Evolution of the Elaphostrongylinae
(Nematoda: Metastrongyloidea: Protostrongylidae)
Parasites of Cervids (Mammalia)

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ABSTRACT: The phylogenetic relationships of the Elaphostrongylinae were evaluated by cladistic analysis. *Elaphostrongylus cervi* is considered the most plesiomorphic member of the subfamily and is the sister-group of *Parelaphostrongylus*. *Parelaphostrongylus*, which consists of *P. andersoni*, *P. odocoilei*, and *P. tenuis*, is monophyletic based on the presence of crura on the gubernaculum and a bifurcate gubernacular corpus. *P. tenuis* is the most plesiomorphic member of the genus and is the sister-group of a monophyletic muscleworm lineage composed of *P. andersoni* and *P. odocoilei*.

*Elaphostrongylus cervi* originated in the nearctic, co-speciating with *Rangifer*. The current holarctic distribution of *E. cervi* is interpreted as colonization of more primitive cervids with the retention of broad coaccommodation within the family. The meningeal worm, *P. tenuis*, originated prior to the formation of extant species of *Odocoileus*. Co-speciation of the muscleworm ancestor with the ancestor of the extant species of *Odocoileus* resulted in *P. andersoni* in *O. virginianus* and *P. odocoilei* in *O. hemionus*.

The extensive distribution of *E. cervi*, a generalist, can be attributed to its broad coaccommodation within the Cervidae, broad coaccommodation with and the ubiquitous nature of suitable molluscan intermediate hosts, and the absence of competitors in Eurasia. The distribution of *P. tenuis*, a specialist, in North America is attributed to the success of white-tailed deer and in part to the pathogenic effects of the meningeal worm in sympatric cervids. Two hypotheses for the current distribution of the species of *Parelaphostrongylus* are presented.

The Elaphostrongylinae (Protostrongylidae) comprise a small but economically important group of nematode parasites of cervids. Although commonly referred to as “lungworms,” all species of the subfamily inhabit extrapulmonary sites in the definitive host. Life cycles are complex, and terrestrial gastropods are used as obligate intermediate hosts (see Anderson, 1968 for a review).

Coevolution of parasitic organisms with their hosts has been considered axiomatic. Cameron (1964) stated, “parasites have obviously evolved co-incidentally with their hosts” and that “parasite phylogeny and classification can only be interpreted in terms of host phylogeny and classification.” However, Inglis (1965) stated, “evolution of most groups of nematodes has tended to occur in hosts with similar ecological requirements.” Brooks (1979a) recently reexamined the concept of coevolution and identified two distinct components: coaccommodation, “the mutual adaptation of a given parasite species and its host through time” and cospeciation, “cladogenesis of an ancestral parasite species as a result of or, concomitant with, host cladogenesis.” This distinction forms an important framework for the study of the evolution of host–parasite systems, as it emphasizes the historical relationship of host and parasite but does not disregard colonization as an alternative means of parasite acquisition.

Recent studies of host–parasite evolution and zoogeography have centered exclusively on the relationship between the parasite and the definitive host (Brooks, 1977, 1978, 1979b; Brooks et al., 1981; Chabaud and Bain, 1976). The role of intermediate hosts however has not been given equal attention. The following analysis of the Elaphostrongylinae includes an evaluation of the role of the intermediate and definitive hosts as they relate to the distribution and evolution of the parasite.

Materials and Methods

Specimens of *P. odocoilei* were obtained from experimentally infected mule deer (*Odocoileus h. hemionus*) as reported by Platt and Samuel (1978a, b). Specimens of *P. tenuis* were obtained from naturally infected wapiti (*Cervus elaphus canadensis*) in Pennsylvania. Type specimens of *P. andersoni* were obtained from the USNM Helm. Coll., Beltsville, Maryland. Specimens of *E. cervi* were not available, and the description by Lankester and Northcott (1979) was used as a source of morphological characters.

The direction of change of characters within the Elaphostrongylinae was determined through the use of out-group comparison (Hennig, 1966; Wiley, 1981).

