

Research Note

A revised checklist of *Cooperia* nematodes (Trichostrongyloidea), common parasites of wild and domestic ruminants

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Summary

This review updates the current knowledge on the taxonomy of intestinal nematodes of the genus *Cooperia* parasitizing in wild and domestic ruminants. The emphasis is put on revision of 19 valid species belonging to the genus. This analysis focuses on main features of the genus *Cooperia*, including its geographic occurrence and the life cycle details. The most widespread congeners are *Cooperia curticei*, *C. oncophora*, *C. pectinata*, and *C. punctata*, having nearly worldwide distribution. The fifth species, referred by electronic databases from the European territory as *Cooperia asamati* Spiridonov, 1985, is unveiled here originally as *nomen nudum*.

Keywords: roundworms; species spectrum; geography; morphology; *Cooperia asamati nomen nudum*

Introduction

Gastrointestinal nematodes of the genus *Cooperia* Ransom, 1907, belong to the most important group parasitizing ruminants, trichostrongylids (Amarante *et al.*, 2014). Up to now, more than 30 species were proven within this genus (Skrjabin *et al.*, 1954; Yamaguti, 1961; Rees, 2018; Ramúnke *et al.*, 2018). However, the detailed review of taxonomic and systematic studies discovered new information in validity of some taxa. A correct species designation is important from both, the theoretical and practical point of view since mixed gastrointestinal nematode infections are common in domestic ruminants and various parasite species may differ significantly in their fertility and pathogenicity (Amarante *et al.*, 2014). Shared infections among wild and domestic ruminants also occur, and co-infections with other trichostrongylid parasites, such as *Ostertagia* spp. or *Haemonchus contortus*, are common (Vlassoff & McKenna, 1994).

Nematodes of the genus *Cooperia* parasitize the small intes-

tines in a wide spectrum of domestic and wild ruminants. Several species have a worldwide distribution as well as broad ruminant host spectrum. Meanwhile, others have been described only in a single host species. In fact, *Cooperia* spp. are considered less pathogenic than the other gastrointestinal roundworms of cattle and sheep. On the other hand high worm burden may substantially reduce the production in host animals where the infection has been associated with their inappetence and insufficient weight gain (Ramúnke *et al.*, 2018).

The abundance of various species of the genus *Cooperia* can be different depending on climate conditions and geographic location. In general, a higher temperature and a humid environment are more favourable for these parasites (Gibbons, 1981). On average, a richer species spectrum was referred in Africa than in Europe or the North America. The infectivity of *Cooperia* spp. in cattle and goats reaches nearly 40 % in subtropical or tropical regions (Coelho *et al.*, 2012; Mahmuda *et al.*, 2012; Kulišić *et al.*, 2013; Radavelli *et al.*, 2014). In livestock, *Cooperia* spp. have recently become

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the most prevalent parasites in the United States. This is partially due to the widespread use of veterinary drugs, macrocyclic lactones what resulted in reduced drug effectiveness (Stromberg *et al.* 2012). The trichostrongylid roundworms including *Cooperia* spp., have acquired a multi-species anthelmintic resistance what was, for instance, experimentally demonstrated on cattle in the western parts of the United States (Gasbarre *et al.* 2009; Edmonds *et al.* 2010).

Nematodes of the genus *Cooperia* are monoxenous parasites with a direct life cycle where pre-parasitic larval phase is completely free-living. Eggs, produced by females located in host intestine, are passed through host faeces and hatch in the "faecal pat". The first stage larvae (L₁) feed on soil and faecal bacteria. Then, two subsequent moults to L₂ and L₃ are completed between 24 and 36 hours (Ciordia & Bizzel, 1963; Kotrlá *et al.*, 1984). The temperature range for larval development is 5 °C and 33 °C (Knapp-Lawitzke *et al.*, 2016). The L₃ larvae do not feed and are enclosed by a sheath composed of the retained L₂ cuticle. They migrate from the "faecal pat" to the grass, where they develop within 1 to 6 weeks (depending on the time of year) and become infectious to the host (Fiel *et al.*, 2012). Infective larvae can survive for up to one year, until they are swallowed by the ruminant host (Kotrlá *et al.*, 1984). Then the L₃ larvae release from the sheath, move into mucosa of small intestine, and undergo the third and fourth moults to L₄ and L₅ larvae. Within 2-3 weeks, the L₅ larvae develop into sexually mature adult males or females (Jennings *et al.*, 1966; Leland, 1967; Kotrlá *et al.*, 1984). The fertilised females then begin producing eggs and entire cycle repeats.

