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Eric P. Hoberg

*United States Department of Agriculture, Agricultural Research Service, geocolonizer@gmail.com*

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## PARASITE BIODIVERSITY AND EMERGING PATHOGENS: A ROLE FOR SYSTEMATICS IN LIMITING IMPACTS ON GENETIC RESOURCES

**Eric P. Hoberg**

*Biosystematics and National Parasite Collection Unit, USDA, Agricultural Research Service, Beltsville, MD 20705, U.S.A.*

*"The larger ecological explosions have helped to alter the course of world history, and ... can often be traced to a breakdown in isolation of continents and islands..."*  
C.S. Elton (1958, pg. 19)

*"...the distribution of a pathogen is wider than the disease caused by it, and the latter cannot be understood without understanding the former as a whole...."* J.R. Audy (1958, pg. 309).

### Abstract

Emergence of pathogenic organisms continues as a threat to overall biodiversity and genetic resources. Macroparasites including helminths constitute a potential threat to economically important resources in agriculture and conservation biology. Limitation of this threat can be achieved through survey and inventory for biodiversity and the application of systematics to understand the host range, biogeography and history of faunas. Systematics constitutes the foundation for recognition of endemic and introduced elements of faunas and the basis for predicting the behavior of pathogens introduced to new ecological settings or host groups. The basis for emergence of pathogens has both a deep historical and a contemporary component. These concepts are addressed through an examination of the history of emergence of nematode parasites of ruminants, including *Nematodirus battus* in sheep and *Umingmakstrongylus pallikuukensis* in muskoxen. Anthropogenic factors, particularly translocation of hosts and parasites leading to introduction and establishment of exotic species, continue as determinants of emergence. Ownership of biodiversity and genetic resources also constitutes responsibility to control the introduction and dissemination of pathogenic organisms.

### Introduction

Pathogenic parasites represent potential threats to economically important genetic resources within the context of agriculture (Hoberg et al., 1985), conservation (Dobson & May, 1986b; Samuel et al., 1992), and management of recovering, threatened or endangered species (Scott, 1988; Hoberg et al., 1995b). Macroparasites such as helminths are ubiquitous, and have characteristic historical relationships, host and geographic distributions, predictable life cycles, and patterns of transmission (e.g. Brooks &

McLennan, 1993). Documentation of parasite biodiversity through survey and inventory is requisite to defining endemic versus introduced elements of faunas. Systematics provides the foundation for understanding the phylogenetic, coevolutionary and biogeographic history of parasite-host assemblages. Such historical data constitutes the predictive framework for elucidating contemporary interactions with naive host-groups, and the behavior of parasites introduced into new geographic and ecological settings. A robust knowledge of the occurrence of parasitic helminths is necessary as parasites and pathogens may limit the ability of countries to export and import economically significant biological resources (e.g. Gajadhar et al., 1994; Mason, 1994).

Translocation of hosts and the introduction and establishment of “exotic” parasites is a historical and a continuing problem (e.g. Elton, 1958; Gajadhar et al., 1994; Hoberg et al., 1986; Mason, 1994; Rickard et al., 1993; Samuel et al., 1992; Scott, 1988). Establishment of exotic parasites of terrestrial vertebrates has occurred throughout the world largely coinciding with movements of domestic stock from Europe to the Western Hemisphere in the 17th century and more recently with the establishment of populations of exotic bovinds, cervids and ratites for economic purposes in North and South America, Australia and New Zealand (e.g. Hoberg et al., 1995a; Rickard et al., 1993). In this context, the history of the agriculturally important nematode, *Nematodirus battus* Crofton & Thomas, 1951, demonstrates the concept of introduction and the factors involved in later emergence (Helle, 1969; Hoberg et al., 1985, 1986).

