Tokyo, 506 pp.

Oishi, I. and Kume, S. 2003. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 55: 213–314. [in Japanese]

Ohishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.

Oishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.

Oishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.

Oishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.

Oishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.

Oishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.

Oishi, I. and Kume, S. 1973. Helminth parasites of cats in Tokyo area. Journal of Veterinary Medical Sciences 35: 793–801.
Uchida, A., Uchida, K., Kawakami, Y., Doi, R., Kanda, E., and Nihei, N. 2001. Epidemiological Surveys of Helminths in Wild Mammals of Central Japan. Journal of the Japan Veterinary Medical Association 54: 635–638.

Uga, S., Matsumura, T., Yamada, T., Onishi, T., and Goto, M. 1983. A helminthological survey on cats in Hyogo Prefecture. Japanese Journal of Parasitology 32: 91–98.

Uraguchi, K., Yamamura, K., and Sai, T. 2009. Estimating number of families for an urban fox population by using two public data sets. Population Ecology 51: 271–277.

Vilas, R., Criscione, C. D., and Blouin, M. S. 2005. A comparison between mitochondrial DNA and the ribosomal internal transcribed regions in prospecting for cryptic species of platyhelminth parasites. Parasitology 131: 839–846.

Weinland, D. F. 1858. Human Cestodes: An Essay on the Tapeworms of Man: Giving a Full Account of Their Nature, Organization, and Embryonic Development; the Pathological Symptoms They Produce, and the Remedies which Have Proved Successful in Modern Practice, to which is Added an Appendix, Containing a Catalogue of All Species of Helminthes Hitherto Found in Man. Cambridge, England, x+93 pp.

Yagi, K., Takahashi, K., Hattori, K., and Ishige, M. 1986. The hepatic helminths of small mammals in Hokkaido, Japan. Report of the Hokkaido Institute of Public Health 36: 30–42. [In Japanese]

Yagisawa, M. 1978. Studies on zoonotic helminths from mammals in northern Honshu, Japan. Hirosaki Medical Journal 30: 67–76. [In Japanese]

Yamaguti, S. 1935. Studies on the helminth fauna of Japan. Part 7. Cestodes of mammals and snakes. Japanese Journal of Zoology 6: 233–246.

Yamaguti, S. 1954. Helminth fauna of Mt. Ontake. Part 2. Trematoda and Cestoda. Acta Medicinae Okayama 8: 393–405.

Yamaguti, S. 1959. Systema Helminthum. Vol. II. The Cestodes of Vertebrates. New York & London: Interscience Publishers, Inc., New York, 860 pp.

Yamashita, J. 1956. Studies on Echinococcosis: II. Echinococcosis in Japan. Japanese Journal of Veterinary Research 4: 64–74.

Yasuda, N., Toda, C., Miyoshi, N., Iizawa, M., and Akuzawa, M. 2005. Survey on Causes of Death in the Japanese Wildcats. Bulletin of Faculty of Agriculture, Kagoshima University 55: 23–30. [In Japanese]

Zeder, J. G. H. 1800. Erster Nachtrag zur Naturgeschichte der Eingeweidewürmer, mit Zusätzen und Anmerkungen herausgegeben. Leipzig, Germany, xx + 320 pp.