Trichostrongylids, including *Cooperia* spp., have developed an exclusive strategy to arrest their development in the host via hypobiosis during conditions that are unfavourable for the free-living stages (Michel *et al.*, 1974; Armour & Duncan, 1987). For instance, large number of arrested L₄ larvae of *Cooperia* spp. may persist in a host digestive tract for up to six months (Kotrlá *et al.*, 1984). Thus, outbreaks of this parasitic disease can occur at times when natural infection would not arise (Armour & Duncan, 1987; Eysker, 1993).

Material and Methods

The revision of the current species spectrum is based on the fundamental taxonomic works of Skrjabin *et al.* (1954) and Yamaguti (1961) and subsequent publications about the taxonomy and systematics of the *Cooperia* spp. The data included in various current electronic databases were also considered and scrutinised.

Ethical Approval and/or Informed Consent

This article does not contain any studies with human participants or animals by any of the authors.

Results and Discussion

According to the most relevant systematics of Nematoda (de Ley & Blaxter, 2002), the genus *Cooperia* belongs to the class Chromadorea, order Rhabditida, suborder Strongylida, superfamily Trichostrongyloidea, and the family Trichostrongylidae. Based on morphology and DNA analyses, the family Trichostrongylidae has been recognised as monophyletic, comprising of six subfamilies (Durette-Desset, 1974; Lichtenfels *et al.*, 1997). Of these subfamilies, primarily Ostertagiinae, Haemonchinae, Trichostrongylinae and Cooperiinae include economically important and taxonomically problematic genera (Wyrobisz *et al.*, 2016).

The genus *Cooperia* is a well-defined group of species that are characterised by a typical anterior cephalic cuticular swelling (vesicle), transverse cuticular striations in the oesophageal region, a pair of typical spicules, a lyre-shaped dorsal ray within the male bursa, and the special morphology of cuticular ridges system - so called synlope system (Lichtenfels *et al.*, 1997). Both males and females are relatively small, measuring from 5.0 to 14.8 mm (Skrjabin *et al.*, 1954). The buccal capsule is reduced. Three lips and small papillae surround the mouth (phasmids are present). The oesophagus possesses the usual cylindrical shape and it is slightly thickened distally. The excretory pore is situated near the end of oesophagus (Durette-Desset, 1974). Cuticular ridges (striations) longitudinally stripe most of the outer surface of the body; this body surface type was named synlope by Durette-Desset (1969). The striations assist in the locomotion of the worm or in its attachment to the host stomach or intestinal mucosa. The number and pattern of the cuticular ridges may serve as additional diagnostic characteristics.

Males have a large bursa with two lateral lobes and a distinctly demarcated dorsal lobe, typical for the genus *Cooperia*. Each lateral lobe contains six bursal rays: ventral rays are widely separated; postero-lateral ray is separated from the laterals. The dorsal ray is lyre-shaped. Two identical and relatively short spicules up to 420 µm long are well sclerotized, having a rounded end and a longitudinal line pattern. They display a distinct wing-like expansion in the middle region and often bear ridges. Although several morphotypes might exist, the morphology of spicules is species specific. There is no gubernaculum (Skrjabin *et al.*, 1954; Walker & Becklund, 1968; Gibbons, 1981).

