



## MORPHOLOGICAL AND GENETIC DIVERSITY OF *ANGIOSTRONGYLUS VASORUM*

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### ABSTRACT

*Angiostrongylus vasorum* is an expanding cardiopulmonary nematode of canids and other carnivores. Variations in the morphology of male specimens, particularly the copulatory bursa, may lead to misidentification, especially in non-canid hosts. Diagnostic challenges are further compounded when examining poorly preserved adult specimens or those from wildlife, especially when males are not present. Molecular methods have proven an excellent tool for species confirmation and in revealing significant genetic diversity within *A. vasorum* populations. This review aims to explore the morphological and genetic diversity of *A. vasorum*, update the distribution in Europe, and discuss important epidemiological implications. We propose integrating molecular and morphological diagnostic strategies, particularly when identifying the parasite in non-canid hosts and in non-endemic regions. Understanding the population structure and diversity of *A. vasorum* may influence diagnostic strategies and support control measures of canine angiostrongylosis.

**Key words:** *Angiostrongylus vasorum*, diversity, morphology, diagnosis

### INTRODUCTION

*Angiostrongylus vasorum* (Baillet, 1866) (1), commonly known as „French heartworm“, is a metastrongylid nematode affecting the cardiopulmonary system of dogs and other carnivores. First described over 150 years ago in a dog in France, it has recently become the focus

of extensive studies in parasitology, epidemiology, phylogenetics, and other fields. This species is recognized for its significant global expansion, raising growing concern as it poses a potential global issue (2). Increasing numbers of cases have been reported in dogs, often presenting with severe and variable clinical signs that can sometimes be fatal. *A. vasorum* has a complex biological life cycle that involves not only definitive hosts like dogs and other carnivores but also intermediate hosts such as slugs and snails, as well as paratenic hosts like frogs.

This review article updates the range of *Angiostrongylus vasorum*, critically examining the parasite's genetic diversity, and lists its main morphological and taxonomic distinctions from related species.

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## HOST AND DISTRIBUTION RANGE OF *ANGIOSTRONGYLUS VASORUM*

*Angiostrongylus vasorum* and *A. cantonensis* are the most studied species within the genus *Angiostrongylus*, significantly contributing to the understanding of this genus. *A. vasorum* is primarily associated with canid species, and research has shown that red fox (*Vulpes vulpes*) serves as the main reservoir for this parasite in nature (3). Recent advancements in diagnostic techniques, particularly molecular methods, have revealed a considerable expansion of the host range of *A. vasorum*. The following species have been confirmed as definitive hosts: dogs, domestic cats, wild cats, gray wolves, African golden wolves, red foxes, gray foxes, crab-eating foxes, African desert foxes, hoary foxes, golden jackals, coyotes, stoats, badgers, raccoon dogs, European otters, weasels, meerkats, bears, invasive American minks, and red pandas (2, 3, 4, 5, 6, 7, 8, 9). Furthermore, *A. vasorum* migratory larvae have been discovered in wild boar muscles (10).

Although *A. vasorum* is thought to be a widespread species, it can be difficult to identify and forecast the risk factors for its spread (2). This intricacy is due to the complex developmental cycles in every species of the *Angiostrongylus* genus, including intermediate, paratenic, and definitive hosts. Europe, North America, South America, and Africa are all included in the range of *A. vasorum* (3). In Europe, enzootic regions have demonstrated a rise in incidence in several countries, including the UK, Denmark, France (earlier reports), Germany, and Switzerland. According to continuing epidemiological investigations (11), *Angiostrongylus vasorum* prevalence has been shown to increase annually in endemic regions such as Switzerland.

These areas serve as sources from which the parasite continues to spread, contributing to its increasing prevalence. However, it is not always possible to directly correlate the prevalence of the parasite in dogs and foxes. Variability in prevalence has been observed across different regions of Europe, with recent data suggesting that this cardiorespiratory nematode is less common in Eastern Europe compared to Central and Western Europe (2, 12). There are probably several factors that contribute to the differences in prevalence

and distribution between Eastern and other parts of Europe. Not all reasons for this difference can be attributed to biological factors (climate, vector and host distribution, etc.). Based on our observations, there is a significant difference in the number of epidemiological studies and the priorities of researchers who regularly examine carnivore helminths. For example, in personal communication with parasitologists in the Russian Federation, it was noted that there is a tendency to report only on helminths that show a zoonotic character (*Echinococcus*, *Trichinella*, etc.). Also, the lack of samples in laboratories is an additional factor that may contribute to the scarce data of angiostrongylosis in some countries (this was concluded from communication with colleagues from Montenegro). Finally, a possible scenario is that this parasite is diagnosed in private clinics with the help of now-available serological rapid tests, but such findings remain publicly unpublished.

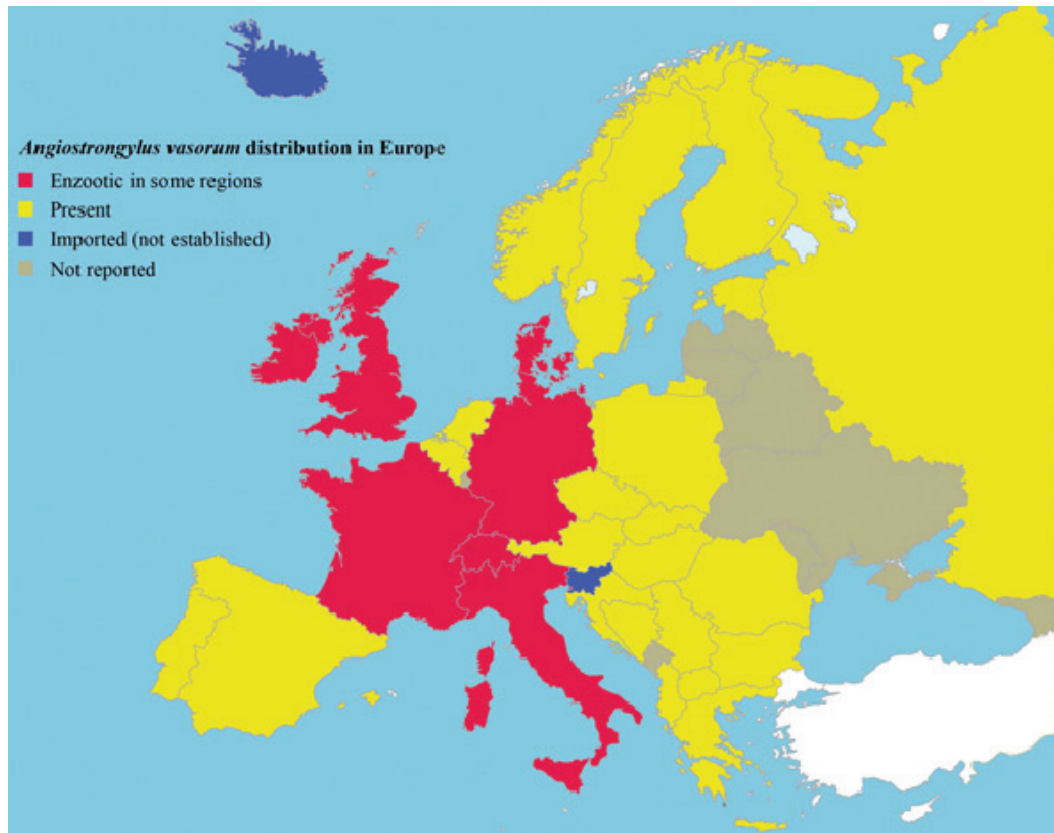
Although many papers dealt with this species, there are still gaps in understanding its presence and prevalence in Eastern Europe. The most recent information regarding the distribution of *A. vasorum* in Europe is summarized in Table 1 and Fig. 1.

In their review article, Morgan et al. (2) examine several hypotheses regarding the biological and social factors that have contributed to the spread of *A. vasorum*. These factors include the movement or migration of owned dogs, climate change, the urbanization of fox populations, increased awareness among veterinarians, and changes in the population of intermediate hosts, such as gastropods. Additionally, other potential risk factors for the spread of this parasite may include the migration of wild canids, specifically jackals, as well as the rising number of owned and stray dogs in certain countries (22). However, it is worth mentioning that epidemiological and clinical studies that investigate the risk factors for spread and distribution can be quite demanding and costly, and the results are not always conclusive. Regardless of the actualization of this problem, in many cases, canine angiostrongylosis (*sensu stricto*) remains under or misdiagnosed.

