Morphological and molecular identification of cyathostomine gastrointestinal nematodes of *Murshidia* and *Quilonia* species from Asian elephants in Myanmar

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**ABSTRACT**

Gastrointestinal nematode parasites have long been recognized in Asian elephants. The most common parasites belong to the subfamily Cyathostominae of the family Strongylidae, which are small to medium-sized with a cylindrical buccal capsule surrounded by coronal leaflets. Diagnostic keys of such parasites are provided from old illustrations in the form of line drawings. However, there are few photomicrographs and no genetic information of these parasites exists. In the present study we obtained adult worm specimens from faeces of Asian elephants after anthelmintic treatment in two elephant camps in Myanmar. Here, we provided photomicrographs for five cyathostomine parasites, *Murshidia falcifera*, *Murshidia indica*, *Murshidia neveulemairei*, *Quilonia renniei*, and *Quilonia travancra* almost 100 years after their original drawings. In addition, we determined the mitochondrial cytochrome c oxidase subunit I (COI) gene sequences of these species. Phylogenetic analysis of the COI genes of *Murshidia* and *Quilonia* species from Asian and African elephants revealed parasite speciation in each elephant host. The present study also indicated that several *Murshidia* and *Quilonia* species were widely distributed in Asian elephants in Myanmar, providing new insight into control strategies and evolution of cyathostomine gastrointestinal parasites in elephants.

**1. Introduction**

Elephants originated in Africa in the late Eocene Epoch and gradually spread to all northern continents and South America. Numerous proboscideans species developed, but many became extinct. Nowadays, the African savannah elephant *Loxodonta africana*, African forest elephant *Loxodonta cyclotis*, and Asian elephant *Elephas maximus* are the only species that survived into the current epoch (Fowler, 2006; Roca et al., 2015). The parasitic fauna of prehistoric proboscideans is unknown, but it is likely that parasitic species similar to present-day elephant parasites infected ancient elephants. Asian and African elephants harbour the same genera of parasites, but species usually differ (Fowler, 2006).

Gastrointestinal nematodes parasitize elephants in large numbers. The parasites in the gastrointestinal tract often produce a protein-losing gastroenteropathy, causing hyperalbuminemia, anaemia, enteritis and even death in younger elephants (Fowler, 2006). From captive and zoo Asian elephant populations in India and China, there have been reported nematodes belonging to subfamily Cyathostominae, including the six *Murshidia* species *M. elephas*, *M. falcifera* (*=M. falcifer*), *M. indica*, *M. murshida*, *M. lanei*, and *M. neveulemairei* (*=M. neveu-lemairei*), the five *Quilonia* species *Q. edentata*, *Q. guptai*, *Q. renniei* (*=Q. quilona*), *Q. simhai*, and *Q. travancra*, and the *Khalilia pileate* (Lane, 1914; Ware, 1924; Witenberg, 1925; Wu, 1934; Gupta and Jaiswal, 1984; Gupta and Trivedi, 1984; Zhang and Xie, 1992). However, *M. lanei* was proposed as a variety of *M. murshida* because of morphological similarity between...
the species (Van der Westhuysen, 1938). Q. edentata, Q. guptai, and Q. simhai were not listed in a review article by Fowler (2006). Meanwhile, 17 species of *Murshidia*, eight species of *Quilonia* and one species of *Khalilia* have been listed in African elephants *Loxodonta africana* (Fowler, 2006).

Genetic identification of some cyathostomine nematode species was conducted for African savannah elephants. The nucleic ribosomal DNA (ITS1, 5.8S and ITS2) and mitochondrial cytochrome c oxidase subunit I gene (COI) were determined for three species of *Murshidia* (M. africana, M. linstowi, and M. longicaudata), *Quilonia africana*, and *Khalilia sameera* (McLean et al., 2012). However, no genetic information is available for cyathostomine nematode parasites of Asian elephants although small subunit (SSU) rDNA sequences of strongyloidal nematodes have been reported in wild Asian elephants in Thailand (Phuphisut et al., 2016).