In contrast, a pathogenic nematode of muskoxen, apparently endemic to a limited region in the Canadian Arctic, represents an enigma with respect to its origins, contemporary host-range and biogeography. The lungworm, *Umingmakstrongylus pallikuukensis* Hoberg, Polley, Gunn & Nishi, 1995, may represent a recently emergent parasite. This remarkable nematode is associated with morbidity and mortality in muskoxen and may have implications for management of wild ruminants in the Arctic (Hoberg et al., 1995b). Additionally, this parasite could have an adverse impact on food resources, by affecting a component of the ruminant prey base historically exploited by native cultures in the Holarctic. In this regard, a tradition of subsistence hunting among villages in the Arctic is directly dependent on the presence of viable populations of large ruminants. This problem is being addressed in a multidisciplinary manner involving parasite systematics and host-parasite coevolution and is dependent on a collaboration among academic scientists, government agencies, and native Inuit hunters in the Arctic.

Factors controlling the emergence of a “new” pathogen are complex. Although often associated with introductions, it is also apparent that altered ecological associations, habitat and climatological variables can influence the potential for “release” of indigenous species leading to detrimental interactions with hosts. The role of systematics and biodiversity assessment in documenting emergence become clear in the following examples concerning nematode parasites of ruminants.

### A History for *Nematodirus battus*

*Nematodirus battus* is considered the most pathogenic gastrointestinal nematode infecting sheep in the Holarctic Region (Dunn, 1978; Hoberg et al., 1985). Recognition of the potential for economic impact attributable to this parasite occurred when the Animal and Plant Health Inspection Service, USDA listed *N. battus* as the only nematode considered as an agent of foreign animal disease in sheep (Hoberg et al., 1985). *Nematodirus battus* is highly distinct morphologically with respect to the broader species-diversity of the genus *Nematodirus* Ransom, 1907. It was unknown in the Western Hemisphere and North America until the 1980's when it was reported from Argentina (Larrieu et al., 1982), Oregon (Hoberg et al., 1985, 1986), Mexico (Romero et al., 1986) and Eastern Canada (Smith & Hines, 1987).

The geographic distribution and history of *N. battus* in sheep can be described as one of continual translocation, introduction and subsequent emergence (Helle, 1969; Hoberg et al., 1986), although the origins of this parasite in the type locality of Great Britain have remained unresolved (Crofton & Thomas, 1951; Jansen, 1973). Current evidence suggests that the parasite was introduced to some areas of Europe and North America via sheep exported from Great Britain (Helle, 1969; Smith & Hines, 1987), albeit there is also some indication that the parasite was historically present in the western Palearctic (Jansen, 1973; Nardi et al., 1974).

In North America, it can be inferred that *N. battus* was first introduced to Eastern Canada, later to Oregon and then secondarily transported to other regions in the United States (Rickard et al., 1989; Smith & Hines, 1987; Zimmerman et al., 1986). Elsewhere in the Western Hemisphere, apparent records from cattle in Mexico (Romero et al., 1986) and guanacos in Argentina (Larrieu et al., 1982) were not completely documented, and conceivably these nematodes could represent a previously unrecognized species (see comments on systematics below). Following introduction, the expected pattern has been a period of dissemination and amplification with subsequent emergence and disease outbreaks (Helle, 1969). Displacement of the typical parasite fauna of sheep, notably other species of *Nematodirus*, has also been observed. The potential for devastating disease in sheep may be directly influenced by local epidemiological factors (Rickard et al., 1989), such that in the region of greatest abundance for this parasite in North America, nematodiriasis of sheep associated with *N. battus* has yet to be unequivocally recognized.

Although the contemporary history of *N. battus* appears strongly tied to domesticated sheep, the ancestral host group for this species is unknown. This nematode is capable of infecting cervids, bovids, some lagomorphs, and camelids and is morphologically similar to some species in Neotropical and Palearctic cervids. However, in all situations in the western Palearctic the occurrence of *N. battus* (except in Italy) has been traced to the recent introduction of sheep. This contemporary history, associated with translocation, parallels the occurrence of *N. battus* in North America.