Table 1. Distribution of *Angiostrongylus vasorum* in Europe

Country	Status	Definitive host	Prevalence/ Diagnostic methods	Presence of congeneric species	References
Albania	present	dog	0.30%/coprology	<i>Angiostrongylus dujardini</i>	13, 14
Andorra	present	fox	3.80%/morphology	no data	15
Austria	present	dog	1.50%/serology 1.30%/coprology	no data	16
Belarus	not reported	NA	NA	not reported	17
Belgium	present	dog	4.70%/serology	no data	18
Bosnia and Herzegovina	present	dog fox jackal	NA/coprology 6.25%/morphology and PCR 6.60%/morphology	<i>Angiostrongylus chabaudi</i> <i>Angiostrongylus daskalovi</i>	19, 20, 21, 22
Bulgaria	present	dog cat	0.70%/serology NA/coprology	<i>Angiostrongylus chabaudi</i> <i>Angiostrongylus daskalovi</i>	23, 24, 25, 26
Croatia	present	fox wolf	1.00%/morphology 3.10%/coprology	no data	27, 28
Czechia	present	dog	1.70%/coprology	no data	29
Denmark	enzootic in some regions	dog fox	3.40%/coprology 80.00%/coprology	no data	30, 31
Estonia	present	fox raccoon dog	2.90%/morphology 1.30%/morphology	no data	32, 33
Finland	present	dog fox	NA/serology and coprology NA/morphology	<i>Angiostrongylus dujardini</i>	34, 35, 36
France	enzootic in some regions	dog fox	1.14%/serology NA/morphology	<i>Angiostrongylus dujardini</i>	37, 38, 39
Georgia	not reported	NA	NA	Not reported	40, 41
Germany	enzootic in some regions	dog fox	2.30%/coprology 4.10%/serology and PCR	<i>Angiostrongylus chabaudi</i>	42, 43, 44
Greece	present	dog	3.00%/serology	<i>Angiostrongylus chabaudi</i>	45, 46
Hungary	present	dog fox jackal	1.40%/serology 17.90%/morphology 10.00%/morphology	<i>Angiostrongylus dujardini</i> <i>Angiostrongylus daskalovi</i>	47, 48, 49, 50, 51
Iceland	imported (not established)	dog	NA/coprology	no data	52
Ireland	enzootic in some regions	dog fox	NA 39.90%/adult morphology	no data	53, 54
Italy	enzootic in some regions	dog fox wolf jackal badger	3.10%/coprology 75.00%/morphology and PCR 66.70%/morphology and PCR 31.70%/morphology and PCR NA/morphology	<i>Angiostrongylus chabaudi</i> <i>Angiostrongylus dujardini</i>	55, 56, 57, 58, 59, 60
Latvia	not reported	NA	NA	no data	61

<b>Lithuania</b>	not reported	NA	NA	not reported no data	62, 63
<b>Luxembourg</b>	not reported	NA	NA	<i>Angiostrongylus</i> spp. in wild cat	12, 64
<b>Moldova</b>	not reported	NA	NA	not reported	65, 66
<b>Montenegro</b>	no data	NA	NA	NA	Stevanović, personal communication
<b>Netherlands</b>	present	dog fox	1.40%/coprology 4.20%/morphology	not reported	67, 68
<b>Norway</b>	present	dog fox	NA/coprology, serology and PCR 3.00%/serology	no data	69, 70
<b>North Macedonia</b>	present	dog	1.70%/coprology	no data	71
<b>Poland</b>	present	dog fox	1.30-1.80%/serology 5.00%/morphology	not reported	72, 73
<b>Portugal</b>	present	dog fox	1.32%/serology 16.10%/morphology	<i>Angiostrongylus dujardini</i>	74, 75, 76
<b>Russian Federation</b>	present	dog fox wolf jackal wild cat	NA/morphology	not reported	4, Stevanović, personal communication
<b>Romania</b>	present	dog fox	2.14%/serology 4.20%/morphology and PCR	<i>Angiostrongylus daskalovi</i> <i>Angiostrongylus chabaudi</i>	77, 78, 79, 80
<b>Serbia</b>	present	dog fox jackal	NA/coprology 54.10%/morphology 24.00%/morphology and PCR	not reported	81, 82, 83
<b>Slovenia</b>	Imported (not established)	dog	NA/NA	no data	12
<b>Spain</b>	present	dog fox wolf badger	1.73/serology 43.20%/morphology 21.60%/morphology 6.40%/morphology	<i>Angiostrongylus daskalovi</i> <i>Angiostrongylus dujardini</i> <i>Angiostrongylus cantonenensis</i>	84, 85, 86, 87, 88, 89
<b>Sweden</b>	present	dog fox	0.10%/serology 0.30%/morphology	not reported	90
<b>Switzerland</b>	enzootic in some regions	dog fox cat meerkat	0.96%/serology Ab+Ag 60.60%/serology and morphology NA/PCR NA/coprology, morphology and PCR	not reported	6, 11, 91, 92
<b>Ukraine</b>	not reported	NA	NA/NA	not reported	93
<b>United Kingdom</b>	enzootic in some regions	dog fox	0.97%/serology (Ag+Ab) 18.30%/morphology	not reported	94, 95



**Figure 1.** Recent data on distribution of *Angiostrongylus vasorum* in Europe

#### **MORPHOLOGICAL DIAGNOSIS: *ANGIOSTRONGYLUS VASORUM* OR NOT?**

In the species *A. vasorum*, the male and female adults exhibit significant morphological differences (Fig. 2). It is visually hard or impossible to establish a valid diagnosis based solely on the characteristics of the females. The basic morphological features of the species are shown in Fig. 3 and Fig. 4.

Morphological descriptions of the species reveal differences in the structure of the copulatory bursa in males. These differences, along with certain morphometric variations, the localization of adults within the host – site of infection, and host specificity, are sufficient to differentiate individual species within the genus *Angiostrongylus*.

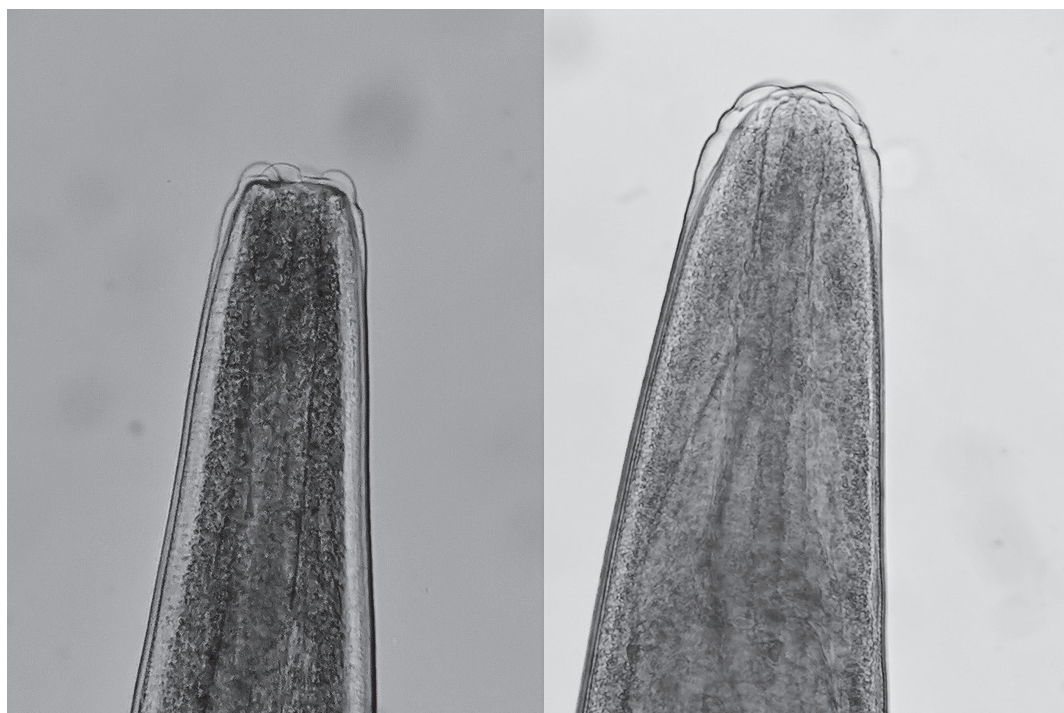
The first taxonomic dilemma concerns classification of the species *A. vasorum*. According to the descriptions by Anderson (96), which were accepted by Ubelaker (97), the genus *Angiostrongylus* is divided into two subgenera: *Parastrongylus* and *Angiostrongylus sensu stricto*. This proposal is significant and influential for many researchers (5). The primary morphological

