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Research article

PHYLOGENETIC VALIDATION OF *ASCARIDIA COMPAR* (SCHRANK, 1790) IN WESTERN CAPERCAILLIE (*TETRAO UROGALLUS*)

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Ascaridia compar (Schrank, 1790) is a nematode parasite of wild galliform birds that has long been surrounded by taxonomic uncertainty due to overlapping morphological features with several historically described species. In this study, we provide molecular evidence supporting the species identity and preliminary phylogenetic placement of *A. compar* isolated from western capercaillie (*Tetrao urogallus*) in Bosnia and Herzegovina. Morphological analysis of seven adult nematodes (six females, one male) revealed diagnostic traits consistent with assignment to the genus *Ascaridia*, however, because morphological characters overlap among several historically described grouse-associated taxa, species-level identification was subsequently supported by molecular analysis of the *ITS1*, *cox1*, and *cox3* gene regions and comparison with homologous sequences available in GenBank. Phylogenetic analysis supported the identification of the capercaillie-derived specimens as *A. compar*, with high bootstrap support distinguishing them from *A. galli*, *A. columbae*, and *A. nymphii*. Pairwise distance analysis showed a 1–4% divergence from the Italian *A. compar* isolate, and significantly greater divergence from congeneric species. This study contributes preliminary molecular evidence relevant to a longstanding taxonomic ambiguity and supports the distinction of *A. compar* from currently compared congeners, although broader sampling across multiple hosts and populations is needed to confirm these patterns. The presented findings highlight the relevance of integrating morphological and molecular data in nematode systematics and point to the need for future studies on parasite dynamics in declining grouse populations.

Keywords: *Ascaridia compar*; morphology; phylogenetic analysis; *Tetrao urogallus*

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INTRODUCTION

Members of the complex genus *Ascaridia* (Dujardin, 1845) are intestinal parasites of a large number of domestic and wild bird species [1,2]. Several *Ascaridia* species have been identified in grouse from Europe, including *Ascaridia galli*, *Ascaridia compar, Ascaridia cylindrica*, and *Ascaridia magnipapilla* [3]. Several species within the genus *Ascaridia* have yet to be molecularly validated, suggesting the presence of numerous synonyms in the morphological descriptions. Despite the morphologically based diagnosis, the taxonomic uncertainty is further complicated by the fact that studies have not employed molecular diagnostic methods for species identification. Instead, species determination has often relied on adult and egg morphology [4,5]. These surveys attribute all ascarid findings in grouse to either *A. compar* or *A. galli* [4,6,7]. In some cases, mixed ascaridid infections in capercaillie were reported [8]. Moreover, only *A. galli* has been extensively investigated through molecular characterization and phylogenetic analysis. New research examining mitochondrial and internal transcribed spacer (*ITS*) gene sequences shows that *A. galli* exhibits significant genetic diversity [9,10]. This knowledge gap underscores the need for more data on how host specificity and host range may influence morphological and genetic variability within *Ascaridia* species. The limited number of studies on the genus *Ascaridia* in certain grouse species, particularly the western capercaillie (*Tetrao urogallus*), can be attributed to a significant decline in hunting practices and the restricted geographical distribution of these tetraonids. As a result, it has become challenging to collect and process high-quality, valid samples. Furthermore, the number of taxonomic studies in systematic parasitology has notably decreased [11]. It is essential not only to confirm the presence of specific ascarid species in these birds but also to investigate the divergence relative to the validated species. This study aims to combine morphological analysis and molecular phylogenetic assessment of *Ascaridia* specimens collected from legally hunted western capercaillie in Bosnia and Herzegovina.

MATERIAL AND METHODS

Morphological study

During the period from 2019 to 2020, four male western capercaillies were legally hunted at two specific locations: Zelengora (43.3544° N, 18.5461° E) and Vučevo (43.3373° N, 18.8254° E) in Bosnia and Herzegovina. The birds exhibited no signs of illness. Following the hunting, all internal organs were excised, marked, and frozen at -20°C for subsequent examination. The parasitological analysis was conducted at the Laboratory for Diagnostics of Infectious Diseases at the Veterinary Institute of the Republic of Srpska "Dr. Vaso Butozan" in Banja Luka. The small intestines were carefully prepared, cut into sections of up to 30 cm, and rinsed with saline in Petri dishes. These intestinal washings were thoroughly examined under a stereomicroscope.