*Elephas maximus* is listed as an endangered species and extant in Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Lao, Malaysia, Myanmar, Nepal, Sri Lanka, Thailand, and Vietnam (IUCN, 2020). In Myanmar, elephants have been domesticated and are used for timber harvesting. There are approximately 3000 captive Asian elephants and half of these are owned by the governmental institution, Myanmar Timber Enterprise (MTE, 2020). Gastrointestinal parasites are extremely common and cause enteritis, especially in younger elephants (Leimgruber et al., 2011; Oo, 2012). Although elephants are regularly treated with anthelmintic drugs, the eradication of gastrointestinal parasites is difficult because captive elephants reside in a group in MTE elephant camps, where elephants feed via free ranging in forest areas. Precise morphological and genetic identification of cyathostomine gastrointestinal nematodes have never been attempted within this population in Myanmar. However, we recently reported genetic identification of stomach bot fly larva from a Myanmar elephant (Chel et al., 2020).

In the present study, we report microscopic identification and provide photomicrographs of three *Murshidia* and two *Quilonia* species from Asian elephants in Myanmar. We also determined the mitochondrial COI gene sequences of these parasite species and compared them to related species from African elephants.

### 2. Materials and methods

#### 2.1. Sample collection

We collected fresh elephant faecal boluses as described (Lyndale et al., 2015). Faeces were collected in December 2018 from two elephants in the Taung Kya (TK) elephant camp (N19°55′, E96°30′) and

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**Table 1**

The number of *Murshidia* and *Quilonia* adult worms identified in Asian elephants in Myanmar.

| Elephant | No. of worms collected from faeces | No. of worms identified |
|----------|-----------------------------------|-------------------------|
|          | M† F‡ | M falcifera | M indica | M neveulemairei | Q. renniei | Q. travancra |
|          |       | M | F | M | F | M | F | M | F |
| HYG-1    | F 4  | 5 | 2 | 2 | 1 |
| HYG-2    | F 14 | 12 | 15 | 1 | 2 | 1 |
| HYG-3    | F 58 | 3 | 2 | 1 | 1 |
| HYG-4    | M 7  | 3 | 5 | 1 | 1 |
| HYG-5    | M 8  | 12 | 23 | 1 |
| HYG-6    | F 67 | 1 | 1 |
| HYG-7    | F 8  | 16 | 21 | 3 | 7 |
| HYG-8    | M 1  | 7 | 6 | 1 | 2 |
| TK-1     | F 30 | 47 | 83 | 2 | 2 |
| TK-2     | M 6  | 9 | 4 | 11 | 18 | 3 | 1 |

* M, male.  
† F, female.

**Table 2**

Morphometrical data of *Murshidia* and *Quilonia* species from Asian elephants in Myanmar.

| Species | M. falcifera | M. indica | M. neveulemairei | Q. renniei | Q. travancra |
|---------|--------------|-----------|------------------|------------|--------------|
|         | M (1) * a | F (2) * b | M (1) | M (6) | M (11) | F (18) | M (3) | F (1) |
| Total length (mm) | 24 | 29.6–32 | 15.7 | 17–23 | 25–28.8 | 15–17.2 | 19.7–26.4 | 16.6–19 | 25.8 |
| Mean total length (mm) | 30.8 | 21.1 | 27.2 | 16 | 22.7 | 18 |
| Maximum diameter (mm) | 0.7 | 1.0–1.3 | 0.54 | 0.6–0.8 | 0.9–1.1 | 0.6–0.7 | 0.8–1.1 | 0.7 | 0.9 |
| Diameter of head (μm) | 245 243 | 135 | 134–144 | 136–149 | 199–232 | 242–322 | 231–261 | 322 |
| No. of coronal leaflets | 80–80 | 40–40 | 12–18 | 18–18 | 16–18 | 18–18 | 18–18 | 18–18 |
| Length of buccal capsule (μm) | 114 | 120–122 | 64 | 67–101 | 84–113 | 44–79 | 50–104 | 53–85 | 136 |
| Diameter of buccal capsule (μm) | 131 | 111–136 | 65 | 53–64 | 55–65 | 123–149 | 158–211 | 94–121 | 198 |
| Length of oesophagus (μm) | 792 | 956–1058 | 517 | 698–776 | 724–880 | 611–667 | 668–812 | 746–790 | 956 |
| Maximum diameter of oesophagus (μm) | 238 | 290–328 | 146 | 182–231 | 192–270 | 156–234 | 206–284 | 175–229 | 221 |
| Cervical papillae from anterior end (μm) | 1154 | 670 |
| Excretory pore from anterior end (μm) | 1147–1169 | 1383 | 509–564 | 713 | 909–1228 |
| Nerve ring from ant. end (μm) | 411 | 497–526 | 213 | 353–384 | 391–413 | 267–375 | 317–470 | 405–413 | 504 |
| Length of spicules (right) (μm) | 1750 | 939 | 1213–1338 | 559–1055 | 932–958 |
| Length of spicules (left) (μm) | 954 | 1209–1321 | 613–1024 | 937 |
| Length of gubernaculum (μm) | 117–215 | 87–266 | 217–248 |
| Length of female tail (μm) | 1763–1880 | 1326–1584 | 1527–2177 | 1600 |
| Vulva from tail end (μm) | 2575–3150 | 1767–2079 | 4873–6859 | 2663 |