Females are didelphic and the excretory pore is situated not far from the anterior end. The vulva lies in the posterior quarter of the body and the ovijector is well developed. Vulvar flaps are limited to the immediate vicinity of the vulva and they expand only slightly from the surrounding cuticular ridges. The longitudinal striations are interrupted in the vulvar region. The tail is sharply pointed and lacks spine. The eggs are thin-shelled and vary from ovoid to elongated shape (Skrjabin *et al.*, 1954; Durette-Desset, 1974; Gibbons, 1981).

Table 1. Species of the genus *Cooperia* listed since Skrjabin *et al.* (1954).

| | <i>Cooperia</i> species [sources of synonymization] | References | Europe | Africa | Other regions |
|---|---|--|---------------|---------------|--------------------------|
| 1 | <i>C. acutispiculum</i> Boomker, 1982 | Boomker (1982); Rees (2018) | | + | |
| X | <i>C. africana</i> Mönnig, 1932: Synonym of <i>C. punctata</i> [Gibbons (1981); Rees (2018)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961) | | + | |
| X | <i>C. asamati</i> Spiridonov, 1985 <i>Nomen nudum</i> [this paper] | Gibson (2017); Rees (2018) | + | | |
| X | <i>C. bisonis</i> Cram, 1925: Synonym of <i>C. oncophora</i> [Yamaguti (1961); Lichtenfels (1977)] | Skrjabin <i>et al.</i> (1954), Besch (1965); Gibson (2017); Rees (2018) | + | | USA |
| X | <i>C. borgesii</i> Gutteres, 1947: <i>Species inquirendae</i> [Gibbons (1981)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Rees (2018) | | + | |
| 2 | <i>C. chabaudi</i> Diaouré, 1964 | Gibbons (1981); Rees (2018) | | + | |
| 3 | <i>C. connochaeti</i> Boomker, Horak et Alves, 1979 | Gibbons (1981); Rees (2018) | | + | |
| 4 | <i>C. curticei</i> (Giles, 1892) (type species of the genus) | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Lichtenfels (1977); Gibbons (1981); Gibson (2017); Rees (2018) | + | + | nearly worldwide |
| X | <i>C. fieldingi</i> Baylis, 1929: Synonym of <i>C. punctata</i> [Yamaguti (1961)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961) | | | Australia |
| 5 | <i>C. fuelleborni</i> Hung, 1926 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Gibbons (1981); Taylor <i>et al.</i> (2013); Rees (2018) | | + | |
| 6 | <i>C. hamiltoni</i> (Mönig, 1932) | Gibbons (1981); Rees (2018) | | + | |
| X | <i>C. hippotragusi</i> Gutteres, 1947: <i>Species inquirendae</i> [Gibbons (1981)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Rees (2018) | | + | |
| 7 | <i>C. hrantahensis</i> Wu, 1965 | Wu (1965) | | | China |
| 8 | <i>C. hungi</i> (Mönnig, 1931) | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Gibbons (1981); Taylor <i>et al.</i> (2013); Rees (2018) | | + | |
| 9 | <i>C. laterouniformis</i> Chen, 1937 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Singh & Pande (1963); Rees (2018) | | | China India |
| X | <i>C. mcmasteri</i> Gordon, 1932: Synonym of <i>C. oncophora</i> [Lichtenfels (1977); Ramünke <i>et al.</i> (2018)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Besch (1963); Gibson (2017); Rees (2018) | + | | USA |