criterion for this taxonomic classification is the structure of the lateral rays of copulatory bursa. In the subgenus *Parastrongylus*, these rays emerge from a common trunk, while in the subgenus *Angiostrongylus*, anteriolateral and the other lateral rays have no common trunk (98, 99). The defining and latest morphological features of *A. vasorum* suggest that its lateral rays share a common trunk (100). That means that *A. vasorum* has morphology typical of the subgenus *Parastrongylus* (101). However, Souza et al. (101) found that the *A. vasorum* present in dogs in Brazil lacks trunk that separates the anteriolateral ray from the mediolateral and posteriolateral rays. In the original drawings and pictures of the male *A. vasorum* by Guilhon and Cens (99), a difference in the structure of the lateral rays is evident, suggesting possible misdescription. Souza et al. (101) highlights a morphological asymmetry between the right and left lateral rays in *A. vasorum*. The original description of the male *A. vasorum* from present-day Russia, as noted by Kozlov (4), indicates that the anteriolateral ray does not share a common trunk with the other two lateral rays supporting original descriptions of the species



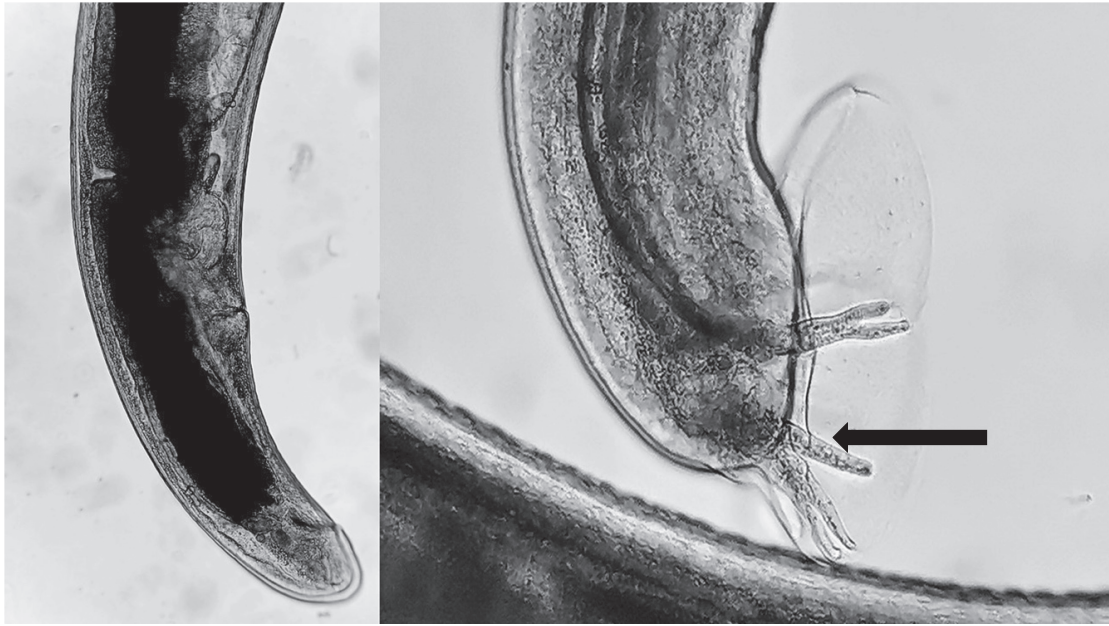
**Figure 2.** Male (left) and female (right) of *Angiostrongylus*

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**Figure 3.** Male (left) and female (right) of *Angiostrongylus vasorum*: note that cephalic vesicle is poorly developed (x200)

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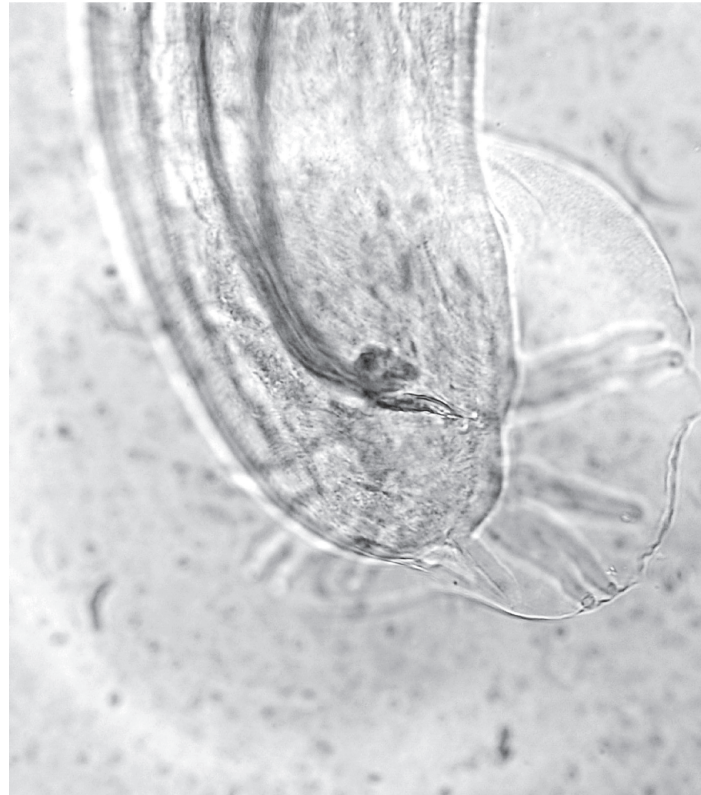
**Figure 4.** Female (left) and male (right) of *Angiostrongylus vasorum*: note that anteriolateral ray is deeply clefted (arrow) and arise separately from mediolateral and posterolateral ray (x200)

by Rosen (98) and Guilhon and Cens (99). In general, the morphological variation and associated dilemma in the case of *A. vasorum* involve whether the anterolateral ray is part of the same common trunk as the mediolateral and posterolateral rays. Additionally, there is uncertainty regarding how deep the cleft of the anteriolateral ray is within the trunk of the copulatory bursa (102, 103).

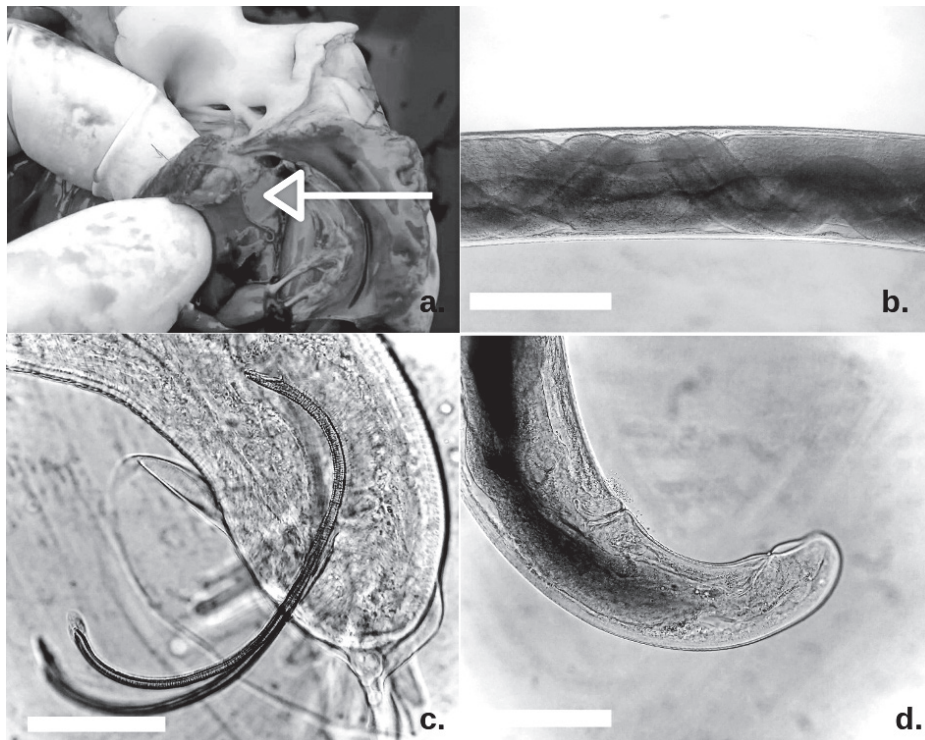
Another significant difference is the length of the spicules. According to Kozlov (4), the spicules of male *A. vasorum* measure 360-400  $\mu\text{m}$ , while Guilhon and Cens (99) describe them as considerably longer, ranging from 460-500  $\mu\text{m}$ . Additionally, the structure of the gubernaculum differs among sources: Guilhon and Cens (99) describe it as triangular, whereas Costa et al. (100) characterize it as more tongue-shaped. The gubernaculum can be difficult to observe, as it is often covered by spicules (Fig. 5). Differences reported in the foundational literature strongly suggest the presence of distinct intraspecific morphological variations, which may complicate the definitive identification of *A. vasorum*.