Selected nematode specimens were processed using Amman's lactophenol. The morphological analysis of the isolated nematodes relied on descriptions and taxonomic keys from Kung [12], Mozgovoi [1], Barus [3], and Brglez et al. [8]. Key morphological and morphometrical features were assessed and compared with available historical records mentioned above. The limited number of examined birds and recovered nematodes reflects the restricted availability of samples due to the species' protected status [13].

Molecular phylogenetic analysis

Genomic DNA was extracted from a single female worm using the GeneJET Genomic DNA Purification Kit (Thermo Scientific, USA). The *ITS1*, *cox1*, and *cox3* genes were amplified using previously reported primers [9,14,15]. In parallel with the sequencing of the mentioned genes from the *Ascaridia* specimen isolated from western capercaillie, comparative sequencing of the *cox1* and *cox3* genes was performed on a female *Ascaridia galli* specimen recovered from a chicken (*Gallus gallus*) in the Banja Luka area. The obtained PCR products were sequenced in both directions using the Sanger method. The obtained sequences were aligned, trimmed, and consensus sequences were analyzed using BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Phylogenetic analysis and pairwise distance calculations were performed in MEGA 12 including analogous sequences available in the GenBank database (https://www.ncbi.nlm.nih.gov/genbank/) [16]. The downloaded sequences were trimmed and aligned with sequences obtained in this study. Maximum likelihood (ML) trees were constructed using the Tamura [17], Tamura-Nei [18], and Hasegawa-Kishino-Yano [19] nucleotide substitution models, with 1000 bootstrap replicates, for the *ITS1*, *cox1*, and *cox3* datasets, respectively. Sequences obtained in this study were submitted to GenBank and are available under the following accession numbers: PV871199 for *ITS1*, PV848595-PV848596 for *cox1*, and PV863151-PV863152 for *cox3*.

RESULTS

A total of seven adult nematodes belonging to the genus *Ascaridia* were collected from intestinal washings, consisting of one male and six females. Worms were found in two western capercaillies from Vučevo. Females measured up to 8 cm in length, while the male measured up to 4 cm (Figure 1-4). The nematodes exhibited three well-developed lips (one dorsal and two lateroventral). The male had a distinctly rounded precloacal sucker with a papilla. The tail of the male was surrounded by prominent cuticular alae. Furthermore, there were nine pairs of caudal papillae on the tail: four well-developed pairs positioned in front of the cloaca and five smaller papillae located behind the cloaca. The shape of the spicule's radix was nearly round, lacking any angular formations. The spicules were not membranous (lacking alae) and ended with a specific rounded tip, measuring up to 3 mm in length. Based on the examined morphological characters, the specimens were assigned to the genus *Ascaridia*, but morphology alone did not allow sufficiently secure species-level identification. Species-level identification as *A. compar* was then supported by BLAST comparison and phylogenetic analysis of the *ITS1*, *cox1*, and *cox3* sequences.

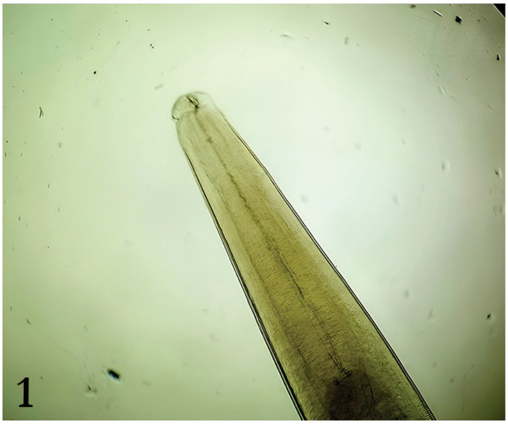

Figure 1. Anterior part of *Ascaridia*: cylindrical oesophagus and prominent lips.

Figure 2. Posterior end of a male *Ascaridia*: long spicules without alae, a round precloacal sucker, and posterior cuticular alae.

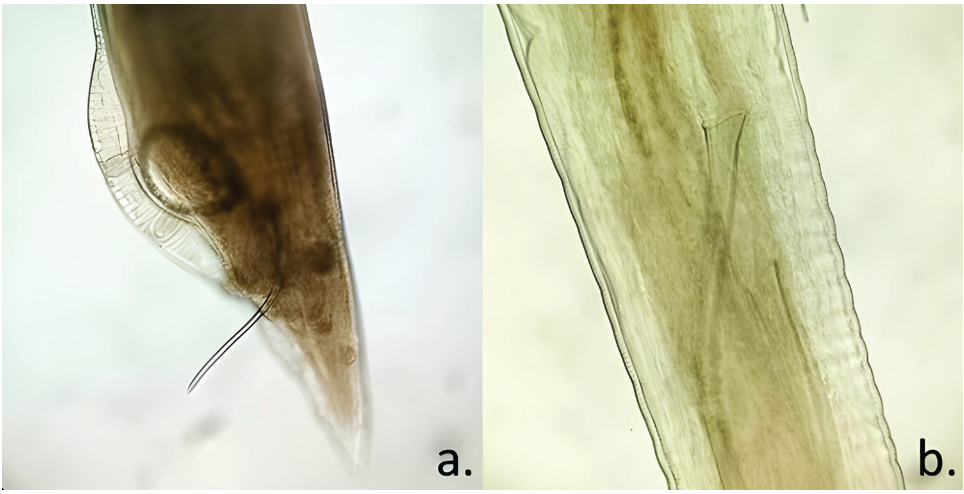

Figure 3. **(a)** Distal end of *Ascaridia* with large caudal papillae and cuticular alae; **(b)** typical radix of the male spicules of *Ascaridia*.

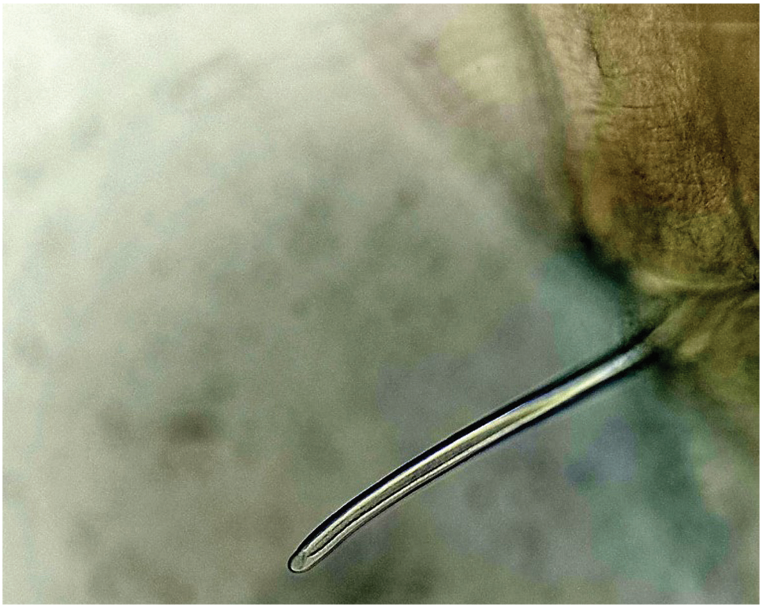

Figure 4. Characteristic rounded spicular tip of *Ascaridia*.

Results of comparative morphological characteristics are presented in Table 1.

Table 1. Results of comparative morphological analysis between *Ascaridia galli, Ascaridia compar, Ascaridia magnipapilla, Ascaridia cylindrica* and *Ascaridia spp.* from this study

Morphological characteristics	*Ascaridia galli* [20]	*Ascaridia compar* [3]	*Ascaridia magnipapilla* [3]	*Ascaridia cylindrica* [8]	*Ascaridia spp.* (this study)
Host	*Gallus gallus*	*Perdix perdix*	*Lyrurus tetrix*	*Tetrao urogallus*	*Tetrao urogallus*
Female length (mm)	72-108	35.2-46.0	35-68	50-70	55-80
Male length (mm)	42-76	25.4-36.2	23.0-24.8	42-60	60
Lips	1 mid-dorsal 2 lateroventral	1 dorsal 2 lateroventral	1 dorsal 2 lateroventral	1 dorsal 2 lateroventral	1 dorsal 2 lateroventral
Cephalic papillae	Present	Present	Present	Not described	Present
Interlabia	Absent	Absent	Absent	Absent	Absent
Precloacal sucker	Round	Round	Round	Round	Round
Papillae on sucker	Not described	Not described	Not described	Present	Present
Cuticular alae	Present	Present	Prominent	Prominent	Prominent
Spicular alae (membrane)	Absent	Absent	Absent	Absent	Absent
Length of spicules (mm)	0.65-2.40	1.84-2.97	2.50-3.04	2.90-3.70	3.00
Tip of spicules	Tapered	Round	Round	Round	Round
Proximal end of spicules	Triangular	Round	Not described	Not described	Round
Number of caudal papillae	10 pairs	9 pairs	9 pairs	9 pairs	9 pairs
Position of caudal papillae	3 precloacal 1 cloacal 3 postcloacal 3 subterminal	4 precloacal 5 postcloacal	2 pairs precloacal 1-2 pairs cloacal 5 pairs postcloacal	4 precloacal 5 postcloacal	4 precloacal 5 postcloacal
Tip of female tail	Blunt end	Cuticular spine	Blunt end	Not described	Cuticular spine
Vulvar opening	Elevated	Not elevated	Elevated	Elevated	Elevated

Only two sequences belonging to the species *A. compar* were available in NCBI GenBank (FM177755 and FM178544) for comparative phylogenetic study. Figure 5 shows that the *ITS1* sequence of our isolate clusters with *A. compar* from black grouse, clearly separating it from *A. galli*, *A. nymphii*, *A. columbae*, and *Heterakis dispar*. In this tree, *A. columbae* does not form a clearly monophyletic cluster, consistent with the limited resolution of this marker for separating some *Ascaridia* taxa.

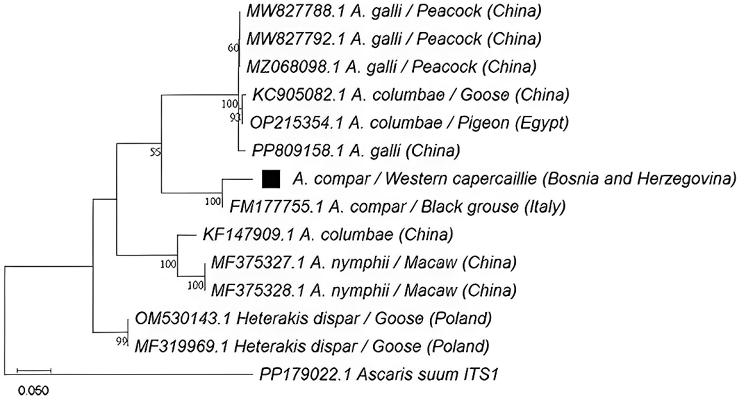

Figure 5. Phylogenetic tree based on 13 partial *ITS1* sequences of *Ascaridia galli*, *A. compar*, *A. columbae*, *A. nymphii*, and *Heterakis dispar*, generated using the Maximum Likelihood method and the Tamura (1992) model of nucleotide substitutions. The tree with the highest log likelihood (-2,681.20) is shown. The percentage of replicate trees in which the associated taxa clustered together (1,000 replicates) is shown below the branches. A partial *ITS1* sequence of *Ascaris suum* (PP179022) was included as the outgroup. Bootstrap values greater than 50% are shown. The final dataset included 629 positions. The sequence from this study is marked with a square.

In Figure 6, the *cox1*-based phylogeny places our sample within the *A. compar* clade, distinct from both *A. galli* and *A. columbae*, with strong bootstrap support. Here again, *A. columbae* does not appear strictly monophyletic. Similarly, Figure 7 supports the identification of our isolate as *A. compar*, which forms a separate position from *A. galli* and *A. columbae* with strong bootstrap support.

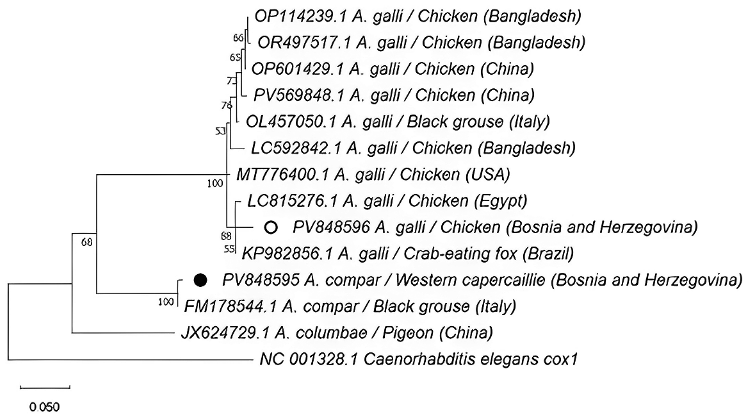

Figure 6. Phylogenetic tree based on 13 partial *cox1* sequences of *Ascaridia galli*, *A. compar*, and *A. columbae*, generated using the Maximum Likelihood method and the Tamura-Nei (1993) model of nucleotide substitutions. The tree with the highest log likelihood (-1,271.36) is shown. The percentage of replicate trees in which the associated taxa clustered together (1,000 replicates) is shown below the branches. A partial *cox1* sequence of *Caenorhabditis elegans* (NC001328) was included as the outgroup. Bootstrap values greater than 50% are shown. The final dataset included 387 positions. Sequences from this study are marked with circles.

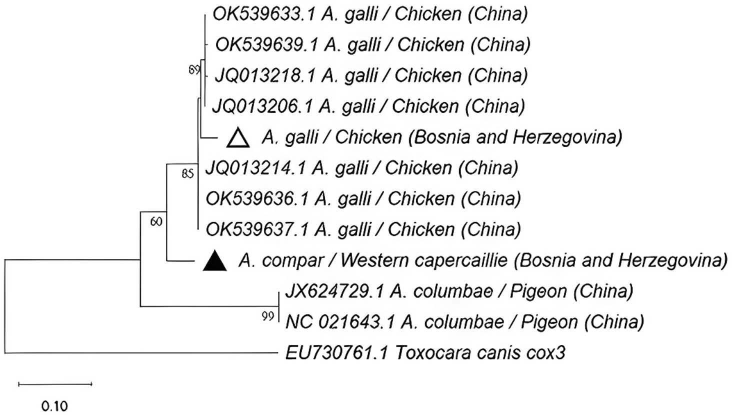

Figure 7. Phylogenetic tree based on 11 partial *cox3* sequences of *Ascaridia galli*, *A. compar*, and *A. columbae*, generated using the Maximum Likelihood method and the Hasegawa-Kishino-Yano (1985) model of nucleotide substitutions. The tree with the highest log likelihood (-978.04) is shown. The percentage of replicate trees in which the associated taxa clustered together (1,000 replicates) is shown below the branches. A partial *cox3* sequence of *Toxocara canis* (EU730761) was included as the outgroup. Bootstrap values greater than 50% are shown. The final dataset included 343 positions. Sequences from this study are marked with triangles.

As shown in Table 2, the *ITS1* sequence showed approximately 4% divergence from the Italian *A. compar* isolate and 21–24% divergence from the other compared taxa (*A. galli*, *A. columbae*, *A. nymphii*, and *H. dispar*). The *cox1* sequence of our isolate differed by approximately 1% from the Italian *A. compar* sequence and by 13–15% from *A. galli* and *A. columbae*. The *cox3* p-distance between our *A. compar* sequence and *A. galli* ranged from 6% to 7%, whereas the distance to *A. columbae* was approximately 15%.

Table 2. Pairwise distances of sequences from *Ascaridia compar* generated in this study compared with analogous sequences of congeneric species

Genomic marker	Gene type	*Ascaridia compar* (Italy)	*Ascaridia galli* (Banja Luka, BiH)	*Ascaridia galli* (China, USA, Egypt, Bangladesh)	*Ascaridia columbae* (China)
ITS-1	Nuclear (rRNA)	4%	-	21%	21-24%
cox1	MtDNA	1%	15%	13-14%	13-15%
cox3	MtDNA	-	7%	6-7%	~15%

Taxonomic remarks

Ascaridia compar was originally described in 1790 in Bavaria (Germany), yet to this day no detailed phylogenetic analysis of this nematode has been reported. The species was first identified by Schrank [21] in willow ptarmigan (*Lagopus lagopus*), but was mistakenly named "*Heterakis compar*". The species was later redescribed by Lauro Travassos in 1913, who reassigned it to the genus *Ascaridia*. Early helminthological studies on wild birds confirmed the presence of *A. compar* in the following species: *Tetrao urogallus, Lyrurus tetrix, Coturnix coturnix, Perdix perdix*, and *Alectoris graeca*. *A. compar* has historically been described under numerous synonymous names, including *Ascaridia urogalli, Ascaridia neocordata, Ascaris compar, Heterakis compar, Ascaridia petrensa, Heterakis infexa, and Heterakis borealis* [22]. Initial investigations suggested that *A. compar* is a dominant nematode species in Europe, specifically among wild gallinaceous birds. It does not occur in domestic chickens (*Gallus gallus*) or in pheasants (*Phasianus colchicus*). Size variation of this nematode associated with geographic origin and host species was noted by Kung [12]. In 1909, Bloome [23] described *Heterakis cylindrica* from the western capercaillie (*Tetrao urogallus*), but this nematode was also later found in *Lyrurus tetrix* and *Lagopus lagopus*. Early distribution records pointed to Eastern Europe and parts of Asia. Huus [24] based on partial descriptions of material from grouse species, concluded that *Heterakis cylindrica* and *Heterakis magnipapilla* (originally described from black grouse) were morphologically identical to the already described *Ascaridia compar*. This conclusion was later supported by Holger Madsen in his seminal 1952 work, "*A study of the nematodes of Danish gallinaceous game-birds*." Subsequently, two additional species, identical to *A. compar*, *Ascaridia alectoris* and *Ascaridia ketzkhovelii* were described [25]. According to previous literature, male morphological traits such as the number and position of caudal papillae, the rounded tip of the spicules, and the presence of cervical papillae were considered sufficient to propose that *Ascaridia alectoris, Ascaridia ketzkhovelii, Ascaridia cylindrica,* and *Ascaridia magnipapilla* are synonyms of the previously described *Ascaridia compar [25].* Although the available morphological evidence and previous taxonomic literature are compatible with the hypothesis that *A. compar* and *A. cylindrica* may represent the same species [22,24,25], *A. cylindrica* was not included in the molecular analysis performed in the present study. Therefore, any inference regarding their relationship remains indirect and should be treated as a hypothesis requiring future integrative taxonomic revision. This question should instead be addressed in a future integrative taxonomic revision based on multiple specimens, host species, geographic populations, and combined morphological and molecular evidence. No consistent morphological characters were found to distinguish the two species. The primary variation observed among these taxa pertains to size (Table 1). This discrepancy in morphology may arise from the fact that the basic descriptions by Barus [3] included specimens of *A. compar* found in the grey partridge (*Perdix perdix*) and not western capercaillie (*Tetrao urogallus*). Brglez et al. [26] noted that the *A. cylindrica* specimens found in capercaillies were larger than those isolated from black grouse (*Lyrurus tetrix*). This may be indicative that size variation could be the result of differences in hosts and ecological factors.

DISCUSSION

A. compar and *A. galli* are sympatric species with similar ecological development conditions in the environment and avian hosts [27]. However, despite sympatry, ecological isolation between the two species is incomplete. Under laboratory conditions, it has been demonstrated that *A. compar* is unable to complete its development in the domestic chicken (*Gallus gallus*), which further supports its specificity for wild galliform birds [27]. A review of the literature, along with our findings, indicates that *A. compar* is a specialized parasite of birds in the tribe Tetraonini, including the genera Tetrao, *Perdix* and *Alectoris* [3,4,27]. In the present study, morphology was sufficient for genus-level diagnosis (*Ascaridia spp.*), whereas species-level identification relied on molecular comparison with available reference sequences. This distinction is important because the available taxonomic literature indicates substantial morphological overlap among nominal taxa such as *A. compar*, *A. cylindrica*, and *A. magnipapilla,* making morphology alone insufficient for a confident species-level diagnosis in the present material. Given that these hosts encompass numerous species, intraspecific morphological and phylogenetic variation is expected. This phenomenon probably led to the several potential synonyms for the species, including *A. ketzkhovelii, A. alectoris*, *A. cylindrica,* and *A. magnipapilla* [22,25]. Our data support the genetic differentiation of *A. compar* from *A. columbae, A. galli*, and *A. nymphii* based on the markers analyzed, although these findings remain preliminary because they are derived from a limited sample set. However, these divergence values should not be interpreted as a formal species-delimitation test, because singlelocus distance thresholds and barcode gaps are known to vary widely among taxa and markers, and there is no universally accepted genetic distance cutoff for nematodes or other metazoans [28,29]. In nematodes, markers such as *ITS* and mitochondrial genes can provide useful evidence for identification and for recognizing potentially distinct lineages, but their interpretive value is marker – and clade-specific [28-30]. Accordingly, the *ITS1*, *cox1*, and *cox3* distances observed here are best interpreted as supportive molecular evidence consistent with the identification of our isolate as *A. compar*, rather than as a standalone basis for delimiting species boundaries [28,29,31]. A robust delimitation framework would require broader sampling across multiple individuals and populations, the application of explicit species-delimitation methods, and the integration of molecular and morphological evidence within an integrative taxonomic approach [31-33]. The pairwise distance and phylogenetic analyses performed in this study indicate that *A. galli* is the closest currently compared species to *A. compar*. Comparison of the *ITS1* and *cox1* sequences of our isolate with those of *A. compar* previously recovered from black grouse (*Lyrurus tetrix*) in Italy revealed a certain degree of intraspecific genetic variation within this species. This interpretation is also consistent with the fact that, in nematodes, intraspecific and interspecific divergence ranges may overlap depending on the marker and taxonomic group [28]. Since our molecular analysis was based on a single specimen, the presented findings should be considered preliminary and interpreted with appropriate caution until confirmed in larger sample sets. The phylogenetic trees based on the *cox1* and *cox3* genes exhibit differences in branching patterns and topology compared to the *ITS1* gene. This is likely due to differences in coalescent times between these markers and may indicate incomplete lineage sorting (ILS). Interestingly, genetic divergence between *A. compar* and *A. galli* is greater than that observed between *A. columbae* and *A. galli*. In fact, the resolution of the *ITS1* marker is insufficient to reliably separate *A. columbae* and *A. galli*, and occasionally yields conflicting phylogenetic signals [10]. From the perspective of the observed genetic distances, *A. compar* may represent an early-diverging lineage relative to the currently compared molecularly validated species within the genus Ascaridia, however, this interpretation should be treated cautiously until tested with broader population-level sampling. This divergence may also be influenced by the evolutionary differences among the hosts, as grouse represent a considerably older taxon than the ancestors of modern domestic chickens [34,35]. Furthermore, the findings of *A. compar* in western capercaillie from Bosnia and Herzegovina provides further evidence that this parasite has a significant geographical distribution closely linked to the ranges of grouse. In the past century *A. cylindrica* was documented in western capercaillies and black grouse in Slovenia [8,26]. The pathogenic impact of *A. compar* has been investigated only to a limited extent, with available evidence from Scandinavia suggesting that parasite burdens may contribute to grouse population dynamics under certain ecological conditions [6]. However, the present study did not include epidemiological, pathological, or population-level data, and therefore no direct conclusions can be drawn regarding the health impact of *A. compar* in western capercaillie from Bosnia and Herzegovina. Nevertheless, the detection of this parasite in a host species of conservation concern highlights the need for future studies addressing its prevalence, pathogenic significance, host–parasite interactions, and possible contribution to broader conservation pressures acting on declining grouse populations in the Balkans [36]. Environmental stressors, habitat degradation, poaching, and changes in prey availability may further exacerbate the effects of *A. compar* infections, posing greater risks to grouse survival. More research is needed to analyze these critical issues.

CONCLUSION

This study provides molecular evidence supporting the species identity of *A. compar* and preliminary phylogenetic support for its placement within the genus *Ascaridia*. Given the unresolved taxonomic complexity among grouse-associated nominal taxa, our findings highlight the need for future integrative taxonomic revision based on broader morphological and molecular sampling. Ultimately, the observed differences in worm size may reflect intraspecific variation associated with host-related and ecological factors rather than speciation alone, but this interpretation requires confirmation through broader morphological and molecular sampling.

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Authors' contributions

OS and SG collected samples in the field, performed macroscopic examinations, and interpreted macroscopic findings. AR and IP performed molecular genetic tests. AR performed the bioinformatic analysis. DK and DN supervised all stages during the study and performed the overall review of the paper. ŽS organized the collection of samples. TI and NJ interpreted the results, reviewed relevant literature, and approved the final version of the paper. AV and AR performed the interpretation of molecular genetic tests. OS carried out the identification of parasites, conducted molecular genetic analyses, interpreted the results of molecular genetic analyses, and worked on the preparation of figures.

Declaration of conflicting interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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FILOGENETSKA POTVRDA VRSTE *ASCARIDIA COMPAR* (SCHRANK, 1790) KOD VELIKOG TETREBA (*TETRAO UROGALLUS*)

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Ascaridia compar (Schrank, 1790) je nematoda divljih galiformnih ptica, koja je dugo bila predmet taksonomske neodumice zbog preklapanja morfoloških karakteristika sa više, ranije opisanih vrsta. U ovoj studiji prikazali smo molekularne dokaze koji podržavaju identitet vrste *A. compar* i njenu preliminarnu filogenetsku pripadnost rodu *Ascaridia*, na osnovu uzorka poreklom od velikog tetreba (*Tetrao urogallus*) iz Bosne i Hercegovine. Morfološka analiza sedam odraslih nematoda (šest ženki i jednog mužjaka) pokazala je osobine koje su u skladu sa prethodnim opisima vrsta roda *Ascaridia*. Da bi se potvrdila vrsta, analizirane su sekvence regiona gena *ITS1*, *cox1* i *cox3*, koje su zatim upoređene sa homolognim sekvencama dostupnim u *GenBank* bazi podataka. Filogenetska analiza ukazuje da su uzorci izolovani iz tetreba identifikovani kao *A. compar*, uz visoku "bootstrap podršku" koja ih jasno razdvaja od vrsta *A. galli*, A. *columbae* i *A. nyphii*. Analiza parnih rastojanja pokazala je odstupanje od 1-4 % u odnosu na italijanski izolovani soj *A. compar*, dok je divergencija u odnosu na srodne vrste bila znatno veća. Ovo istraživanje pruža preliminarne molekularne dokaze koji mogu doprineti razjašnjavanju dugotrane taksonomske nedoumice i ističe razlikovanje vrste *A. compar* u odnosu na druge srodne vrste. Međutim, za potvrdu navedenih podataka potrebna su dodatna istraživanja na većem broju jedinki i populacija. Dobijeni rezultati naglašavaju značaj integracije morfoloških i molekularnih podataka u sistematici nematoda i ukazuju na konzervacione aspekte vezane za dinamiku parazita u opadajućim populacijama tetreba.