* M, male (no. of specimens examined).  
† F, female (no. of specimens examined).
from eight elephants in the Hmaw Yaw Gyi (HYG) elephant camp (N18°22′, E96°24′) one day after oral albendazole administration at a dose of 5–7 mg/kg of body weight. Faecal boluses were kept in a cooler box and transported to a laboratory at the University of Veterinary Science, Nay Pyi Taw. Each faecal bolus in a container was diluted with a large amount of tapped water. We searched for nematode worms using naked eyes in diluted faecal materials and placed parasites in petri dishes using forceps. Most worms were already dead or immobile, but some were still alive and motile (Fig. S1). We separated them into males and females, and randomly selected a total of 47 adult worms (22

Fig. 1. Photomicrographs of Murshidia falcifera. A, anterior end of a female, showing the appearance of two lateral lips of mouth collar with prominent head papillae (arrows) and coronal leaflets (*); B, head of a male, showing cuticular lining of buccal capsule (arrows) and funnel-shaped throat (**); C, dorsal ray of bursa of a male, showing three branches, in which anterior branch is composed of two sub-branches (arrows) and the posterior one is longer (*); D, posterior end of a female, showing anus (arrow).

Fig. 2. Photomicrographs of Murshidia indica. A, anterior end of a male, showing the appearance of plumose sculpturing on anterior portion of oesophagus (arrows); B, head of a male, showing coronal leaflets (*); C, copulatory bursa and spicules (arrow) of a male; D, dorsal ray of bursa of a male, showing two branches (arrows), in which the posterior branch has a pointed extremity (*).

Fig. 3. Photomicrographs of Murshidia neveulemairei. A, anterior end of a female, showing the appearance of plumose sculpturing on anterior portion of oesophagus (arrows); B, posterior extremity of a female, showing anus (arrow) and vulva (*); C, dorsal ray of bursa of a male, showing two branches (arrows), in which the anterior branch is bifurcated in the distal half (*).

Fig. 4. Photomicrographs of Quilonia renniei. A, anterior end of a female, showing cylindrical shape of oesophagus (arrow); B, head of a female, showing a small buccal capsule (arrow) and curved coronal leaflets project above head (*); C, posterior end of a female; D, dorsal ray of bursa of a male, showing two branches (arrows), in which the posterior branch divided two sub-branches and the inner sub-branch is slightly bifid at the extremity (*).
males and 25 females) that seemed to be alive and not denatured. The worms were fixed with absolute alcohol for subsequent morphometric, morphological, and genetic examinations. After measuring worm body length and width, we dissected worms into three parts, anterior, middle, and posterior portions. Anterior and posterior parts were cleared in glycerol and examined under a light microscope. The middle parts were used for DNA isolation.

2.2. Morphological and morphometric identification

We took morphometric data and optical micrographs of parasites using an Olympus SZX16 stereo microscope, CKX41 inverted microscope, and BX50 microscope (Olympus Corp., Tokyo, Japan), equipped with a DP26 digital camera (Olympus) and cellSens. Differential interference micrographs were taken using BX50 microscope. We performed morphological identification of parasite species by comparing to previous descriptions (Lane, 1914; Witenberg, 1925; Van der Westhuysen, 1938; Chabaud, 1957; Popova, 1965; Prahardani et al., 2019) (Figs. S2-4, Table S1). All parasite specimens are stored in the Laboratory of Parasitology, Faculty of Veterinary Medicine, Hokkaido University, Sapporo, Japan.