In a recent reclassification by Cowie (5), four genera, *Angiostrongylus*, *Gallegostrongylus*, *Rodentocaulus*, and *Stefanskostrongylus*, were accepted, designating *Parastrongylus* as a junior synonym of *Angiostrongylus*. However, Cowie (5) focused more on nomenclature than on taxonomy. Another taxonomic issue involves the

morphological similarities between *Angiocaulus raillieti* and *A. vasorum* in South America. The previously described species *A. raillieti*, found in dogs and crab-eating foxes in South America, was reclassified as *A. vasorum* (100). This change has not been universally accepted, as *A. raillieti* is still mentioned in the literature as a separate species, along with comparisons to other species in the *Angiostrongylus* genus (5, 103, 104, 105). A similar taxonomic issue arose concerning the discovery of *A. vasorum* in badgers in Spain and Italy (60, 86). In the original investigation conducted in Spain, the morphological characteristics of the *A. vasorum* specimens collected from badgers were not described. However, subsequent morphometric and molecular analyses confirmed the presence of *A. daskalovi* in the same area (87). Increasing evidence from Europe suggests that *A. daskalovi*, rather than *A. vasorum*, is found in badgers (25, 79, 87). Errors in identification of *Angiostrongylus vasorum* in mustelids are recognized in earlier reports by Ubelaker (97). The third taxonomic challenge is more general. In morphological studies, it has been observed that newly described species in rodents and wild carnivores (such as cats) often lack phylogenetic support (101, 102, 103). Although not yet described in rodents as natural infection, *A. vasorum* is highly similar to *A. schmidtii*, *A. gubernaculatus*, *A. morerai*, *A. lenzii*, and *A. minasensis* (101, 105). The differences between



**Figure 5.** Gubernaculum of *Angiostrongylus vasorum* (specimen is cleared in Amman's lactophenol) (x400)



**Figure 6.** *Angiostrongylus daskalovi* from badger (*Meles meles*), Bosnia and Herzegovina: *in situ* - in right heart (a); middle female body, x200 (b); spicules of males with typical „fan-shaped“ distal end, x200 (c); distal end of female, x200 (d)

these species are based on body length as well as morphometric characteristics of spicules and bursal rays. In Europe, the taxonomic differences are more pronounced, as sympatric species like *A. chabaudi*, *A. daskalovi*, *A. cantonensis* and *A. dujardini* have been molecularly characterized, revealing clearer morphological distinctions. In original specimens of *A. daskalovi* from a badger (shot in 2018 near Srbac, Bosnia and Herzegovina), a sheath (membrane) was observed around the distal part of the spicule, which was not seen in *A. vasorum* found in golden jackals and foxes (22). This spicule sheath gives the appearance that the spicules are expanded at the end in a “fan-shaped” similarity (Fig. 6). Additionally, the spicules in *A. daskalovi* are better developed, wider, and shorter compared to those of *A. vasorum* (79).

*Angiostrongylus daskalovi* is a significantly larger species compared to *A. vasorum*. In this species, the anteriolateral ray shares a common trunk with other lateral rays (25). The main differences between *A. vasorum* and *A. chabaudi* are morphometric, but also include a notably more developed cephalic vesicle in *A. chabaudi* (20). The female *A. dujardini* exhibits a visible papilla at the end of the tail, which is not present in *A. vasorum* (Fig. 4). In male *A. dujardini*, the medio-lateral ray is longer than the other lateral rays, which all originate from a common trunk. Males of *A. cantonensis* possess significantly longer spicules (over 1,000  $\mu\text{m}$ ) compared to those of *A. vasorum*, along with differences in the morphology of the gubernaculum. *A. vasorum* has a shorter, thicker,

and more triangular gubernaculum, while *A. cantonensis* has a filariform gubernaculum. Bursal rays are much shorter in both *A. cantonensis* and *A. dujardini* compared to *A. vasorum*. Despite *A. vasorum* being the most researched species, the morphological descriptions of adults in the literature tend to be scarce. Many studies rely on a phrase stating that the morphological diagnosis is made “according to” certain references. Furthermore, molecular studies have often focused solely on L1 larvae of *A. vasorum*, with inadequate descriptions of adult forms. Morphological diagnosis based on the examination of L1 larvae can be sufficient in enzootic areas; however, in all other cases, confirmation with additional diagnostic methods is required. Therefore, providing a morphological diagnosis without information on the host, geographic location, and site of infection can be problematic for some parasitologists. In practice, additional challenges arise when analyzing adult specimens, such as lower quality samples (especially from wild animals), a limited number of samples, the absence of male specimens, and laboratory personnel lacking sufficient experience. Even in cases where adult forms are absent from the heart and pulmonary artery, this does not entirely rule out the presence of parasites and it is still necessary to examine the lungs for L1 larvae. Finally, many laboratories that do not specialize in the genus *Angiostrongylus* may lack “reference” specimens for comparative morphological analysis (Table 2).

**Table 2.** Basic morphological differences of *Angiostrongylus vasorum* and closely related species from Europe

Species	Spicule	Gubernaculum	Cephalic vesicle	Branching pattern or lateral rays	Female tail
<i>A. vasorum</i>	360–500 $\mu\text{m}$	Triangular	Poorly developed	Antero-lateral ray deep clefted in lateral ray stem	Smooth
<i>A. daskalovi</i>	330-410 $\mu\text{m}$ “fan-shaped” distal tip	Elongated-triangular	Present	All lateral rays share common trunk	Smooth
<i>A. chabaudi</i>	510-555 $\mu\text{m}$	Elongated-triangular	Prominent	All lateral rays share common trunk	Smooth
<i>A. dujardini</i>	Not available	Filariform	Not prominent	All lateral rays share common trunk, mediolateral ray is the longest	Female tail has papilla
<i>A. cantonensis</i>	>1000 $\mu\text{m}$	Filariform	Not prominent	All lateral rays share common trunk, short bursal rays	Angular appearance