Systematics is useful in illuminating the contemporary host and geographic distribution for *N. battus*. Results of phylogenetic analysis of a small subset of *Nematodirus* spp. (11 of approximately 60 nominal taxa) provide a context for understanding the relationships and history for *N. battus* (Fig. 1; Appendix). Host distribution mapped onto the parasite phylogeny is compatible with an early association of *Nematodirus* spp. among bovids of the subfamily Caprinae (sheep and goats), and later diversification among Cervidae (deer) with colonization of other ruminants including Bovinae (cattle) and South American Camelidae in the late Tertiary (see also Hoberg et al., 1989; Hoberg & Rickard, 1988; Lichtenfels & Pilitt, 1983; Rossi, 1983).

*Nematodirus battus* is in a clade containing nematodes which are principally parasites of the Cervidae (Fig. 1). These putative host-parasite relationships suggest: (1) *N. battus* is only distantly related to species typical of domesticated hosts, including *N. spathiger* (Railliet, 1896) and *N. filicollis* (Rudolphi, 1802) from the Caprinae, and *N. helvetianus* (May, 1920) from the Bovinae; (2) *N. battus* is most closely related to those species of *Nematodirus* for which the Cervidae are ancestral hosts, corroborating the hypothesis for this relationship presented by Jansen (1973); (3) host-switching has been an important factor in the speciation process for *Nematodirus* spp.; and (4) with respect to *N. battus*, limited parasite specificity and a concomitant broad host amplitude indicate a contemporary propensity for successful introduction and acquisition of new hosts. Indeed, *N. battus* has been reported from a diversity of bovids, cervids and lagomorphs (reviewed in Hoberg et al., 1986).

The results of this preliminary analysis lead to two predictions: (1) Additional species of *Nematodirus* (similar morphologically to *N. battus*, *N. roscidus* Railliet, 1911 and *N. urichi* Cameron, 1935) may be found in the endemic cervids of the Palearctic and particularly South America (Rickard & Hoberg, 1990). Parasite biodiversity among Neotropical cervids has been poorly documented and to date these deer have received scant attention from parasitologists (Rickard & Hoberg, 1990). (2) There is a reasonable expectation that this nematode can successfully parasitize endemic cervids such as *Odocoileus virginianus* (Zimmermann), *O. hemionus* (Rafinesque), and *Cervus elaphus* Linnaeus in temperate North America.

Systematics provides the background for eventual elucidation of host and biogeographic relationships for *N. battus* and other species of this genus. Relationships depicted here suggest a coevolutionary history for Cervidae and an inclusive group of *Nematodirus* spp. Although such a relationship must eventually be examined within the broader context of the approximately 60 nominal species in the genus, it is clear that the distribution of *N. battus* has been determined on temporal scales which are both historically deep and relatively recent. The currently broad geographic distribution for *N. battus* in North America (Zimmerman et al., 1986) is anthropogenic in its origin and points to the continuing lack of controls on the transport of domestic stock and wild ruminants infected with helminthic parasites.