As some parasitologists may not be familiar with the terminology of phylogenetic systematics, the following definitions are provided (following Wiley, 1981). Ple-
siomorphic and apomorphic refer to the original and derived states, respectively, of a pair of homologous characters. Synapomorphies are “evolutionary novelities” (derived characters) shared by two or more species forming a monophyletic group. Autapomorphies are derived characters restricted to a single species. Homoplasies are structurally similar characters that are thought to be of independent origin.

As the sister-group of the elaphostrongylines is unknown, members of the Metastrongylida, excluding the Protostrongylidae, were employed as the out-group. Each character was assigned a 0 for the plesiomorphic state and a 1, −1, or 2 for the apomorphic state. An outline and explanation for the decision of the determination of character state polarity is presented below.

1. Crura of the gubernaculum.—The gubernaculum of the majority of the Protostrongylidae (sensu Anderson, 1978) is complex, consisting of a corpus, crura, and capitulum. The gubernaculum of the remaining metastrongylids is simple, corpus only, or absent. Two states: crura absent (0); crura present (1) (Fig. 1a–d).

2. Corpus of the gubernaculum.—The corpus is a solid
Table 1. Data matrix of the character state distribution used in the analysis of the Elaphostrongylinea.

<table>
<thead>
<tr>
<th>Species</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. cervi</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>P. tenuis</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P. andersoni</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>P. odocoilei</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>-1</td>
<td>0</td>
</tr>
</tbody>
</table>

Results

Two equally parsimonious cladograms can be constructed based on the distribution of the synapomorphies (Fig. 2). The first (Fig. 2a) recognizes E. cervi as the most plesiomorphic member of the subfamily. *Parelaphostrongylus* is recognized as a monophyletic taxon on the basis of the presence of crura and a notched or distally split gubernacular corpus (Fig. 1a–c). A muscleworm lineage consisting of *P. andersoni* and *P. odocoilei* is monophyletic based on the presence of a compact, bulbous dorsal ray (5). A single homoplasy, the ventral position of the branches of the dorsal ray (6), is shared by *P. tenuis* and *P. odocoilei*. The alternative phylogeny (Fig. 2b) also recognizes *E. cervi* as the most plesiomorphic species and *Parelaphostrongylus* as monophyletic, as described above. This phylogeny differs however in recognizing *P. andersoni* and *P. tenuis*, which are parasites of white-tailed deer, as a monophyletic group based on the position of the branches of the dorsal ray. A single homoplasy, the presence of a compact dorsal ray, is shared by *P. odocoilei* and *P. andersoni*.

Discussion

Although the two cladograms are equally parsimonious based on character distributions, the phylogeny in Figure 2a is preferred based on the location of the adult worms in the definitive host. *Elaphostrongylus cervi*, the most plesiomorphic species, has been reported from the meninges of the brain (Mitskevitch, 1964) as well as the connective tissue of the skeletal muscles (Mitskevitch, 1964; Lankester and Northcott, 1979) and occasionally deep muscle sites (Lankester and Northcott, 1979). Species of *Parelaphostrongylus* are more restricted in their site of maturation. Adult *P. tenuis* have only been found in close association with the central nervous system (CNS) (Anderson, 1968). The muscleworms are restricted to the skeletal muscles and associated connective tissue (Prestwood, 1972; Platt and Samuel, 1978b). Therefore, following the phylogeny in Figure 2a, habitat specialization is a direct process requiring no reversals or parallelisms. In the alternate phylogeny (Fig. 2b) neurotropic behavior would have been lost in the ancestral *Parelaphostrongylus* and then reappeared in *P. tenuis*, or the muscleworms lost their neurotropic behavior independently and *P. tenuis* retained the behavior as a plesiomorphic trait. Both of these scenarios require reversals or parallel evolution, hence Figure 2a is preferred.