## GENETIC DIVERSITY OF *ANGIOSTRONGYLUS VASORUM*: THERE IS MORE THAN MEETS THE EYE

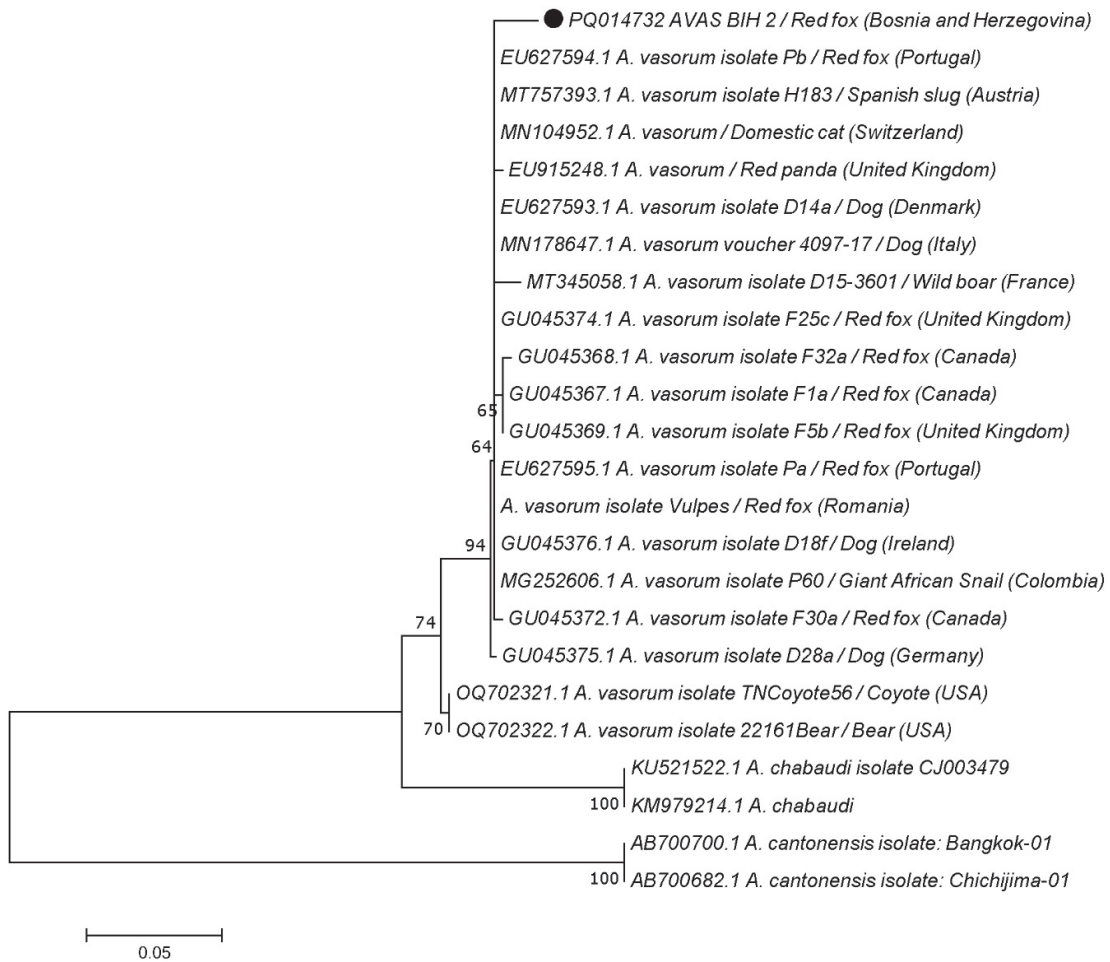
It is generally accepted that significant genetic variation exists within natural populations (106). Nematodes are particularly superabundant, with many species being cosmopolitan. These species (parasites and/or free-living) have adapted to various hosts (parasites) and environmental factors throughout their evolution and coevolution. As a result, they often display notable genetic diversity, which can serve as a resource for adaptation in the face of natural pressure (107). The primary genetic markers studied in *Angiostrongylus vasorum* are 18s (ribosomal RNA), ITS-2 (internal transcribed spacer region 2), and *cox1* (cyclooxygenase 1). Differences in the nucleotide sequences of these loci reflect variations in population dynamics, species history, speciation processes, and evolutionary changes. Most investigations into genetic diversity have focused on the species *A. vasorum*, aiming to establish connections between individual variants – haplotypes and their geographical areas and host species (108). However, it appears that this goal may be overly ambitious, primarily because the high level of genetic diversity can be interpreted more from the perspective of parasite population dynamics (expansion, bottleneck effect, population differentiation, etc.). Understanding whether genetic variants of *A. vasorum* differ in pathogenic potential remains unknown. In their initial study, Jefferies et al. (108) analyzed the internal transcribed spacer region 2 (ITS-2) and cyclooxygenase 1 (*cox1*) genes. They found a significant pairwise nucleotide distance (p-distance) between the ITS-2 sequences from Europe and South America, leading them to propose that *A. vasorum* comprises two distinct genotypes/lineages - European and South American variants. Subsequent research indicated that *A. vasorum* can be divided into Palearctic/Nearctic and Neotropic clades based on ITS-2 and mitochondrial genes (109). This suggests that the Neotropic clade essentially represents a South American lineage

of *A. vasorum*. Different hosts (such as foxes and dogs) sharing identical haplotypes of this species indicate a host-switching effect. However, evidence has demonstrated that populations of this nematode have differentiated in certain Palearctic/Nearctic and Neotropic regions due to geographic isolation and varying microclimatic conditions (109). Some researchers have proposed that the larger p-distance observed in ITS-2 gene sequences between the European and South American genotypes (2 - 2.3%) may signify the existence of two distinct species: *A. vasorum* and *A. raillieti* (103). However, without a detailed comparative analysis of specimens attributed to these species (holotypes), this cannot be conclusively proven. Additionally, there is currently no established “yardstick” p-distance value that can reliably separate species. Blouin (110) suggests that the intraspecies p-distance (ITS-2) might be around 1%, while interspecies p-distances for the *Angiostrongylus* genus usually range from 12.1% to 29.3% (108) (Table 3).

Another challenge is that it is not always feasible to distinguish species based solely on single gene analysis (SGA). A combination of multiple nuclear and mitochondrial genes is often necessary to achieve higher resolution and more comprehensive phylogenetic data. For instance, greater differences in the p-distance of *cox1* gene sequences have been observed in *A. vasorum*, where intraspecies p-distance ranges from 1% to 2%, while interspecies divergence is significantly higher, often between 10% and 20% (110). Recent data supported that global phylogenetic analysis of *A. vasorum* is notably more complex. Lange et al. (111) identified *A. vasorum* larvae in the African giant snail (*Achatina fulica*) in Colombia, where the ITS-2 sequence showed 99% identity with the analogous sequences of the European lineage. The inferred phylogenetic tree clearly grouped the ITS-2 sequences of *A. vasorum* with sequences from Europe, Canada, and Colombia (Fig. 7). The authors speculate that both genotypes of this species circulate in South America and that there has likely been an introduction of this nematode from Europe.

**Table 3.** Genetic markers used for phylogenetical analysis of *Angiostrongylus*

Marker	Type	Diagnostic use	Intraspecific divergence	Interspecific divergence	Molecular traits
ITS-2	Nuclear (rRNA)	Species confirmation	1–2%	12–29%	Limited intraspecific resolution
<i>cox1</i>	MtDNA	Phylogeography and haplotyping	>2%	>10%	High resolution and more informative
18S rRNA	Nuclear (rRNA)	Genus and species confirmation	>1%	1–2%	Highly conserved locus



**Figure 7.** The phylogenetic tree is based on the nucleotide sequences of the partial ITS-2 sequence (Neighbor-joining method in MEGAX, applying the Tamura-Nei model) of *Angiostrongylus vasorum*. ITS-2 sequence of *A. vasorum* from Bosnia and Herzegovina (PQ014732) is marked – original sequence from paper Stevanović et al. (22). *Angiostrongylus cantonensis* and *Angiostrongylus chabaudi* were included as outgroups. The numbers associated with the nodes represent the percentage of 1000 bootstrap iterations supporting the nodes (only percentages greater than 50% are shown)

We offer the following potential explanations for this finding:

1. a single ITS-2 sequence lacks adequate resolution to differentiate intraspecific haplotypic or genotypic variants,
2. the genetic diversity of the *A. vasorum* is greater than previously recognized, and
3. the recommendation to categorize the ITS-2 genotypes of *A. vasorum* based on geographical origin has limited taxonomical significance.