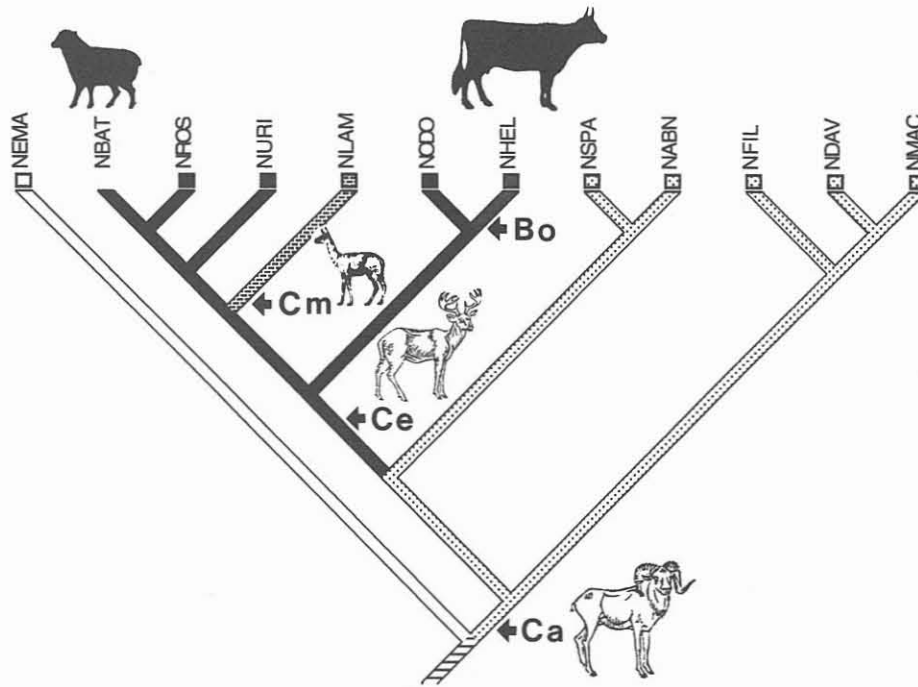


Figure 1. Phylogenetic hypothesis for 11 species of *Nematodirus* from ruminants. The tree shown is one of two equal length hypotheses based on the matrix presented in the Appendix (Consistency Index=0.57; Retention Index=0.63). The structure of the competing trees varied only in the placement of *N. roscidus*, although the basic relationships depicted for host-parasite associations were congruent. Taxon labels are as follows: NEMA=Nematodirinae outgroups; NBAT=*N. battus*; NROS=*N. roscidus*; NURI=*N. urichi*; NLAM=*N. lamae*; NODO=*N. odocoilei*; NHEL=*N. helvetianus*; NSPA=*N. spathiger*; NABN=*N. abnormalis*; NFIL=*N. filicollis*; NDAV=*N. davtiani*; NMAC=*N. maculosus*. Host groups are mapped onto the tree as follows: Ca= Caprinae including wild sheep (stippled), Bo= Bovinae including cattle (gray), Cm= Camelidae particularly alpaca and vicugna (cross-hatched), Ce= Cervidae including deer (black). This hypothesis is compatible with Caprinae as ancestral hosts, colonization and diversification in Cervidae, and independent colonization of Bovinae, Camelidae and domesticated sheep (note relationship for *N. battus*). Based on this analysis, *N. battus* shares a relationship with other species of *Nematodirus* from the Cervidae rather than with those species which occur among the Caprinae, including domesticated sheep and goats.

### **A History for *Umingmakstrongylus pallikuukensis***

A protostrongylid lungworm, recently discovered in muskoxen, *Ovibos moschatus* (Zimmermann) from the central Canadian Arctic, represents an apparently emerging pathogen and provides a contrast to the history of *N. battus* in ruminants (Hoberg et al., 1995b). The nematode, *Umingmakstrongylus pallikuukensis*, was unrecognized prior to 1988 (Gunn & Wobeser, 1993) and appears to have a limited distribution in a local population of muskoxen along the lower drainages of the Rae and Richardson Rivers, near the settlement of Coppermine or Kugluktuk, Northwest Territories. This is not an exotic parasite but a component of what appears to be an endemic fauna in the Arctic. An exceptionally high prevalence of infection (near 90%) and apparent pathogenicity may indicate recent emergence of this nematode as a potential influence on the population dynamics of muskoxen (Hoberg et al., 1995b). Emergence and pathogenicity are not necessarily correlated with the evolutionary age of a host-parasite association (May & Anderson, 1983), and current evidence suggests continuity of this assemblage since at least the Pleistocene (Hoberg et al., 1995b).