2.3. DNA extraction, PCR, and sequencing

We extracted total genomic DNA from the middle parts of all 47 specimens using a DNA extraction kit (DNeasy Blood & Tissue Kit, Qiagen, Hilden, Germany) and measured DNA concentration using a NanoDrop 2000 (ThermoFisher Scientific, MA, USA). To amplify the COI gene, we designed two new primers, COIQF (5′ GGATCAAA 3′) and COIQR (5′ CCACCAGTTCTA GGATCAA 3′) based on the alignment sequences of mitochondrial COI genes of cyathostomine nematodes from African elephants (McLean et al., 2012) because our preliminary experiments showed that some specimens were not amplified using PCR with the universal barcoding primers, LCO-1490 and HCO-2198 (Folmer et al., 1994). The PCR mixture contained 0.3 μM of each primer, 10 ng/μL of template DNA, 0.025 U/μL of Tks GFlex DNA polymerase (Takara Bio Inc., Tokyo, Japan), and 1× GFlex buffer in a volume of 10 μL. After initial denaturation at 94 °C for 1 min, the reaction was carried out with 40 cycles of denaturation at 98 °C for 10 s, annealing at 52 °C for 15 s, and extension at 68 °C for 45 s, followed by a final extension at 68 °C for 5 min, with the SimpliAmp thermal cycler (Applied Biosystems Japan, Tokyo, Japan). PCR products were run on 1.2% agarose gels, stained with GelRed Nucleic Acid Staining Solution (Biotium, Hayward, CA, USA), and photographed under LED light. PCR products were purified with NucleoSpin® Gel and PCR Clean-up kit (Macherey-Nagel AG, Düren, Germany) and subjected to direct sequencing with COIQF and COIQR primers using an Applied Biosystems 3130 Genetic Analyzer with a Big Dye v3.1 Terminator cycle sequencing kit (Applied Biosystems, Inc., Foster City, CA, USA).

2.4. Phylogenetic analysis

We conducted phylogenetic analysis of COI gene nucleotide sequences of 47 nematodes from Asian elephants. The ingroup comprised of K. sameera, M. africana, M. linstowi, M. longicaudata, and Q. africana from African elephants. Strongyloides stercoralis was included as an outgroup. We aligned COI sequences using the MUSCLE (codon) option within MEGA7 (Kumar et al., 2016), and created a maximum likelihood (ML) tree. The Tamura-Nei+G model was adapted as it showed the best fit to all datasets. Bootstrap values were determined by 500 replicates.

We also analyzed distance and diversity of COI genes using MEGA7 with the Tamura-Nei model (Tamura and Nei, 1993). Pairwise sequence comparisons were made to determine the average number of base-pair differences per site between all groups. Standard error was calculated with 1000 bootstrap replications. The analysis between groups involved 47 nucleotide sequences in 411 positions in the final dataset. The average number of base-pair differences per site within each group in 471 positions in the final dataset was also analyzed. The nucleotide sequences of COI genes determined in this study are available in DDBJ/EMBL/GenBank databases under accession numbers LC513767-86, 88, 89, 91–99, LC513800-4, 6–16 (Table S2).
Fig. 6. Molecular phylogenetic analysis of COI gene sequences of cyathostomine species using the maximum likelihood method in MEGA7. The percentage of trees in which associated taxa clustered together is shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. GenBank accession numbers are indicated alongside taxa name.
3. Results

3.1. Morphometric description and morphological identification

We obtained a total of 115 males and 158 females from faeces of 10 elephants, and approximately half the number of parasites were collected from one elephant (TK-1) in TK camp (Table 1). Among them, morphometric data of 47 parasites that seemed alive and not denatured are shown in Table 2. We identified five species, including M. falciمرة (Fig. 1), M. indica (Fig. 2), M. neveulemairei (Fig. 3), Q. renniei (Fig. 4), and Q. travancra (Fig. 5). The number of parasites identified was three for M. falciمرة, one for M. indica, 10 for M. neveulemairei, 29 for Q. renniei, and four for Q. travancra (Table 1). We also took differential interference micrographs to further clarify morphological features (Figs. S5-9). However, we found some difficulty in determining the precise number of coronal leafllets, one of the major characteristics of Murshidia and Quilonia species.