Some studies support some of these observations. Mitochondrial genes are advantageous for investigating evolutionary processes of speciation compared to nuclear genes in veterinary-relevant

nematodes (112). The genetic diversity of the mitochondrial cytochrome c oxidase subunit I (cox1) gene is extremely high in restricted geographical areas with high prevalence and parasitic burden within hosts (113, 114). Comparing two studies conducted in London and Zurich reveals genetic signal for population expansion of *A. vasorum* in enzootic regions (as indicated by negative neutrality tests), with shared haplotypes among populations. Although  $F_{st}$  (fixation test) and AMOVA analyses were not performed between these populations, the results suggest the high gene flow and low population differentiation into subdivisions. From an epidemiological perspective, these findings imply that the expansion of a species, underpinned by genetic diversity, is progressive and cannot be

halted merely by implementing control measures for this parasite. Additionally, *A. vasorum* exhibits significantly greater genetic diversity compared to *A. cantonensis*, another species experiencing recent geographical expansion (9). This high genetic diversity is further supported by the discovery of new ITS-2 variants of *A. vasorum* in coyote and black bear in Tennessee, USA (7). Analysis of ITS-2 sequences indicates that these isolates demonstrate a higher p-distance (95%-96% similarity) compared to the European clade (Fig. 7), suggesting the presence of a distinct genetic lineage. Studies on the phylogeny of *A. vasorum* indicate the potential occurrence of cryptic diversity or speciation (*sensu lato*). The p-distance of *cox1* sequences from *A. vasorum* in Costa Rica was found to be 8.6% compared to homologous sequences from Europe and Brazil (9). Similar to the isolates from the USA, *A. vasorum* from Costa Rica does not fall within the variants originally proposed by Jefferies et al. (108, 109). The concept of cryptic diversity - or the notion that *A. vasorum* contains cryptic variants - requires thorough revision. A limitation of the study by Robleto-Quesada et al. (9) is that it analyzed only two samples and did not include adult forms of *A. vasorum*, which would be necessary for detailed morphological analysis. It is difficult to define cryptic diversity without precise morphological descriptions of the species, supported by statistical validity concerning the number and origin of samples at all phyletic and ecological levels (115). Further complication is that speciation and diversity in this case are typically inferred from genetic divergence, which is often overemphasized, whereas essential ecological criteria - particularly reproductive isolation - are largely overlooked. A greater divergence in mitochondrial DNA (mtDNA) and other genes may result from the higher population differentiation observed in the species *A. vasorum*. This differentiation often arises from spatio-temporal and ecological isolation (host-associated divergence). Although this process can occur independently, it is faster and more ephemeral compared to speciation (116).

If there is a lack of biological or ecological data on the species and interpretations are solely based on gene data, it is possible that incomplete lineage sorting (ILS) could introduce noise, leading to misleading conclusions about divergence. As shown in the review, *A. vasorum* displays significant morphological variations that have unresolved taxonomic implications (e.g., *A. vasorum* and/or *A. railletii*). Furthermore, the species exhibits considerable genetic diversity that is expanding in

terms of geographical range and host distribution. This indicates that new variants in terms of haplotypes, genotypes, or lineages of this species may emerge, presenting varying p-distances and other indicators of genetic diversity.

## CONCLUSION

*Angiostrongylus vasorum* exhibits substantial morphological and genetic variability, challenging morphological diagnosis and phylogenetic interpretation. Morphological ambiguities have limited impact in general practice but are essential in taxonomic and epidemiological studies. When assessing the genetic diversity of *Angiostrongylus vasorum*, it is important to avoid premature conclusions, as population dynamics in this species are known to be highly fluid and complex. We emphasize that identification in non-canid hosts should always be supported by molecular confirmation. The high genetic variability within *A. vasorum* may reflect a combination of factors, including reproductive capacity and environmental pressures, rather than host and geographical range alone. Future research should adopt a more integrative approach, incorporating standardized diagnostic protocols and exploring host-parasite coevolution and population genetics.

## CONFLICT OF INTEREST

The authors declare that they have no financial or non-financial conflict of interest regarding authorship and publication of this article.

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## AUTHORS' CONTRIBUTIONS

OS wrote the manuscript. DD, AR, DN, TI, AV and IP edited the final version of the manuscript.

## REFERENCES

1. Baillet, C.C. (1957). Strongyle of the vessels and the heart of the dog *Strongylus vasorum*. [Strongle des vaisseaux et du coeur du chien *Strongylus vasorum* (Nobis).] *N Dict Paract Med Vet.* 8, 587-588. [In French]
2. Morgan, E.R., Modrý, D., Paredes-Esquivel, C., Foronda, P., Traversa, D. (2021). *Angiostrongylosis* in animals and humans in Europe. *Pathogens.* 10(10): 1236.  
<https://doi.org/10.3390/pathogens10101236>  
PMid:34684185 PMCID:PMC8538298
3. Spratt, D.M. (2015). Species of *Angiostrongylus* (Nematoda: Metastrongyloidea) in wildlife: A review. *Int J Parasitol Parasites Wildl.* 4(2): 178-189.  
<https://doi.org/10.1016/j.ijppaw.2015.02.006>  
PMid:25853051 PMCID:PMC4381133
4. Kozlov, D.P. (1977). Key to the helminths of carnivores in the USSR. *Nauka.* 276.
5. Cowie, R.H. (2019). Annotated catalogue of species of *Angiostrongylus* and the related genera *Gallegostrongylus*, *Rodentocaulus* and *Stefanskostrongylus* (Nematoda: Metastrongyloidea, Angiostrongylidae). *J Helminthol.* 93(4): 389-423.  
<https://doi.org/10.1017/S0022149X19000270>  
PMid:31064435
6. Gueldner, E.K., Schuppisser, C., Borel, N., Hilbe, M., Schnyder, M. (2019). First case of a natural infection in a domestic cat (*Felis catus*) with the canid heart worm *Angiostrongylus vasorum*. *Vet Parasitol Reg Stud Reports.* 18, 100342.  
<https://doi.org/10.1016/j.vprsr.2019.100342>  
PMid:31796174 PMCID:PMC7104072
7. Riese, K., Baker, E., Dennis, M.M., Williamson, R., Gerhold, R. (2024). Two cases of *Angiostrongylus vasorum*, a cardiopulmonary nematode, in a wild black bear and coyote of Tennessee. *Vet Parasitol Reg Stud Reports.* 54, 101079.  
<https://doi.org/10.1016/j.vprsr.2024.101079>  
PMid:39237243
8. Mechouck, N., Deak, G., Ionică, A.M., Toma, C., Negoescu, A.G., Taulescu, M., Bouslama, Z., Mihalca, A.D. (2024). First report of *Angiostrongylus vasorum* in an African golden wolf (*Canis lupaster*) in Algeria. *Parasit Vectors.* 17(1): 441.  
<https://doi.org/10.1186/s13071-024-06534-9>  
PMid:39468624 PMCID:PMC11520683
9. Robleto-Quesada, J., Umaña-Blanco, F., Solano-Barquero, A., Allen, J., Levi, T., Gori, F., Schnyder, M., Rojas, A. (2024). Seek, and you will find: Cryptic diversity of the cardiopulmonary nematode *Angiostrongylus vasorum* in the Americas. *Acta Trop.* 258, 107337.  
<https://doi.org/10.1016/j.actatropica.2024.107337>  
PMid:39098751
10. Karadjian, G., Kaestner, C., Laboutière, L., Adicéam, E., Wagner, T., Johne, A., Thomas, M., et al. (2020). A two-step morphology-PCR strategy for the identification of nematode larvae recovered from muscles after artificial digestion at meat inspection. *Parasitol Res.* 119(12): 4113-4122.  
<https://doi.org/10.1007/s00436-020-06899-7>  
PMid:32979104
11. Gillis-Germitsch, N., Tritten, L., Hegglin, D., Deplazes, P., Schnyder, M. (2020). Conquering Switzerland: the emergence of *Angiostrongylus vasorum* in foxes over three decades and its rapid regional increase in prevalence contrast with the stable occurrence of lungworms. *Parasitol.* 147(10): 1071-1079.  
<https://doi.org/10.1017/S0031182020000700>  
PMid:32372743 PMCID:PMC10317728
12. Fuehrer, H.P., Morelli, S., Unterköfler, M.S., Bajzer, A., Bakran-Lebl, K., Dwuznik-Szarek, D., Farkas, R., et al. (2021). *Dirofilaria* spp. and *Angiostrongylus vasorum*: Current Risk of Spreading in Central and Northern Europe. *Pathogens.* 10(10): 1268.  
<https://doi.org/10.3390/pathogens10101268>  
PMid:34684217 PMCID:PMC8537668
13. Shukullari, E., Hamel, D., Rapti, D., Pfister, K., Visser, M., Winter, R., Rehbein, S. (2015). Parasites and vector-borne diseases in client-owned dogs in Albania. Intestinal and pulmonary endoparasite infections. *Parasitol Res.* 114(12): 4579-4590.  
<https://doi.org/10.1007/s00436-015-4704-8>  
PMid:26350379
14. Kontrimavichus, V.L. (1979). Subfamily *Angiostrongylinae* Boehm and Gebaur, 1934. In: V.L. Kontrimavichus, S.L. Delyamure, (Eds.), *Principles of nematology. Volume 29. Filaroids of domestic and wild animals* (pp. 55-138). Moscow: Nauka Publishers
15. Segovia, J.M., Torres, J., Miquel, J. (2004). Helminth parasites of the red fox (*Vulpes vulpes* L., 1758) in the Iberian Peninsula: an ecological study. *Acta Parasitol.* 49(1): 67-79.
16. Globokar, M., Pantchev, N., Hinney, B., Leschnik, M., Peschke, R., Schaper, R., Schnyder, M. (2021). Serological and faecal detection of *Angiostrongylus vasorum* in dogs from Austria. *Vet Parasitol Reg Stud Reports.* 26, 100641.  
<https://doi.org/10.1016/j.vprsr.2021.100641>  
PMid:34879952
17. Shimalov, V., Shimalov, V. (2003). Helminth fauna of the red fox (*Vulpes vulpes* Linnaeus, 1758) in southern Belarus. *Parasitol Res.* 89(1): 77-78.  
<https://doi.org/10.1007/s00436-002-0701-9>  
PMid:12474048