Strict adherence to the rules of phylogenetic classification (Hennig, 1966) would result in a major change in nomenclature for the subfamily. Application of the sequencing convention (Wiley, 1979) would permit the inclusion of the four species of elaphostrongylines in a single genus, *Elaphostrongylus* Cameron, 1931. I prefer to retain the current nomenclature at the present time for the following reasons. Pryadko and Boev (1971) reduced *E. rangiferi* Mitskevitch, 1958, and *E. panticola* Liubimov, 1945, to synonyms of *E. cervi* in the absence of morphometric criteria to separate these forms. Additional investigation, however may validate one or both of these species and would require the reinstatement of *Parelaphostrongylus*. In addition, both taxa as currently defined are monophyletic based on criteria presented by Platnick (1977). Rec-
The elaphostrongyline genera show some specificity for the intermediate host (Panin, 1964; Lankester and Anderson, 1968; Platt, 1978). A number of species in two of the four suborders (Heteraurethra and Sigmaurethra) of the pulmonate order Stylommatophora, are capable of serving as suitable intermediate hosts. Therefore, it can be assumed that a modern terrestrial gastropod fauna was present when modern cervids were becoming established during the late Miocene and early Pliocene (Flerov, 1952) as suggested by Pryadko and Boev (1971). The continuity of the gastropod fauna during the late Tertiary and Pleistocene would have given the elaphostrongylines a long association with, and relatively little selection pressure from, the intermediate host. Thus, the current distribution of these nematodes must be explained as a function of the evolution and distribution of the definitive hosts.

The family Cervidae consists of 11–17 extant genera, with representatives occurring naturally on all continents except Australia and Antarctica. Cervus and Mazama will be treated sensu lato, consisting of the following: Cervus s.l. (=Cervus, Dama, and Axis) and Mazama s.l. (=Mazama, Blastocerus, Ozotocerus, Hippocamelus, and Pudu).

There have been few attempts to formally reconstruct the phylogenetic relationships of the genera of cervids. Flerov (1950) presented a general evolutionary scheme for the cervids based on paleontological, as well as neontological data that is at variance with more traditional schemes (e.g., Lydekker, 1898; Simpson, 1945). These follow Brooke's (1878) original designation of two primary lineages based on the type of reuction of the second and fifth metacarpals. Giffin (1974) analyzed the phylogeny of the cervids using cladistic methods in a more inclusive study of the relationships of the Artiodactyla. Her work was based on a combination of gross cerebral characters as well as noncerebral characters taken from the literature. Giffin (1974) did not use the condition of the metacarpals in her analysis, and hence it serves as an independent test of that character. The results provide more support for the traditional classifications than that of Flerov (1952).

The most parsimonious hypothesis of the origin of the elaphostrongylines is a nearctic origin prior to the formation of Rangifer and the subsequent cospeciation of Parelaphostrongylus spp. with Odocoileus spp. (Fig. 3). E. cervi originated with Rangifer, a northern-adapted, tundra specialist. At the same time the ancestor of O. virginianus—
O. hemionus, a temperate and subtemperate generalist (Brokx, 1972), originated harboring the ancestor of Parelaphostrongylus spp. Alternatively, the elaphostrongylines could be regarded as eurasian in origin (Pryadko and Boev, 1971). This would require strict speciation of the parasite and host with subsequent extinction of the parasites of Cervus s.l. through Mazama s.l. preceding or as a result of colonization of these hosts by E. cervi. There is no evidence to support these extinctions, nor is the hypothesis testable in any way. A second alternative involves the survival of E. cervi in the more primitive cervids and recognizing E. cervi as ancestral to Parelaphostrongylus. However, since E. cervi is not plesiomorphic for all characters examined it does not meet the minimum requirements of an ancestor. The presence of E. cervi or an undescribed species of Elaphostrongylus in South American cervids (Mazama s.l.) would falsify the nearctic origin of the group, due to the geographic isolation of the hosts and the unlikely possibility of long-distance dispersal of the nematode to the southern hemisphere.

The second speciation event gave rise to the neurotropic specialist P. tenuis, which exhibits narrow coaccommodation and is the ancestor of the muscleworm lineage (Figs. 2, 3). The variant event responsible for this speciation event is unknown. It was not however, a response to speciation in the host lineage (Fig. 3). Speciation in the muscleworm lineage followed the separation of Odocoileus into a western population, O. hemionus, and an eastern form, O. virginianus, as described by Brokx (1972). Vicariance could have been accomplished by the formation of the midwestern plains during the Pliocene (Clements and Chaney, 1937) or by a later re-establishment of the plains during the Pleistocene (Blair, 1958).

The current distribution of elaphostrongylines can be explained as a function of dispersal (mobilism), coaccommodation, and possibly ecologic factors. Overlap between sister-taxa is indicative of mobilism (Croizat et al., 1974). Elaphostrongylus cervi has an extensive distribution in Europe and Asia (see Kontramavichus et al., 1976). Naturally occurring infections of E. cervi have been reported from reindeer in Newfoundland (Lankester, 1976; Lankester and Northcott, 1979), which is evidence for a holartic distribution. Parelaphostrongylus is known only from North America (Anderson, 1972). P. tenuis has been reported from a wide variety of
locations in eastern North America (Anderson, 1956; Prestwood and Smith, 1969; Gilbert, 1973) and as far west as western Manitoba (Bindernagel and Anderson, 1972) and eastern Oklahoma (Carpenter et al., 1972; Kocan et al., 1982). The distribution of *P. andersoni* has been well documented in the southeastern United States (Prestwood et al., 1974). Pybus and Samuel (1981) have reported this species from white-tailed deer in southeastern British Columbia. *P. odocoilei* has been reported from central California (Hobmaier and Hobmaier, 1934; Brunetti, 1969), west-central Alberta (Platt and Samuel, 1978a), and Vancouver Island, British Columbia (Platt, unpubl.).

The current holarctic distribution of *E. cervi* could be attributed to the colonization of more plesiomorphic cervids (e.g., *Alces, Capreolus*, and *Cervus*) (Fig. 3) as a result of a period of westward mobilism of *Rangifer*, broad coaccommodation within the Cervidae, and the apparent absence of competitors in Europe and Asia. Natural infections have been reported from five genera of cervids (Anderson, 1968; Konramavichus et al., 1976; Kotrlá and Kotrlý, 1977). Larvae identical to those described for other elaphostrongylineb, as well as other protostrongylids, have been reported from caribou in Ontario and Manitoba (Lankester et al., 1976), suggesting that *E. cervi* is sympatric with *P. tennis* in some parts of its range. White-tailed deer show no ill effects of infection with *E. cervi* in limited experimental trials (Lankester, 1976) or under field conditions (Kotrlá and Kotrlý, 1977). Although white-tailed deer can harbor infections of *E. cervi*, competition from *P. tennis*, which is extremely pathogenic to reindeer, could have resulted in competitive exclusion and may have prevented the introduction of *E. cervi* into populations of *O. virginianus*.

The absence of neurotropic elaphostrongylineb in mule deer from western North America may be explained by a low tolerance of the *protohemionus* population for CNS-inhabiting species. Experimental infections of *P. tennis* in mule deer resulted in paralysis and death of the host (Anderson et al., 1966; Tyler et al., 1980). The absence of CNS-inhabiting species could be further tested by experimentally infecting mule deer with *E. cervi*. The prediction being that mule deer would succumb to the infection or at least show signs of CNS disturbance, thereby reducing host fitness. This would have prevented sympathy between mule deer and wapiti where *E. cervi* was present and the subsequent spread of *E. cervi* into areas occupied only by *O. hemionus*.

The current pattern of distribution of muscleworm species is considerably more difficult to explain. The recent report of *P. andersoni* from British Columbia (Pybus and Samuel, 1981) occupying an area of overlap with *P. odocoilei* indicates a period of mobilism for *P. andersoni* associated with the expansion of the range of white-tailed deer. The timing of this movement is unclear. Krämer (1972) hypothesized that the white-tailed deer in British Columbia represent an autochthonous population that survived the last glacial period in western refugia.

The meningeal worm, *P. tennis*, has not been reported from white-tailed deer in western Canada (British Columbia, Alberta, and western Saskatchewan) despite intensive investigation (Bindernagel and Anderson, 1972; Bindernagel, 1973; Samuel and Holmes, 1974). There are two possible explanations for the absence of *P. tennis* from western North America. The first involves two separate periods of mobilism from white-tailed deer; one, reaching the west coast and, preceding the last glaciation, which resulted in deer harboring *P. andersoni* but not *P. tennis*, and a later period of mobilism of white-tailed deer infected with *P. tennis*. If this scenario is correct, *P. tennis* may eventually reach cervid populations in and west of the Rocky Mountains, as suggested by Bindernagel and Anderson (1972).

A more parsimonious hypothesis may relate to differences in biological valence between the muscleworm species and *P. tennis*. Shostak and Samuel (1979) demonstrated significant lowered infectivity of the first-stage larvae of *P. tennis* to gastropods after exposure to freezing conditions. Larvae of *P. odocoilei* did not show a similar decline in infectivity. Larvae of *P. andersoni* have not been tested, however this species would be expected to have a response similar to its sister-sppecies, *P. odocoilei*, and to have the capacity to survive freezing conditions. This would result in an ecological limitation to the spread of *P. tennis*, but not *P. andersoni*, in accord with the general hypothesis proposed by Samuel and Holmes (1974). They stated that, "some ecological feature, possibly associated with drier conditions" prevented the westward spread of *P. tennis*. This would predict that *P. tennis* has reached the westernmost limits of its range and cannot move farther west without significant ecological changes.
or human intervention. Recent ecological studies (Kocan et al., 1982) provide circumstantial evidence for this hypothesis. Single or multiple periods of mobilism of white-tailed deer would be consistent with this scenario.

Success of the host(s) may also play a prominent role in determining the distribution of the parasite. This is exemplified by the wide distribution of *P. tenuis* and *P. andersoni* in North America. Range expansion of these species is directly related to the success of the white-tailed deer and the wide availability of suitable intermediate hosts. The case of *P. tenuis*, which exhibits narrow coaccommodation and is pathogenic to ecologically similar hosts, is particularly intriguing.

Barbehenn (1969) proposed a “germ warfare” theory of species diversity as a mechanism for the maintenance of a competitively inferior host in the presence of a superior competitor. Coevolution of the host–parasite complex would produce a more successful competitor than the host alone. Barbehenn (1969), citing the work of Karns (1966), recognized *Pneumostrongylus (=Parelaphostrongylus) tenuis*–*O. virginianus* as a possible example of a host–parasite complex that could adversely affect sympatric ungulates. Investigations in Maine (Gilbert, 1973, 1974) and Ontario (Saunders, 1973) have provided circumstantial evidence for the reduction of moose (*Alces alces*) populations in areas where they are sympatric with white-tailed deer that have a high prevalence of infection of *P. tenuis*. The pathologic effects of *P. tenuis* infections in moose (Anderson, 1964; Kurtz and Schlothauer, 1966) support his hypothesis. Kellsall and Telfer (1973) suggested that *P. tenuis* may have had a role in restricting the range of moose. Experimental infections of *P. tenuis* in reindeer have also proved lethal (Anderson, 1971) and Dauphiné (1975) hypothesized that the failure of reindeer (*Rangifer tarandus*) to establish in Nova Scotia was a result of the acquisition of *P. tenuis* from resident white-tailed deer.

Wapiti (*Cervus elaphus*) were widely distributed in the northern and central United States following the last glacial period (Hall and Kelso, 1959), however they are currently restricted to higher elevations in western North America and northern habitats where white-tailed deer do not typically occur. This tremendous reduction in range may be associated with the expansion of the *O. virginianus–P. tenuis* complex. The pathogenic effects of *P. tenuis* in wapiti have been well documented (Carpenter et al., 1973; Trainer, 1973).

The role of parasites in altering the range of host organisms can only be approached circumstantially, as presented above. Range extension is undoubtedly a complex process involving a variety of factors. Climate and concomitant changes in vegetation during the Pleistocene have been used to explain significant shifts in the distribution of a variety of mammals (Blair, 1958); however, the possibility of a host–parasite complex acting as a selective agent must be considered where the evidence warrants.

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