3.2. Phylogenetic analysis

The PCR amplifications produced ~469 bp nucleotide sequences for the COI gene of Murshidia and Quilonia species with a primer set of CO1QF and CO1QR. A ML phylogenetic tree constructed from CDS (~453 bp) of the COI genes of 47 specimens from Myanmar elephants and five ingroup sequences from African elephants in GenBank clearly showed that the genera Murshidia and Quilonia formed in separate clades (Fig. 6). We found a close genetic relationship between Q. renniei from Asian elephants and Q. africana from African elephants, and likewise between M. indica and M. africana. However, M. falciمرة and M. neveulemairei had no counterparts from African elephants in this study. All 29 Q. renniei specimens formed one clade that was separated from Q. africana. Four Q. travancra specimens formed a clade separated from Q. renniei.

3.3. Nucleotide diversity

Mean distances of nucleotide sequences of COI genes between parasite species in this study were in the range of 0.104–0.166 (Table 3). The highest level of interspecific nucleotide diversity (16.6%) was detected between M. neveulemairei and Q. travancra. The mean diversity (± SE) within species were 0.0071 ± 0.0030, 0.0101 ± 0.0033, 0.0099 ± 0.0019, and 0.0149 ± 0.0040 for three M. falciمرة, ten M. neveulemairei, 29 Q. renniei, and four Q. travancra specimens, respectively. Namely, the range was 0.71%–1.49% across species, and Q. travancra had the highest level of nucleotide diversity.

4. Discussion

Here, we report of detection and genetic analysis of three species of Murshidia (M. falciمرة, M. indica, and M. neveulemairei) and two species of Quilonia (Q. renniei, and Q. travancra) from Asian elephants in Myanmar for the first time. We provided photomicrographs of these adult parasites almost 100 years after their original drawings, but photomicrographs and scanning electron photomicrographs were recently reported for Q. travancra from Sumatran elephants in Indonesia (Prahardani et al., 2019). The photomicrographs taken by optical microscopy here clearly showed species-specific morphological characteristics, including mouth collar, buccal capsule, plumose sculpturing on the oesophagus, and dorsal bursal rays of the parasites.

Phylogenetic analysis of COI genes from Murshidia species in Asian and African elephants suggested that M. indica and M. africana were closely related species. The ancestor of these species may have evolved to M. indica in E. maximus and to M. africana in L. africana. Taken together with a proposed evolutionary lineage of M. africana, M. linstowi, and M. longicaudata in African elephants (McLean et al., 2012), the early divergence of M. falciمرة was suggested. This was followed by an ancestor of M. linstowi and M. longicaudata before M. neveulemairei. However, a detailed Murshidia lineage will be required for further genetic studies because the lack of M. elephasi and M. murshidia COI gene sequences from Asian elephants and other Murshidia species from African elephants. Currently, only three of 17 African Murshidia species have yielded COI gene sequences (McLean et al., 2012).

Phylogenetic tree of COI genes from Quilonia species suggested that Q. renniei from Asian elephants was closely related to Q. africana from African elephant rather than Q. travancra from Asian elephants. Likewise, better understanding of the evolutionary lineage between Quilonia species in elephants awaits further genetic studies because of the lack of sequence data from Q. edentata, Q. simbai, and Q. guptai from Asian elephants and the other seven Quilonia species from African elephants.

The number of coronal leafllets is one of the major taxonomic keys for species identification, but the numbers were very close to each other 20, 24, 20–22, and 18, for Q. edentata, Q. guptai, Q. simbai, and Q. renniei, respectively. The morphology of Q. edentata was like Q. simbai in general features, but it can be distinguished by shapes like cervical papillae, gubernaculum, and buccal capsules in both sexes (Zhang and Xie, 1992). Furthermore, variation in the number of coronal leafllets in Q. simbai was accepted by the authors (Gupta and Trivedi, 1984). Thus, genetic analysis of Q. edentata, Q. guptai, and Q. simbai will be required to elucidate whether these species are real species or variations in Quilonia species. Here, 29 Q. renniei specimens showed a lower level of nucleotide diversity in the COI gene (0.99 ± 0.19%) at 471 positions of CDS sequences) and no obvious separation in the phylogenetic tree, indicating intraspecific variation in the gene. Meanwhile, for six Q. africana specimens from African elephants, intraspecific nucleotide diversity in the COI gene was 2.20 ± 0.39% at 655 positions (McLean et al., 2012) and 2.22 ± 0.38% at 654 positions of CDS sequences by our analysis. Determination of the precise number of coronal leafllets of these Q. renniei specimens using scanning microscopy is needed to clarify whether leafllets variation exists within Q. renniei populations in Myanmar. The consistency of ten coronal leafllets in Q. travancra was shown using scanning electron microscopy (Prahardani et al., 2019). Thus, further scanning electron microscopic studies will clarify an association between the number of coronal leafllets and genetic separation of Quilonia species from Asian elephants.

Two elephant genera, Elephas (Asia) and Loxodonta (Africa), diverged 5 million years ago, and African savannah elephants (L. africana) and forest elephant (L. cyclotis) diverged approximately 2.63

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**Table 3**

Mean distance (± SE) of nucleotides of the COI genes between Murshidia and Quilonia species from Asian elephants in Myanmar.

| Species (no. of specimens) | 1   | 2   | 3   | 4   |
|---------------------------|-----|-----|-----|-----|
| 1. M. falciمرة (3)        | 0.108 ± 0.018 |
| 2. M. indica (1)          | 0.104 ± 0.016 |
| 3. M. neveulemairei (10) | 0.110 ± 0.016 |
| 4. Q. renniei (29)        | 0.127 ± 0.020 |
| 5. Q. travancra (4)       | 0.127 ± 0.020 |

Pairwise sequence comparisons were made to determine the average number of base-pair differences per site between all groups using MEGA7 with the Tamura-Nei model. Standard error was calculated with 1000 bootstrap replications. The analysis involved 47 nucleotide sequences in 411 positions in the final dataset.
Here, we showed molecular evidence of the presence of the same genus but different species of *Murshidia* and *Quilonia* nematode parasites in Asian (*E. maximus*) and African (*L. africana*) elephants. Recently, we also showed molecular evidence of the presence of the same genus but different *Cobboldia* species, stomach bot fly, in Asian and African elephants (Yan et al., 2019; Chel et al., 2020). A phylogenetic tree revealed that *Cobboldia elephantis* from an Asian elephant formed one clade with *C. loxodontis* from an African elephant but separated from stomach bot fly species in rhinoceros and equids. It is unknown whether parasite speciation and separation in Asian and African elephants is associated to host-shift speciation or cospeciation in host-parasite associations (de Vienne et al., 2013) because numerous proboscideans species became extinct.

A much higher number of *Quilonia* species was detected compared to *Murshidia* species in Myanmar elephants. Both *Quilonia* and *Murshidia* species were detected in the HYG elephant camp whereas only *Quilonia* species were found in the TK camp. Particularly, one elephant excreted various *Quilonia* and *Murshidia* species in the HYG camp. The reasons for parasite species geographic separation are unknown. These two elephant camps are located greater than 150 km distance, and elephants in camps are cared for under semi-captive conditions, in which elephants can eat plants freely in the surrounding forest. More than 30 MTE elephant camps are currently scattered throughout Myanmar and artificial movement of animals between camps is common for natural mating. In our preliminary experiments, however, we could obtain COI gene sequences from single third stage larva after the cultivation of elephant faeces, indicating infection of elephants with *Q. renniei* in both TK and HYG camps (unpublished). Thus, development of genetic markers using nematode eggs and subsequent cultured larvae will facilitate identification of parasite species. Nationwide distribution and abundance of cyathostomine parasite species await further epidemiological surveys in different elephant camps of Myanmar.

5. Conclusions

In conclusion, we report morphological and genetic identification of *Murshidia* and *Quilonia* species from Asian elephants in elephant camps in Myanmar. Phylogenetic analysis of COI gene sequences was performed for 47 adult nematode specimens. The results showed that *Murshidia* and *Quilonia* species in Asian elephants were closely related to but different from those in African elephants. Further studies, including genetic analysis of more samples in other elephant camps in Myanmar as well as Asian elephants in other countries, are needed to elucidate control strategies, evolution and parasitism of gastrointestinal parasites in elephants.

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Compliance with ethical standards

Collection of parasitological samples from elephants was approved by the University of Veterinary Science, Ministry of Agriculture, Livestock and Irrigation, and Myanmar Timber Enterprise, Ministry of Natural Resources and Environmental Conservation, Myanmar.

Declaration of competing interest

There are no conflicts of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jippaw.2020.03.005.

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