Data available from surveys of parasite biodiversity in the Arctic suggest an historically limited distribution for *U. pallikuukensis* in muskoxen. Endemism for this nematode may be related to events in the Pleistocene or more recent extirpation of muskoxen in the Arctic (Hoberg et al., 1995b). Additionally, a complex life cycle involving molluscan intermediate hosts (slugs) indicates that the distribution of the parasite is likely to be limited by both abiotic (temperature and moisture) and biotic factors (occurrence of mollusks; longevity of larval nematodes in the environment) characteristic of harsh environments at high latitudes. Alternative definitive hosts such as caribou, *Rangifer tarandus* (Linnaeus) are not known to be infected by *U. pallikuukensis*.

The host and geographic range for this parasite are enigmatic, as no other protostrongylid lungworms are currently known from ruminants in the mid- to high Arctic (Hoberg et al., 1995b). Thus, systematics becomes important in documenting distribution and historical relationships for this parasite assemblage. It is critical in predicting the potential for interactions with other ruminants, and as a consequence forms the basis for protection of host-genetic resources. In this instance, such information will be necessary to understand if there is a potential threat to large herbivores on which the Inuit of the Arctic are dependent. Current management practices for muskoxen, often involving translocation and reintroduction to former range (Gunn, 1982), make it requisite that accurate information be available for the contemporary biogeography and host distribution for this parasite. This situation provides a model for the interactions of scientists and local communities in defining the distribution, occurrence and severity of infection by *U. pallikuukensis* and in documenting potential influences on populations of animals that are of significance in subsistence societies.

### **A Conceptual Framework for Emerging Parasites**

The axiom that "...the distribution of a pathogen is wider than the disease caused by it..." (Audy, 1958) provides the rationale for development of well documented concepts

for the distribution of parasitic organisms. Accurate survey and inventory, linked to a strong phylogenetic foundation for hosts and parasites, provide a context for distinguishing indigenous versus exotic elements of parasite faunas.

The respective histories of *N. battus* and *U. pallikuukensis* indicate that the phenomenon of emergence may be associated with macroparasites introduced into new geographic regions (or through exposure of naive animals) or may involve indigenous parasites potentially responding to changing ecological interactions or climatological factors. The potential for emergence is multifaceted and is dependent largely on a breakdown in control mechanisms with either a geographic or ecological basis.

Emergence is directly influenced by the availability of a susceptible host population. Subsequent factors controlling amplification and dissemination are the density and vagility of the host population, and a history of prior exposure (high density and low vagility promote higher levels of infection, and greater species richness) (Dobson & May, 1986b). Thus, rapid and long distance transport, introduction and maintenance of domesticated stock or establishment of captive herds on small reserves exacerbate amplification and dissemination. Additionally, emergence may follow introduction of parasite-naive animals onto the endemic range of a parasite-host assemblage.

Successful establishment following introduction is also a function of the ecological or environmental setting which must be conducive to either acquisition of new hosts, or elimination of controls due to competition; limiting factors must be minimal. Thus, a lag time (amplification) prior to emergence, followed by displacement and disruption of local patterns of distribution and abundance of related pathogens might be observed. This pattern was typical of the introduction of *N. battus* into new geographic localities in Norway (Helle, 1969), but has yet to be recognized in North America (Rickard et al., 1989).

Life history patterns also directly influence establishment and later amplification. The potential is enhanced when dealing with helminths that do not require an intermediate host for development and transmission, such as strongylate nematodes with direct life cycles (e.g. Dobson & May, 1986a; Hoberg et al., 1995a; Rickard et al., 1993). However, protostrongylid nematodes with indirect cycles requiring molluscan intermediate and cervid definitive hosts have been translocated and successfully introduced with their definitive hosts in North America, Australia and New Zealand (Gajadhar et al., 1994; Mason, 1994). This highlights the risk in conservation or wildlife management which relies on reintroductions of large mammals (or other vertebrates) onto historical range following extirpation. Such practices with muskoxen (see Gunn, 1982) could influence the distribution of *U. pallikuukensis* and ultimately the re-establishment of this ruminant in the Arctic (Hoberg et al., 1995b).

As Audy (1958) implied, potential pathogens can be widespread but may not be associated with disease. Natural host-parasite assemblages can be maintained in areas not influenced by man (Rausch, 1972b). Encroachment and disruption of ecological continuity of naturally existing parasite-host assemblages, particularly through the formation of ecotones, will enhance the potential for emergence (Rausch, 1972b).



Clearly, historical events such as climatic fluctuations, habitat disruption and isolation during the Pleistocene have been significant determinants for distribution of some assemblages. (Hoberg et al., 1995b; Hoberg & Lichtenfels, 1994; Rausch, 1972b, 1994). Contemporary climate may also be a determinant of geographic range for some parasites. For instance in the Arctic, *U. pallikuukensis* may not occur at high latitudes due to severe conditions which may limit the distribution of intermediate hosts or directly affect survival of larvae in the environment (Hoberg et al., 1995b). In such situations a change in the dynamics of transmission might be expected with amelioration of environmental conditions associated with global warming.

In order to elucidate the patterns of emergence for pathogenic organisms it is necessary to understand the interaction between historical and anthropogenic influences. However, within this context, "While the distribution of numerous natural-focal diseases is limited by biotic parameters.... the most important.... owe their extensive geographic occurrence to the influence of man. The cosmopolitan occurrence of many communicable diseases is largely the result of the *breaking down of isolating barriers* and the patterns of disease continue to change as populations grow and redistribute" (Rausch, 1972a). Thus, alteration of historical associations through ecological disruption and long range translocation will figure prominently in the continued emergence of pathogenic macroparasites, which constitute significant components of global biodiversity.

### **Emerging Pathogens: Responsibility and Accountability**

There are positive and negative ramifications to "ownership" of genetic or biological resources. The concept of ownership cannot be limited to those organisms or genetic products that are considered to be beneficial. It must include a broader view of all biotic diversity. If taken to this logical extreme, then the concept of compensation for the accidental or inadvertent introduction and establishment of an exotic free-living organism or a pathogen also must be considered.

Ownership of components of biodiversity implies accountability. Is there a responsibility to attempt to limit dissemination or introduction of known exotic species, including pathogens? Subsequently, how do we measure the impact and compensate for losses related to the introduction and establishment of allochthonous taxa? It must be the obligation of "source" or "donor" nations to limit the dissemination of pathogens, by adequate surveillance and controls on export. Conversely there is a responsibility of the "receiver" nations to provide adequate diagnostic, quarantine and control capabilities to regulate or limit the importation of pathogens. Both aims are accomplished by documentation, survey and inventory to determine the host and geographic distribution of helminthic and other parasites. Hence there is a rationale, indeed a necessity, for exhaustive survey and inventory of faunas. The potential for introduction of a parasite or free-living species and its economic impact should drive the development of more robust methods of surveillance, survey and monitoring in source and receiver countries. This broader concept of ownership also provides a counterpoint to the current paradigm of anticipated economic gains expected from the exploitation of genetic and biotic resources.

## The Role of Systematics

Systematics is the cornerstone for limiting the potential impacts of pathogenic organisms that may be detrimental to genetic resources at a number of levels. Hierarchical and predictive information from systematic analyses is requisite to understanding such aspects as host range, specificity of parasites and the potential for host switching leading to detrimental interactions. Patterns of transmission, epizootiology and pathogenicity can also be understood within this context. Phylogenetic information for macroparasites and hosts is the foundation for understanding the linkage between historical and contemporary biogeography and a primary element in controlling the dissemination and emergence of pathogenic organisms.

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### Appendix: Phylogenetic Analysis of *Nematodirus* spp.

Phylogenetic analysis was conducted on a subset of 11 species of *Nematodirus* for which accurate comparative morphological data was available either by direct examination of specimens or from the literature. Analysis was based on 16 characters (4 multistate and 12 binary), in which polarity was determined initially by taxonomic outgroup (basal Nematodirinae including the genera *Murielus*, *Nematodiroides*, and *Rauschia*) and secondarily by functional outgroup criteria for one attribute (Watrous, L.E. & Q.D. Wheeler. 1981. *Systematic Zoology* 30:1-11). A character matrix (0=plesiomorphic; 1,2=apomorphic) and taxon labels are presented below along with descriptions of characters. The matrix was analyzed using PAUP 3.1.1 (Swofford, D.L. 1993. *Phylogenetic analysis using parsimony*. Version 3.1. Illinois Natural History Survey) with the following options: Branch and Bound with multistate characters unordered; no character weights were assigned. Character and host distributions were examined with MacClade 3.0 (Maddison, W.P. & D.R. Maddison, 1992. *MacClade: Analysis of phylogeny and character evolution*. Version 3.0. Sinauer Associates, Sunderland, Massachusetts).

**Character descriptions:** 1) Perioral denticles (number): 0=  $\leq$  35-40; 1= $>$ 40. 2) Bursal rays, position of rays 5 and 6: 0= parallel; 1= divergent (this character was recoded with reference to functional outgroup criteria, basal species of *Nematodirus*, following preliminary analysis). 3) Bursal lobes, structure of dorsal ray: 0= divided; 1= not divided. 4) Cephalic expansion: 0= length  $<$ 2X width; 1= length  $>$ 2X width. 5) Spicule tips (length): 0= short,  $<$ 25 $\mu$ m; 1= long,  $>$ 30 $\mu$ m. 6) Spicule tips (shape): 0= lanceolate; 1= heart shaped; 2= spatulate. 7) Vulva position: 0= in far posterior fourth of body; 1= at junction of middle and posterior fourth of body; 2= in third fourth of body. 8) Egg shell (pigmentation): 0= absent; 1= present. 9) Egg shell (sculpturing): 0= absent; 1= present. 10) Tail of female: 0= truncate; 1= conical. 11) Synlophe (number of ridges at midbody): 0= 14-18; 1= $\geq$ 20; 2= $>$ 30. 12) Synlophe (structure of ridges): 0= fin-like; 1= not fin-like. 13) Synlophe (number of postcervical ridges): 0= $\leq$ 18; 1= 22-26; 2= $<$ 30. 14) Synlophe (alternation in ridge height): 0= absent; 1= present; 15) Synlophe (hypertrophy of dorsal and ventral ridges): 0= absent; 1= present. 16) Egg (length): 0= $<$ 200 $\mu$ m; 1= $>$ 200 $\mu$ m.

CHARACTER MATRIX	TAXON:	HOST:
NEMA 0000000000000000-	(Nematodirinae outgroups)	Lagomorpha
NBAT 0101012111110000-	( <i>Nematodirus battus</i> )	Caprinae?
NROS 1101101110212000-	( <i>N. roscidus</i> )	Cervidae
NODO 1000101000212100-	( <i>N. odocoilei</i> )	Cervidae
NSPA 1000021000010001-	( <i>N. spathiger</i> )	Caprinae
NFIL 0011001000000000-	( <i>N. filicollis</i> )	Caprinae
NHEL 1000101000211001-	( <i>N. helvetianus</i> )	Bovinae
NURI 1001012001212100-	( <i>N. urichi</i> )	Cervidae
NABN 1000002000110001-	( <i>N. abnormalis</i> )	Caprinae
NDAV 0011000000000011-	( <i>N. davtiani</i> )	Caprinae
NLAM 0000011000212000-	( <i>N. lamae</i> )	Camelidae
NMAC 1011021000000011-	( <i>N. maculosus</i> )	Caprinae