18. Lempereur, L., Martinelle, L., Marechal, F., Bayrou, C., Dalemans, A.C., Schnyder, M., Losson, B. (2016). Prevalence of *Angiostrongylus vasorum* in southern Belgium, a coprological and serological survey. *Parasit Vectors*. 9(1): 533.  
<https://doi.org/10.1186/s13071-016-1820-y>  
PMid:27716374 PMCID:PMC5052934
19. Stevanović, O., Dobrijević, M., Vujanić, D., Nedić, D., Ilić, T., Trbojević, I. (2020). First report of autochthonous canine angiostrongylosis in Bosnia and Herzegovina. *Vet Glasnik*. 7(1): 85-91.  
<https://doi.org/10.2298/VETGL2001085S>
20. Stevanović, O., Diakou, A., Morelli, S., Paraš, S., Trbojević, I., Nedić, D., Sladojević, Ž., et al. (2019). Severe verminous pneumonia caused by natural mixed infection with *Aelurostrongylus abstrusus* and *Angiostrongylus chabaudi* in a European wild cat from Western Balkan area. *Acta Parasitol*. 64(2): 411-417.  
<https://doi.org/10.2478/s11686-019-00029-9>  
PMid:30756237
21. Stevanović, O., Vujanić, D., Dobrijević, M., Trbojević, I., Gajić, N., Nedić, D., Sladojević, Ž. (2019). Cardiorespiratory nematode in carnivores from Republic of Srpska, Lecture by Invitation. 24rd Annual Counselling of Doctors of Veterinary Medicine of Republic of Srpska (Bosnia and Herzegovina), 81-82. [In Serbian]
22. Stevanović, O., Despotović, D., Ilić, T., Jovanović, N., Trbojević, I., Radaljić, A. (2024). *Angiostrongylus vasorum* in golden jackals (*Canis aureus*) and red foxes (*Vulpes vulpes*) from Northern Bosnia and Herzegovina. *Parasitol Res*. 123, 352.  
<https://doi.org/10.1007/s00436-024-08377-w>  
PMid:39414642
23. Kamenov, Y., Radev, V., Zlateva, N. (1999). On diagnosis and clinic of angiostrongylosis of cats. *Exp Pathol Parasitol*. 2, 51-54.
24. Pantchev, N., Schnyder, M., Vrhovec, M.G., Schaper, R., Tsachev, I. (2015). Current surveys of the seroprevalence of *Borrelia burgdorferi*, *Ehrlichia canis*, *Anaplasma phagocytophilum*, *Leishmania infantum*, *Babesia canis*, *Angiostrongylus vasorum* and *Dirofilaria immitis* in dogs in Bulgaria. *Parasitol Res*. 114(Suppl. 1): 117-130.  
<https://doi.org/10.1007/s00436-015-4518-8>  
PMid:26152413
25. Panayotova-Pencheva, M., Trifonova, A., Dakova, V., Salkova, D., Movsesyan, S.O. (2017). On the parasites of genus *Angiostrongylus* (Nematoda: Angiostrongylidae) and some cases of *Angiostrongylus daskalovi* in badgers from Bulgaria. *Russ J Parasitol*. 40(2): 124-128.
26. Giannelli, A., Kirkova, Z., Abramo, F., Latrofa, M.S., Campbell, B., Zizzo, N., Cantacessi, C., et al. (2016). *Angiostrongylus chabaudi* in felids: New findings and a review of the literature. *Vet Parasitol*. 228, 188-192.  
<https://doi.org/10.1016/j.vetpar.2016.09.007>  
PMid:27692325
27. Rajković-Janje, R., Marinculić, A., Bosnić, S., Benić, M., Vinković, B., Mihajlević, Ž. (2003). Prevalence and seasonal distribution of helminth parasites in red foxes (*Vulpes vulpes*) from the Zagreb County (Croatia). *Z Jagdwiss*. 48, 151-160.  
<https://doi.org/10.1007/BF02189989>
28. Hermosilla, C., Kleinertz, S., Silva, L.M., Hirzmann, J., Huber, D., Kusak, J., Taubert, A. (2017). Protozoan and helminth parasite fauna of free-living Croatian wild wolves (*Canis lupus*) analyzed by scat collection. *Vet Parasitol*. 233, 14-19.  
<https://doi.org/10.1016/j.vetpar.2016.11.011>  
PMid:28043382
29. Vernerová, E., Dvorakova, N., Svobodová, V., Bures, J. (2020). Factors affecting the occurrence of gastrointestinal parasites and lungworms in dogs and assessment of antiparasitic drugs use patterns. *Acta Vet Brno*. 91(2): 171-177.  
<https://doi.org/10.2754/avb202291020171>
30. Lundsgaard, K. (2024). Epidemiology of *Angiostrongylus vasorum* and *Crenosoma vulpis* infection in dogs in Denmark. *J Small Anim Pract*. 65(10): 737-748.  
<https://doi.org/10.1111/jsap.13762>  
PMid:38973253
31. Bolt, G., Monrad, J., Henriksen, P., Dietz, H.H., Koch, J., Bindseil, E., Jensen, A.L. (1992). The fox (*Vulpes vulpes*) as a reservoir for canine angiostrongylosis in Denmark. Field survey and experimental infections. *Acta Vet Scand*. 33(4): 357-362.  
<https://doi.org/10.1186/BF03547302>  
PMid:1488951 PMCID:PMC8117834
32. Laurimaa, L., Moks, E., Soe, E., Valdmann, H., Saarma, U. (2016). *Echinococcus multilocularis* and other zoonotic parasites in red foxes in Estonia. *Parasitol*. 143(11): 1450-1458.  
<https://doi.org/10.1017/S0031182016001013>  
PMid:27279259
33. Laurimaa, L., Süld, K., Davison, J., Moks, E., Valdmann, H., Saarma, U. (2016). Alien species and their zoonotic parasites in native and introduced ranges: The raccoon dog example. *Vet Parasitol*. 219, 24-33.  
<https://doi.org/10.1016/j.vetpar.2016.01.020>  
PMid:26921035

34. Tiškina, V., Lindqvist, E.L., Blomqvist, A.C., Orav, M., Stensvold, C.R., Jokelainen, P. (2019). Autochthonous *Angiostrongylus vasorum* in Finland. *Vet Rec Open*. 6(1): e000314.  
<https://doi.org/10.1136/vetrec-2018-000314>  
PMid:30997112 PMCID:PMC6446214
35. Isomursu, M., Salin, N., Oksanen, A. (2010). Rare canine parasites survive in the wild fox population. *Acta Vet Scand*. 52(Suppl. 1): S22.  
<https://doi.org/10.1186/1751-0147-52-S1-S22>  
PMCID:PMC2994299
36. Tenora, F., Henttonen, H., Haukisalminen, V. (1983). On helminths of rodents in Finland. *Ann Zool Fenn*. 20, 37-45.
37. Schnyder, M., Bilbrough, G., Hafner, C., Schaper, R. (2017). *Angiostrongylus vasorum*, 'The French heartworm': a serological survey in dogs from France introduced by a brief historical review. *Parasitol Res*. 116(Suppl. 1): 31-40.  
<https://doi.org/10.1007/s00436-017-5489-8>  
PMid:28717947
38. Ferdushy, T., Hasan, M.T. (2010). *Angiostrongylus vasorum*: the 'French heartworm'. *Parasitol Res*. 107(4): 765-771.  
<https://doi.org/10.1007/s00436-010-2026-4>  
PMid:20714748
39. Graille, M., Ferté, H., Petit, T., Courtois, F.O., Gauchot, J.Y., Nougailon, J.L., Vitaud, C., et al. (2015). Fatal *Parastrostrongylus dujardini* infection in captive callitrichids. *Vet Pathol*. 52(2): 364-368.  
<https://doi.org/10.1177/0300985814531496>  
PMid:24793826
40. Pochverya, Sh.O., Shikvishvily, M.I., Gvaladze, A.Z., Turmanidze, M.O. (2015). On the issue of helminth infection in dogs of the population of Tbilisi. *Theory and Practice of Combating Parasitic Diseases [К вопросу об инвазированности гельминтами собак населения г. Тбилиси. Теория и практика борьбы с паразитарными болезнями.]* 16, 352-353. [In Russian]
41. Kurashvili, B.E., Matsaberidze, G.V., Sadikhov, I.A., Rodonaia, T.E. (1989). Parasitic worms of small mammals of the Transcaucasian fauna. *Metsniereba, Tbilisi*, 196.
42. Maksimov, P., Hermosilla, C., Taubert, A., Staubach, C., Sauter-Louis, C., Conraths, F.J., Vrhovec, M.G., Pantchev, N. (2017). GIS-supported epidemiological analysis on canine *Angiostrongylus vasorum* and *Crenosoma vulpis* infections in Germany. *Parasit Vectors*. 10(1): 108.  
<https://doi.org/10.1186/s13071-017-2054-3>  
PMid:28241853 PMCID:PMC5330135
43. Schug, K., Krämer, F., Schaper, R., Hirzmann, J., Failing, K., Hermosilla, C., Taubert, A. (2018). Prevalence survey on lungworm (*Angiostrongylus vasorum*, *Crenosoma vulpis*, *Eucoleus aerophilus*) infections of wild red foxes (*Vulpes vulpes*) in central Germany. *Parasit Vectors*. 11(1): 85.  
<https://doi.org/10.1186/s13071-018-2672-4>  
PMid:29409523 PMCID:PMC5801722
44. Bisterfeld, K., Raulf, M.K., Waindok, P., Springer, A., Lang, J., Lierz, M., Siebert, U., Strube, C. (2022). Cardio-pulmonary parasites of the European wildcat (*Felis silvestris*) in Germany. *Parasit Vectors*. 15(1): 452.  
<https://doi.org/10.1186/s13071-022-05578-z>  
PMid:36471378 PMCID:PMC9724372
45. Angelou, A., Gelasakis, A.I., Schnyder, M., Schaper, R., Papadopoulos, E. (2020). The 'French heartworm' in Greece: A countrywide serological survey of *Angiostrongylus vasorum* infection by combined detection of circulating antigens and specific antibodies. *Vet Parasitol Reg Stud Reports*. 19, 100376.  
<https://doi.org/10.1016/j.vprsr.2020.100376>  
PMid:32057383
46. Diakou, A., Psalla, D., Migli, D., Di Cesare, A., Youlatos, D., Marcer, F., Traversa, D. (2016). First evidence of the European wildcat (*Felis silvestris silvestris*) as definitive host of *Angiostrongylus chabaudi*. *Parasitol Res*. 115(3): 1235-1244.  
<https://doi.org/10.1007/s00436-015-4860-x>  
PMid:26637312
47. Schnyder, M., Schaper, R., Lukács, Z., Hornok, S., Farkas, R. (2015). Combined serological detection of circulating *Angiostrongylus vasorum* antigen and parasite-specific antibodies in dogs from Hungary. *Parasitol Res*. 114(Suppl. 1): 145-154.  
<https://doi.org/10.1007/s00436-015-4520-1>  
PMid:26152415
48. Tolnai, Z., Széll, Z., Sréter, T. (2015). Environmental determinants of the spatial distribution of *Angiostrongylus vasorum*, *Crenosoma vulpis* and *Eucoleus aerophilus* in Hungary. *Vet Parasitol*. 207(3-4): 355-358.  
<https://doi.org/10.1016/j.vetpar.2014.12.008>  
PMid:25547643
49. Takács, A., Szabó, L., Juhász, L., Takács, A., Lanszki, J., Takács, P., Heltai, M. (2014). Data on the parasitological status of golden jackal (*Canis aureus* L., 1758) in Hungary. *Acta Vet Hung*. 62(1): 33-41.  
<https://doi.org/10.1556/avet.2013.058>  
PMid:24334089
50. Mészáros, F. (1972). The occurrence of *Angiostrongylus* (P.) *dujardini* Drozd et Doby, 1970 (Nematoda) in rodents in Hungary. *Parasitol Hung*. 5, 163-176.

51. Nagy, E., Benedek, I., Zsolnai, A., Halász, T., Csivincsik, Á., Ács, V., Nagy, G., Tari, T. (2021). Habitat characteristics as potential drivers of the *Angiostrongylus daskalovi* infection in European badger (*Meles meles*) populations. *Pathogens*. 10(6): 715.  
<https://doi.org/10.3390/pathogens10060715>  
PMid:34200340 PMCID:PMC8228055
52. Skirnisson, K., Pálsdóttir, G.R., Eydal, M. (2018). Parasites of dogs and cats imported to Iceland during 1989-2017 with remarks on parasites occurring in the native populations. *Icel Agric Sci*. 31, 49-63.  
<https://doi.org/10.16886/IAS.2018.04>
53. Gallagher, B., Brennan, S.F., Zarelli, M., Mooney, C.T. (2012). Geographical, clinical, clinicopathological and radiographic features of canine angiostrongylosis in Irish dogs: a retrospective study. *Ir Vet J*. 65, 5.  
<https://doi.org/10.1186/2046-0481-65-5>  
PMid:22433388 PMCID:PMC3349590
54. McCarthy, G., Ferrand, M., De Waal, T., Zintl, A., McCrath, G., Byrne, W., O'Neill, E.J. (2016). Geographical distribution of *Angiostrongylus vasorum* in foxes (*Vulpes vulpes*) in the Republic of Ireland. *Parasitol*. 143(5): 588-593.  
<https://doi.org/10.1017/S0031182016000032>  
PMid:26940534
55. Traversa, D., Morelli, S., Di Cesare, A., Astuti, C., Barlaam, A., Colombo, M., Veronesi, F., et al. (2025). Current Enzooticity of *Dirofilaria immitis* and *Angiostrongylus vasorum* in Central and Southern Italy. *Animals (Basel)*. 15(2): 172.  
<https://doi.org/10.3390/ani15020172>  
PMid:39858171 PMCID:PMC11758344
56. Tieri, E.E., Saletti, M.A., D'Angelo, A.R., Parisciani, G., Pelini, S., Cocco, A., Di Teodoro, G., et al. (2021). *Angiostrongylus vasorum* in foxes (*Vulpes vulpes*) and wolves (*Canis lupus italicus*) from Abruzzo region, Italy. *Int J Parasitol Parasites Wildl*. 15, 184-194.  
<https://doi.org/10.1016/j.ijppaw.2021.05.003>  
PMid:34136344 PMCID:PMC8182381
57. Orioles, M., Fabbri, D., Miani, G., Pesaro, S., Dorigo, L., Bregoli, M., Saccà, E., et al. (2024). Double trouble: Co-infection of *Angiostrongylus vasorum* and *Dirofilaria immitis* in golden jackal (*Canis aureus*) in Friuli Venezia Giulia, Italy. *Int J Parasitol Parasites Wildl*. 24, 100969.  
<https://doi.org/10.1016/j.ijppaw.2024.100969>  
PMid:39165606 PMCID:PMC11334653
58. Varcasia, A., Tamponi, C., