

***Haemonchus contortus* (Rudolphi, 1803) Cobb, 1898 (Nematoda: Trichostrongylidae) from a goat on Mindanao, Philippines: genetic diversity of the widespread species**

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Summary. *Haemonchus contortus* is one of the most pathogenic and economically important gastrointestinal nematodes of small ruminants worldwide, causing anemia, reduced productivity and substantial losses in goat and sheep production systems. During the slaughter of three goats for meat in Iligan City, Mindanao, Philippines, trichostrongylid nematodes were detected in the abomasum of one animal. Using an integrative approach that combined light microscopy, scanning electron microscopy, morphometric analysis, and DNA-based characterisation, a subset of these specimens was identified as *H. contortus*. In one specimen, direct sequencing of the ITS rDNA amplicon produced overlapping peaks in the ITS1 region, so the product was cloned for further analysis. Phylogenetic analyses based on ITS rDNA and *CoxI* mtDNA, together with a *CoxI* haplotype network and pairwise distance estimates, were used to assess the genetic diversity and taxonomic affinities of the *Haemonchus* specimens. The ITS data revealed three closely related sequence variants with low divergence, supporting their interpretation as intraspecific variation rather than taxonomic heterogeneity. In turn, analysis of the *CoxI* sequence showed that the Philippine specimens belonged to a widespread *H. contortus* assemblage while representing a unique haplotype. This pattern suggests local genetic differentiation within a broadly distributed and genetically heterogeneous species. Minor incongruence between ITS- and *CoxI*-based relationships should be interpreted cautiously, given marker-specific evolutionary histories and the still limited regional sampling in public databases.

Keywords: *Haemonchus contortus*, goats, abomasum, ITS rDNA, *CoxI*, phylogeny, Philippines.

The trichostrongylid species, *Haemonchus contortus* (Rudolphi, 1803) Cobb, 1898, is regarded as one of the most pathogenic and economically important gastrointestinal nematodes of small ruminants worldwide, being associated with anemia, reduced productivity, and substantial losses in goat- and sheep-breeding systems (Hoberg & Zarlenga, 2016; Flay *et al.*, 2022). The species is generally considered to be of African origin, but is now distributed widely across tropical, subtropical, and temperate regions, including the Americas, Eurasia, and numerous island systems (Hoberg & Zarlenga, 2016). Owing to its broad distribution, veterinary

importance and apparent dispersal capacity, considerable attention has been paid to the genetic structure and phylogeography of *H. contortus* (Gharamah *et al.*, 2012; Laosutthipong & Eardmusic, 2019; Parvin *et al.*, 2024).

For molecular characterisation of *H. contortus*, both mitochondrial and nuclear ribosomal markers have been widely used, especially the cytochrome c oxidase subunit I gene (*CoxI*) and the internal transcribed spacer region (ITS), which provide complementary information on genetic diversity and phylogenetic relationships (Blouin, 2002; Nabavi *et al.*, 2014; Bogale *et al.*, 2020; Pimenov *et al.*, 2024;

Maurizio *et al.*, 2025). A high level of mitochondrial variation has been documented in geographically distant isolates, whereas the ITS region, despite its common use in species identification and comparative analyses, has been shown to exhibit intra-individual polymorphism in *H. contortus* (Chen *et al.*, 2000; Gomes *et al.*, 2002; Aksenov & Spiridonov, 2013; Pitaksakulrat *et al.*, 2021). This feature should be taken into account in the interpretation of ITS data and, in some cases, sequence variants may need to be resolved by cloning (Ellegren *et al.*, 1992; Aksenov & Spiridonov, 2013).

Although *H. contortus* has been studied in various parts of the world, sequence data from Southeast Asia remains relatively limited (Gharamah *et al.*, 2012; Laosutthipong & Eardmusic, 2019), and material from the Philippines appears to be insufficiently represented in public datasets, with most of the data being coprological (Rupa & Portugaliza, 2016; Sabirin *et al.*, 2024, 2025; Balbin *et al.*, 2025). In the present study, *H. contortus* specimens collected from a goat in the Philippines were characterized using mitochondrial (*CoxI*) and nuclear (ITS) markers. Phylogenetic relationships were reconstructed for both loci, mitochondrial affinities were examined using a haplotype network in the context of previously published GenBank sequences, and ITS variation was additionally assessed through cloning of one amplicon because of intra-individual polymorphism detected in one male specimen. The aim of this study was to determine the phylogenetic position of the Philippine material and its relationship to the broader diversity of *H. contortus*.

MATERIAL AND METHODS

On November 28th, 2023, during the slaughter of three goats (*Capra hircus* Linnaeus, 1758) for meat in Iligan City, Mindanao, Philippines (8.23581 N, 124.26131 E), trichostrongylid nematodes were detected in the abomasum of one animal. Using an integrative approach combining light microscopy, scanning electron microscopy, morphometric analysis and DNA-based characterisation, a subset of these specimens was identified as *H. contortus* (Loginova *et al.*, 2026). For molecular characterisation, two individual specimens were subjected to amplification of the ITS rDNA region and the mitochondrial *CoxI* gene. DNA was obtained from single male worms with the QIAamp DNA Micro Kit (QIAGEN, Germany), following the protocol supplied by the manufacturer. The ITS rDNA marker was represented by a partial fragment

generated with primers TW81 (5'-GTT TCC GTA GGT GAA CCT GC-3') and AB28 (5'-ATA TGC TTA AGT TCA GCG GGT-3'), in accordance with the protocol of Joyce *et al.* (1994). All ITS PCR reactions were set up in a final volume of 25 µl using the Encyclo Plus PCR Kit (Evrogen, Russia). Cycling conditions included an initial denaturation step at 95°C for 3 min, followed by 35 amplification cycles consisting of denaturation at 95°C for 45 s, annealing at 57°C for 45 s, and extension at 72°C for 70 s; the program was completed with a final extension at 72°C for 5 min. For the mitochondrial marker, a partial *CoxI* fragment was amplified with the primer set COI_F1 (5'-CCT ACT ATG ATT GGT GGT TTT GGT AAT TG-3') and COI_R2 (5'-GTA GCA GCA GTA AAA TAA GCA CG-3'), originally proposed by Kanzaki and Futai (2002). The amplification regime consisted of an initial denaturation at 95°C for 2 min, followed by 35 cycles of 95°C for 30 s, 45°C for 15 s, and 72°C for 60 s, with a terminal extension step at 72°C for 5 min. For each set of reactions, negative controls lacking template DNA but containing all other PCR components were processed in parallel. Following amplification, PCR products were examined on agarose gels. Bands corresponding to the target fragments were excised and purified with the HiPure Gel DNA Mini Kit (Magen Biotechnology Co., Ltd., China). The resulting amplicons were sequenced directly by Genotech Ltd. (Moscow, Russia) using the same primers as those employed for PCR. In one specimen of *H. contortus*, direct sequencing of the ITS rDNA product produced overlapping peaks in the ITS1 region. To resolve this, the amplicon was cloned after ligation into the pGEM-T vector, followed by transformation into JM109 High Efficiency Competent Cells (Promega, The Netherlands) in accordance with the manufacturer's instructions. Clones containing inserts were subsequently amplified and sequenced with primers TW81 and AB28, *i.e.*, the same primers used in the primary PCR. This procedure revealed three distinct cloned ITS sequences from the single *H. contortus* specimen.

The newly generated sequences were queried against the NCBI GenBank database using the BLAST algorithm. The obtained sequences, together with those identified as most similar by BLAST, were aligned using MAFFT Version 7.520, RRID:SCR_011811 (Katoh & Standley, 2013). Prior to the phylogenetic analyses, the best-fit models of nucleotide substitution were selected with jModelTest2 (Darriba *et al.*, 2012). The TPM3uf + G model was applied to the partial ITS rDNA dataset, whereas the GTR + G + I model was used

for the partial *CoxI* mtDNA dataset. Bayesian inference analyses were performed in MrBayes Version 3.2.7a, RRID:SCR_012067 (Ronquist *et al.*, 2012). Markov chain Monte Carlo simulations were run for 15,000,000 generations, and the final 75% of sampled trees were used to construct the consensus trees. Posterior probability (PP) values above 0.95 were considered statistically significant in the Bayesian inference trees. For haplotype analysis, 55 aligned *H. contortus* *CoxI* sequences of 566 bp each, retrieved from GenBank and including one sequence generated in the present study, were analysed in DnaSP version 6.12.03, RRID:SCR_003067 (University of Barcelona, Barcelona, Spain) (Rozas *et al.*, 2017) to identify haplotypes. All relevant *CoxI* sequences available in GenBank at the time of analysis were included. No gaps or missing data were present in the alignment. This dataset yielded 52 haplotypes. A median-joining haplotype network was reconstructed in PopART version 1.7, RRID:SCR_021924 (University of Otago, Dunedin, New Zealand) (Leigh & Bryant, 2015) using the variable sites only; in total, 104 polymorphic positions were identified in the 566-bp *CoxI* alignment and retained for network analysis.