| | | | | | | |
|----|--|--|---|---|------------------------------|---|
| X | <i>C. minor</i> Gutierrez, 1947: <i>Species inquirendae</i> [Gibbons (1981)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Rees (2018) | | | | + |
| 10 | <i>C. neitzi</i> Mönnig, 1932 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Gibbons (1981); Rees (2018) | | | | + |
| 11 | <i>C. okapi</i> Leiper, 1935 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Gibbons (1981); Rees (2018) | | | | + |
| X | <i>C. okapiae</i> Bearghe et Vuylsteke, 1937 [Skrjabin <i>et al.</i> (1954)] | Yamaguti (1961) | | | | + |
| 12 | <i>C. oncophora</i> (Railliet, 1898) | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Lichtenfels (1977); Gibbons (1981); Gibson (2017); Rees (2018); Avramenko <i>et al.</i> (2017) | + | + | nearly worldwi- de | |
| 13 | <i>C. pectinata</i> Ransom, 1907 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Lichtenfels (1977); Gibbons (1981); Gibson (2017); Rees (2018) | + | + | USA | |
| 14 | <i>C. pigachei</i> Boomker et Taylor, 2004 | Boomker & Taylor (2004); Rees (2018) | | | | + |
| 15 | <i>C. punctata</i> (von Linstow, 1906) | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Walker & Becklund (1968); Lichtenfels (1977); Gibbons (1981); Gibson (2017); Avramenko <i>et al.</i> (2017); Rees (2018) | + | + | nearly worldwi- de | |
| X | <i>C. reduncai</i> Gutierrez, 1947: <i>Species inquirendae</i> [Gibbons (1981)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Rees (2018) | | | | |
| 16 | <i>C. rotundispiculum</i> Gibbons et Khalil, 1980 | Gibbons (1981); Rees (2018) | | | | + |
| X | <i>C. spatulata</i> Baylis, 1938: Synonym of <i>C. punctata</i> [Ramünke <i>et al.</i> (2018); Sun <i>et al.</i> (2020)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Walker & Becklund (1968); Lichtenfels (1977); Gibbons (1981); Rees (2018) | | | Australia Malaysia USA | + |
| X | <i>C. surnabada</i> Antipin, 1931: Synonym of <i>C. oncophora</i> [e.g. Isenstein (1971a); Gibbons (1981); Newton <i>et al.</i> (1998); Ramünke <i>et al.</i> (2018)] | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Besch (1963); Lichtenfels (1977); Gibson (2017); Rees (2018) | + | + | USA | |
| 17 | <i>C. svanetica</i> Burdjanadze et Tschotschischvili, 1942 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961) | | | Gruzia | |
| 18 | <i>C. verrucosa</i> Mönnig, 1932 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Gibbons (1981); Rees (2018) | | | | + |
| 19 | <i>C. yoshidai</i> Mönnig, 1939 | Skrjabin <i>et al.</i> (1954); Yamaguti (1961); Gibbons (1981); Rees (2018) | | | | + |

Notes: The species currently valid are numbered; invalid species are marked as X and highlighted in grey.

The comprehensive lists of the *Cooperia* species were published by Skrjabin *et al.* (1954) and Yamaguti (1961). The first inventory contained 22 species while the second one 21 species. The differences were that Skrjabin *et al.* (1954) suppressed *C. okapiae* as a synonym of *C. okapi* while Yamaguti (1961) suppressed *C. fieldingi* and *C. bisonis* as synonyms of *C. punctata* and *C. oncophora*, respectively. This information is marked in Table 1. Later on, several other species were originally described, re-described, synonymised with congeners, or designated as *species inquirendae* (Isenstein, 1971a; Lichtenfels, 1977; Gibbons, 1981; Newton *et al.*, 1998; Ramünke *et al.*, 2018).

For instance, Gibbons published in 1981 a merit work revising African species of the genus *Cooperia*. Out of 20 species reported from Africa, 14 were redescribed, four (*C. borgesii*, *C. hippotragusi*, *C. minor*, and *C. redunca*), were considered as *species inquirendae*, and two (*C. africana* and *C. surnabada*) were discussed as synonyms of valid species *C. punctata* and *C. oncophora* (see Table 1).

The species *C. surnabada* has had adaptable story and now is considered a synonym of *C. oncophora*. This proposal was first published by Isenstein (1971a) on the basis of mating experiments and high morphological similarities between both species. Later, Lichtenfels (1977) tried to show that those two species are valid on the basis of different cuticular ridge patterns (synlope). Nevertheless, the invalidity of *C. surnabada* was finally accepted by Gibbons (1981), Humbert & Cabaret (1995), Lichtenfels *et al.* (1997), Newton *et al.* (1998), and Ramünke *et al.* (2018) (Table 1).

Cooperia mcmasteri was initially synonymized with *C. surnabada* by Karamendin (1967) and Lichtenfels (1977) and then later, with *C. oncophora* (Ramünke *et al.*, 2018).

Two other morphologically similar species are *C. spatulata* and *C. punctata* (Table 1). Walker & Becklund (1968) thoroughly compared their morphology and revealed slight differences in the shape of the concavity and ventral flange of the spicule. They also found overlapping in other features, such as size and the spicule length. The authors therefore confirmed a very high level of similarity between the congeners. Using molecular analysis, Ramünke *et al.* (2018) recently found out extreme similarities between the two species and suggested *C. spatulata* as a synonym of *C. punctata*. This was also confirmed by the latest analysis performed by Sun *et al.* (2020) (Table 1).

Cooperia asamati represents a special issue of the controversial species. The species name *C. asamati* Spiridonov, 1985 is currently reported in several Web databases (Fauna Europaea; YRMNG; BioLib.cz, Nederlands Soortenregister ID: 136135; Global Biodiversity Information - Facility ID: 7034224; YRMNG ID: 11474162 - Rees 2018). The main European zoological index, Fauna Europaea (de Jong, 2014), refers the occurrence of *C. asamati* exclusively from the Netherlands despite the facts that no further data are available. Moreover, the original description of *C. asamati* does not exist at all. The Spiridonov paper (1985) described the rhabditid nematode species *Angiostoma asamati* n.

sp. from slugs in Kyrgyzstan, and the species name of *A. asamati* was dedicated a Kyrgyz's colleague (S.E. Spiridonov, personal communication). This nematode has never been re-described or transferred into another genus. Therefore, we consider *C. asamati* as *nomen nudum*.

Overall, 19 species of the genus *Cooperia* are currently recognized as valid (Table 1). Four of these, the *C. curticei*, *C. oncophora*, *C. pectinata* and *C. punctata* occur nearly worldwide, remaining taxa have been found on selected continents (Table 1). Perhaps the most thorough research was carried out in Africa (Gibbons, 1981; Boomker, 1982; Boomker & Taylor, 2004) but many regions of the world have not been sufficiently explored. In Europe, only *C. curticei*, *C. oncophora*, *C. pectinata*, and *C. punctata* represent the valid taxa.

Due to polymorphism and/or inter-species hybridization which may occur within the members of the genus (Wyrobisz *et al.*, 2016) species boundaries of currently deemed valid *Cooperia* spp. may be rather unclear. For instance, the experimental evidence of successful interspecific cross-breeding between *C. oncophora* and *C. pectinata* was provided by Isenstein (1971b) where the hybrid generation of nematodes had morphological characters from both purebred parental species. This phenomenon is particularly important since mixed infections comprising several *Cooperia* species may occur in ruminant hosts (Giudici *et al.*, 1999).

In conclusion it is evident that the true species spectrum can be objectivized solely with modern integrative approaches. As yet, only several molecular studies have been applied to the *Cooperia* spp. The first molecular characteristics of *C. oncophora* were accomplished by van der Veer & de Vries (2003) and van der Veer *et al.* (2003). In addition, various genes were sequenced from *C. punctata* and *C. oncophora* in North and South America (Avramenko *et al.*, 2015, 2017). Amarante *et al.* (2014) developed the rDNA marker specific for *C. curticei*. Recent study of Ramünke *et al.* (2018) provided molecular data about two mitochondrial and two nuclear genes that allow diagnosis of four common *Cooperia* spp. commonly infecting cattle. Currently, *C. oncophora*, as a model species, is being investigated for transcriptomic data, and the complete genome sequencing is expected to be completed at the Washington University Genome Sequencing Center (Borloo *et al.*, 2013; Heizer *et al.*, 2013; https://en.wikipedia.org/wiki/Cooperia_oncophora). The latest comparative analysis of mitochondrial DNA of Chinese *Cooperia* sp. showed probable existence of a new species. However, further integrative studies involving classical taxonomy, population genetics and probably cytogenetics are urgently needed to accomplish.

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Conflict of Interest

Authors declare no conflict of interest.

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