The ITS and *CoxI* nucleotide sequences of *H. contortus* obtained in this study were deposited in GenBank under accession numbers: PZ122374 (for *CoxI* of the specimen 1), PZ754459 (for *CoxI* of the specimen 2), PZ122197 (for ITS region of the specimen 1), PZ124337, PZ124339 and PZ124339 (for the clones 1, 2 and 3 of the ITS region of the specimen 2, respectively). Specimen 1 of *H. contortus* was archived in the Museum of Helminthological Collections of the IEE RAS (Moscow, Russia) under voucher number IPEE_Parasites 14466; specimen 2 was archived under voucher number IPEE_Parasites 14472. Voucher specimens consisted of the anterior and posterior ends of the same males from which the middle body portions were used for DNA extraction.

RESULTS

BLAST comparison of the ITS and *CoxI* nucleotide sequences obtained from trichostrongylids preliminarily identified as *H. contortus* against GenBank records showed high sequence similarity, reaching up to 100% with reference sequences of these species. To complement BLAST-based identification and phylogenetic placement, sequence divergence was additionally quantified using uncorrected pairwise distances (*P*-distance) and numbers of nucleotide differences between the obtained sequences and

their closest GenBank matches. For *H. contortus* *CoxI*, the Philippine sequence showed the lowest divergence from two Mexican reference sequences (OP785768, OP785767), differing by 8 bp (*P*-distance $1.4\% \pm 0.5\%$), and from one Indian sequence ON005159, differing by 17 bp ($3.1\% \pm 0.7\%$). Greater divergence was observed relative to a Bangladeshi sequence LC716177 (31–32 bp; $6.5\% \pm 1.1\%$) and to several African sequences (31–35 bp; $5.6\text{--}6.9\% \pm 1.3\%$). Notably, the Philippine *H. contortus* *CoxI* sequence differed from the congeneric species *H. longistipes* Railliet et Henry, 1909 sequence KJ724420 by 37 bp ($7.1\% \pm 1.2\%$), supporting its assignment to *H. contortus*. For the three ITS rDNA variants of *H. contortus*, pairwise differences among clones were limited to 4–5 nucleotide positions, corresponding to *P*-distances of $0.6\text{--}0.8\% \pm 0.4\%$, which is consistent with intraspecific variation. The Philippine ITS sequences differed from the closest *H. contortus* reference sequences (*e.g.*, EU086380, EU086384 and related sequences) from giraffe (*Giraffa camelopardalis* Linnaeus, 1758) by 10–12 bp ($1.7\% \pm 0.6\%$), and from an Iranian *H. contortus* sequence (HQ389229) by 12–14 bp ($2.6\% \pm 0.6\%$). By contrast, divergence from *H. longistipes* ITS sequences was higher, amounting to 23–27 bp ($3.9\text{--}4.7\% \pm 0.8\%$).

Bayesian inference analysis of the partial mitochondrial *CoxI* sequences placed the Mindanao *H. contortus* specimen within a well-supported clade together with isolates from Mexico and India (PP = 1.0), while the sequence from Pakistan clustered within the same lineage (Fig. 1). By contrast, most Nigerian isolates formed a separate highly supported clade (PP = 1.0). It should be noted that the *CoxI* dataset was geographically unbalanced, as the majority of comparative sequences originated from goats in Nigeria.

Analysis of partial ITS sequences provided a broader representation of *H. contortus* haplotypes (Fig. 2). The species formed a strongly supported monophyletic group (PP = 1.0), although relationships among most intraspecific lineages remained unresolved. Only a few internal clades received strong support (PP > 0.95). In several cases, clustering corresponded to geographic origin or host association, for example, in specimens from Chinese forest musk deer (*Moschus berezovskii* Flerov, 1929) in Shanxi Province of China (PP = 1.0). However, some strongly supported clades included isolates from geographically distant regions and different hosts. The three ITS clones obtained from the Mindanao specimen grouped into a single strongly supported clade (PP = 1.0). A

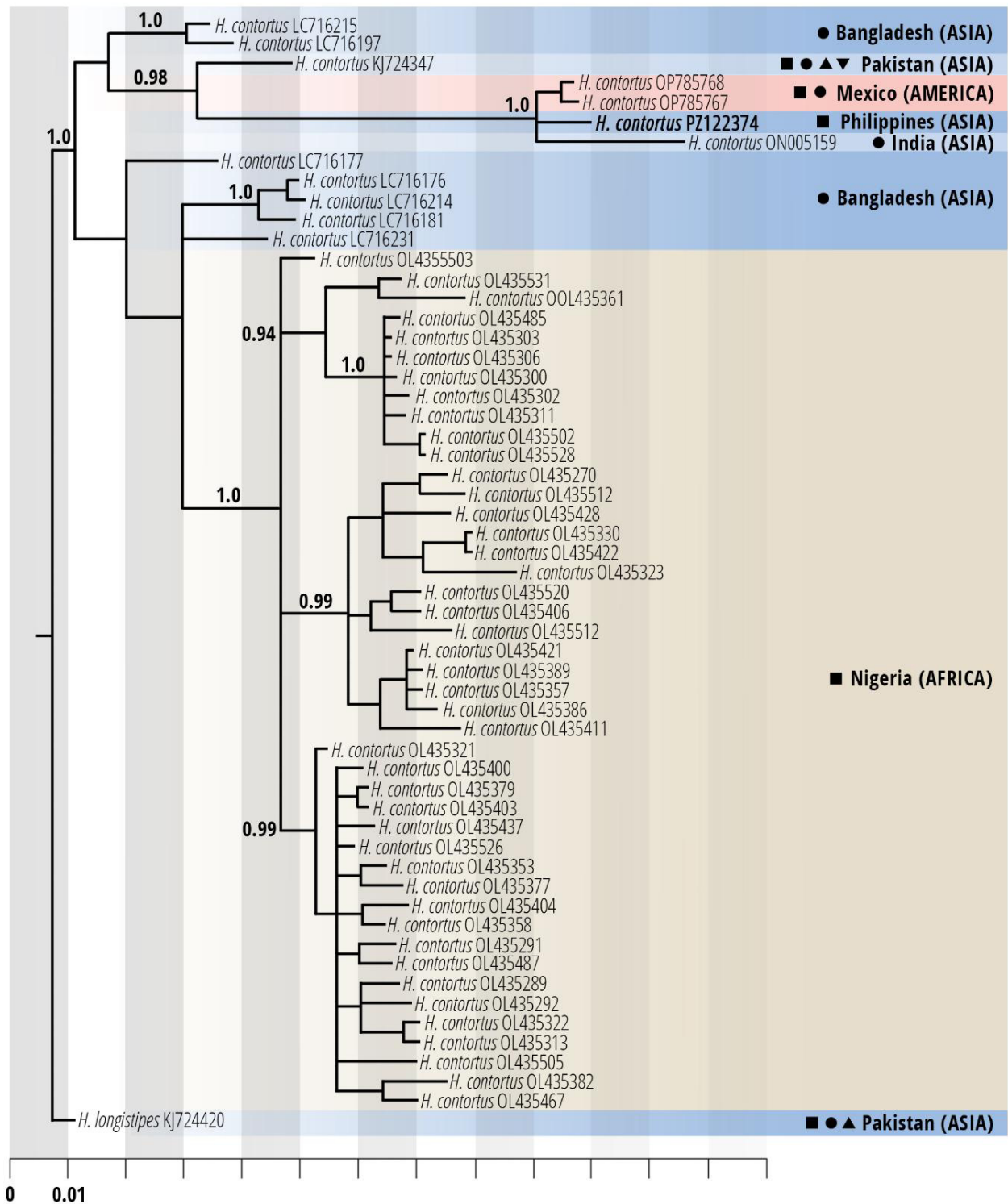


Fig. 1. Bayesian inference phylogenetic tree of *H. contortus* (Rudolphi, 1803) Cobb, 1898 recovered from the abomasum of the goat in the Philippines based on partial mitochondrial *CoxI* sequences. *H. longistipes* Railliet et Henry, 1909 was used as the outgroup. Sequences generated in the present study are indicated in bold. Posterior probability values are indicated at the nodes. Circle indicates domestic sheep (*Ovis aries* Linnaeus, 1758), square indicates domestic goat (*Capra hircus* Linnaeus, 1758), triangle indicates cattle (*Bos taurus* Linnaeus, 1758), and inverted triangle indicates water buffalo (*Bubalus bubalis* Linnaeus, 1758).

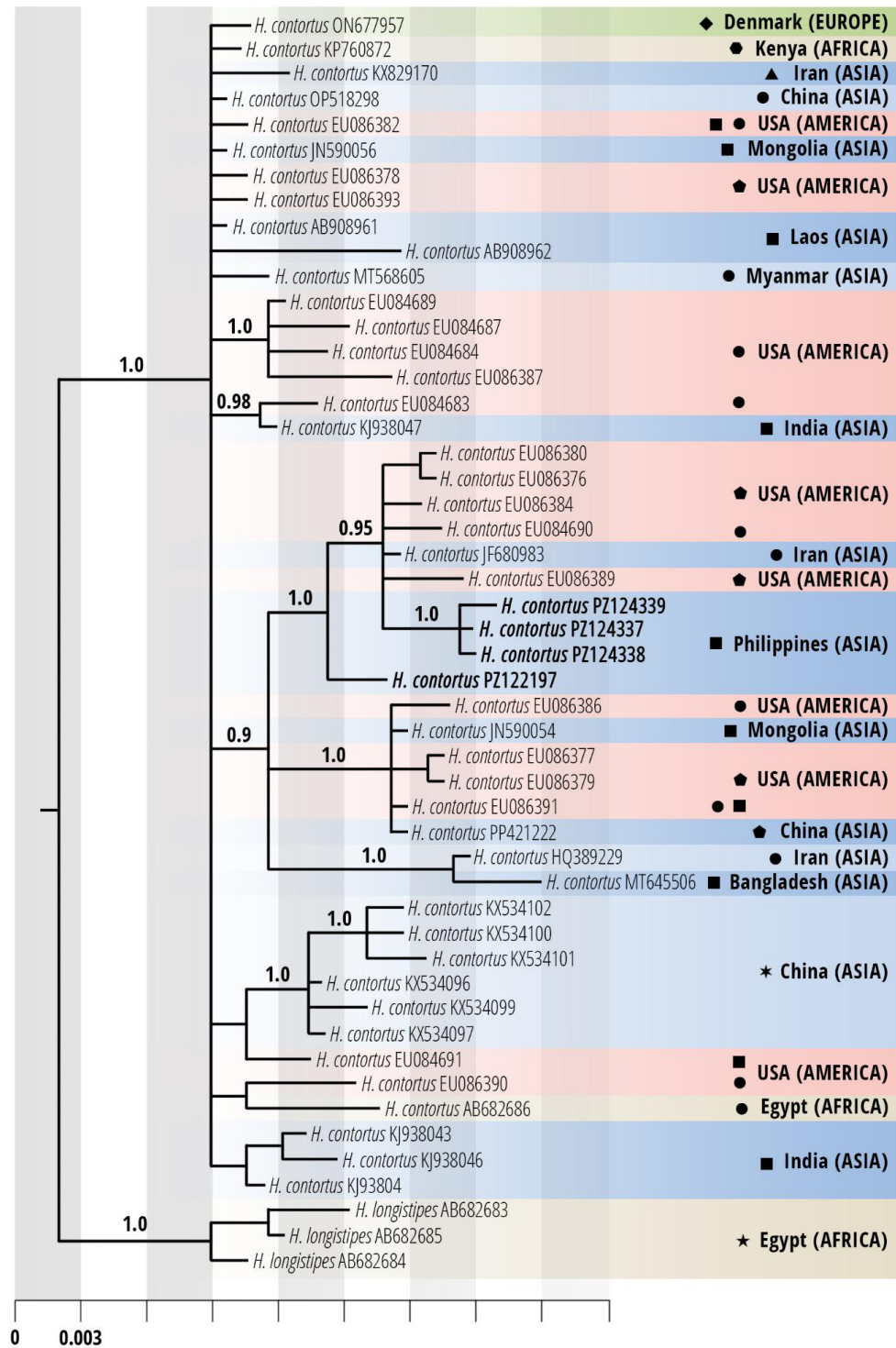


Fig. 2. Bayesian inference phylogenetic tree of *H. contortus* (Rudolphi, 1803) Cobb, 1898 recovered from the abomasum of the goat in the Philippines based on partial nuclear ITS sequences. *H. longistipes* Railliet et Henry, 1909 was used as the outgroup. Sequences generated in the present study are indicated in bold. Posterior probability values are indicated at the nodes. Rhombus indicates European bison (*Bison bonasus* Linnaeus, 1758), triangle indicates cattle (*Bos taurus* Linnaeus, 1758), circle indicates domestic sheep (*Ovis aries* Linnaeus, 1758), square indicates domestic goat (*Capra hircus* Linnaeus, 1758), pentagon indicates giraffe (*Giraffa camelopardalis* Linnaeus, 1758), six-pointed star indicates Chinese forest musk deer (*Moschus berezovskii* Flerov, 1929), and five-pointed star indicates dromedary (*Camelus dromedaries* Linnaeus, 1758).

Table 1. Alphabetical list of countries and the corresponding numbers of *H. contortus* *CoxI* control-region haplotypes inferred from a 104-bp fragment, with the corresponding numbers of haplotypes and source sequences.

Country (REGION)	Haplotype	Sequence
Bangladesh (ASIA)	7	7
India (ASIA)	1	1
Mexico (AMERICA)	2	2
Nigeria (AFRICA)	40	43
Pakistan (ASIA)	1	1
Philippines (ASIA)*	1	1

*This study.

median-joining haplotype network based on 566-bp *CoxI* sequences of *H. contortus* revealed high haplotypic diversity across the dataset (Fig. 3).

Analysis of 55 sequences identified 52 haplotypes, with 104 polymorphic sites and 119 mutational events. Haplotype diversity was very high ($H_d = 0.998 \pm 0.004$), indicating extensive sequence variation within the analysed sample. The sequence generated in the present study represented a distinct haplotype and did not cluster identically with any previously available sequence. The network was constructed from the same dataset as that used for Figure 1, with the exception of *H. longistipes*, which was excluded from the haplotype analysis because it had been included there solely as an outgroup. A country-level summary of inferred haplotypes is provided in the Table 1.

DISCUSSION

In the present study, phylogenetic analyses based on ITS rDNA and *CoxI* mtDNA, together with a *CoxI* haplotype network and pairwise distance estimates, were used to assess the genetic diversity and taxonomic affinities of *Haemonchus* specimens recovered from goats in Mindanao. Taken together, these complementary analyses consistently support the assignment of the examined specimens to *H. contortus* while also indicating detectable intraspecific variation.

The ITS data revealed three sequence variants, but their low pairwise divergence (0.6–0.8%) and their closer affinity to one another than to reference sequences of other congeners are consistent with interpretation as intraspecific variants rather than evidence of taxonomic heterogeneity (Nabavi *et al.*, 2014). Conversely, the larger distances separating these variants from other *Haemonchus* species support species-level distinction and are congruent with the phylogenetic placement of the Mindanao

specimens within *H. contortus* (Chaudhry *et al.*, 2015). The inclusion of *P*-distance estimates therefore provides a useful quantitative complement to BLAST similarity values and tree topology by helping to distinguish variation within species from divergence among species.

The *CoxI* results likewise support identification as *H. contortus*, but they also point to broader genetic heterogeneity within the species. In the *CoxI*-based phylogenetic trees and haplotype network, the Philippine sequence was recovered within a widely distributed assemblage of *H. contortus* haplotypes but appeared as a unique haplotype relative to sequences currently available in GenBank. This pattern is more consistent with geographic differentiation within a genetically diverse species than with conflict in taxonomic assignment (Blouin *et al.*, 1995; Chaudhry *et al.*, 2015; Wei *et al.*, 2025). At the same time, the relationships of the Mindanao isolates to other *H. contortus* sequences were not fully congruent between the ITS- and *CoxI*-based phylogenies. Such incongruence is not unexpected, because nuclear and mitochondrial markers may capture different evolutionary histories, differ in rates of lineage sorting, and be differentially influenced by demographic processes such as gene flow, drift, or host movement (Cushner, 1965; Slatkin, 1985; Masel, 2011; Dampier, 2012). Interpretation is further constrained by the uneven representation of localities, hosts and study designs among publicly available reference sequences (Harris, 2003; Meyer *et al.*, 2015).

The molecular patterns observed here are compatible with the view that *H. contortus* represents a broadly distributed and genetically heterogeneous parasite with limited or uneven geographic structuring across parts of its range (Blouin *et al.*, 1995; Salle *et al.*, 2019). One plausible explanation is the long-term movement of domestic ruminants through trade,

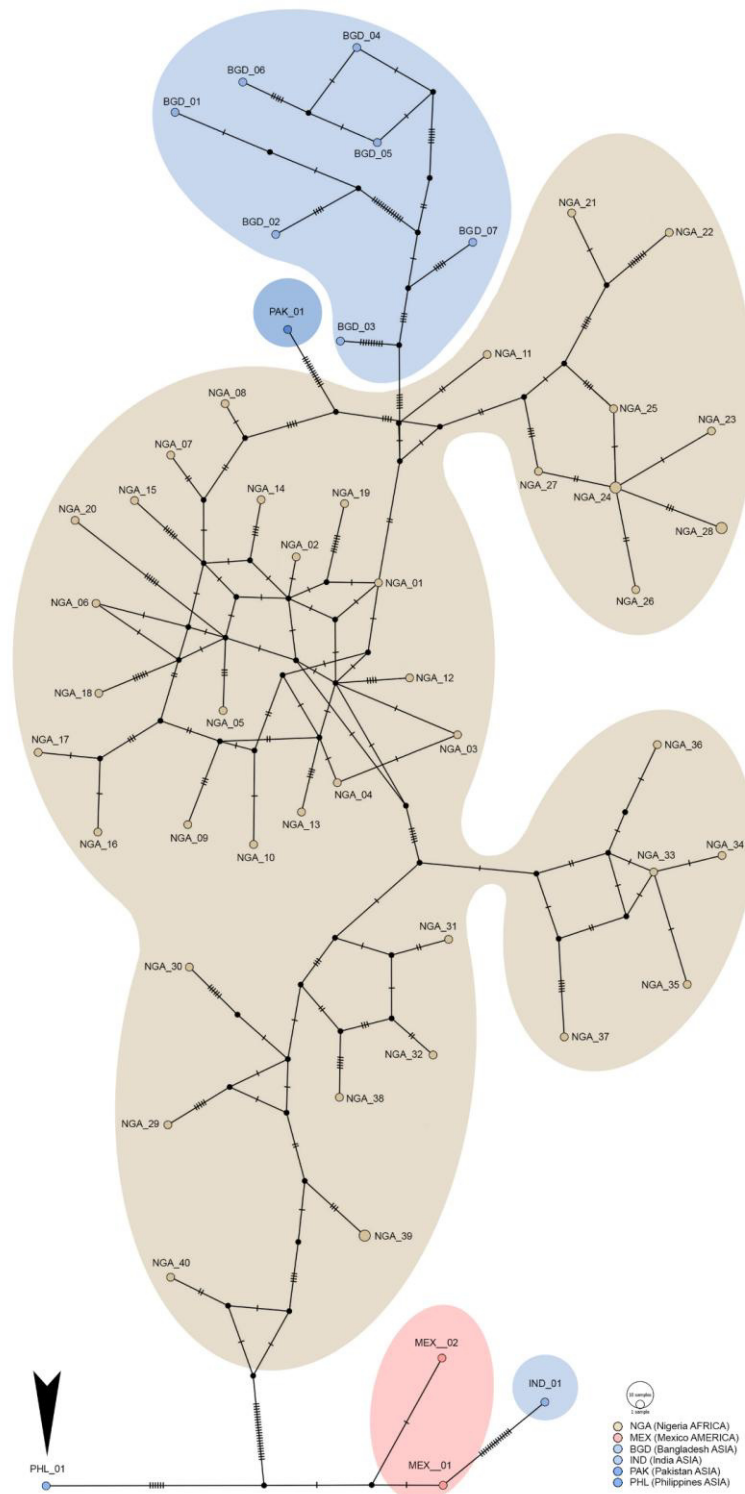


Fig. 3. Median-joining haplotype network of *H. contortus* (Rudolphi, 1803) Cobb, 1898 based on *CoxI* sequences. The network was constructed from the same sequence dataset used in Figure 1, excluding *H. longistipes* Railliet et Henry, 1909, which was included there as an outgroup. A total of 55 sequences, including one generated in the present study, yielded 52 haplotypes; the sequence obtained in this study constituted a distinct haplotype. Circles represent haplotypes, with circle size proportional to haplotype frequency, and hatch marks on the connecting lines indicate mutational steps. The haplotype identified in the present study is indicated by a black arrowhead.

translocation and agricultural exchange, which may have facilitated repeated introduction, circulation and admixture of parasite lineages across regions (Cushner, 1965; Dampier, 2012; Salle *et al.*, 2019). Under this scenario, the distinct Philippine *CoxI* haplotype may reflect local differentiation within a globally dispersed lineage complex rather than deep historical isolation. However, its apparent uniqueness should be interpreted cautiously, as it may also result from undersampling (Gaytán *et al.*, 2020), especially given the current absence of comparable molecular data from the Philippines and the still incomplete representation of Asian isolates in public databases (Gharamah *et al.*, 2012; Laosutthipong & Eardmusic, 2019; Pitaksakulrat *et al.*, 2021).

An important limitation of the present study is the restricted sampling design. Although three goats were examined, all sequenced parasites were recovered from a single infected host. Consequently, the present dataset does not allow assessment of parasite prevalence, haplotype frequency, within-population diversity, regional transmission dynamics, or broader population structure in the Philippines. For the same reason, it is not possible to infer specific historical introduction routes or to determine whether the detected ITS variants and *CoxI* haplotype are widespread locally or represent host-level sampling effects. The present results should therefore be regarded as preliminary comparative molecular evidence that establishes the occurrence and detectable genetic variation of *H. contortus* in the sampled locality, while also providing a basis for broader future surveys.

Future work should include expanded sampling across multiple hosts, farms and geographic regions of the Philippines, ideally integrating both nuclear and mitochondrial markers and a denser comparative framework from neighbouring parts of Asia (Parvin *et al.*, 2024). Such data will be necessary to determine whether the patterns observed here reflect localised diversity, repeated introductions, or broader regional circulation of *H. contortus* lineages.

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Loginova O. A., Luneva A. V., Sumaya N. H. N. and S. E. Spiridonov. *Haemonchus contortus* (Rudolphi, 1803) Cobb, 1898 (Nematoda: Trichostrongylidae), обнаруженный у козы на острове Минданао, Филиппины: генетическое разнообразие широко распространенного вида.

Резюме. *Haemonchus contortus* рассматривают как один из наиболее патогенных и экономически значимых видов желудочно-кишечных нематод мелких жвачных во всём мире, вызывающий анемию, снижение продуктивности и значительные потери в козо- и овцеводстве. При убое трёх коз на мясо в городе Илиган, Минданао, Филиппины, у одного животного в сычуге были обнаружены нематоды из группы трихостронгилид. При использовании интегративного подхода, сочетавшего световую микроскопию, сканирующую электронную микроскопию, морфометрический анализ и анализ ДНК, часть этих экземпляров была идентифицирована как *H. contortus*. У одного экземпляра прямое секвенирование ампликона ITS рДНК дало перекрывающиеся пики в области ITS1, поэтому продукт был клонирован для дальнейшего анализа. Для оценки генетического разнообразия и таксономических связей особей *Haemonchus* были использованы филогенетические анализы на основе ITS рДНК и митохондриального *CoxI*, а также сеть гаплотипов *CoxI* и оценки попарных генетических дистанций. Данные ITS выявили три близкородственных варианта последовательностей с низким уровнем дивергенции, что подтверждает их интерпретацию как внутривидовой вариации, а не таксономической неоднородности. В свою очередь, анализ последовательности *CoxI* показал, что филиппинский образец относится к широко распространённой группе *H. contortus*, но при этом представляет собой уникальный гаплотип. Такая картина указывает на локальную генетическую дифференциацию в пределах широко распространённого и генетически гетерогенного вида. Незначительное несоответствие между отношениями, реконструированными на основе ITS и *CoxI*, следует интерпретировать с осторожностью, учитывая специфическую для маркеров эволюционную историю и всё ещё ограниченную региональную выборку в общедоступных базах данных.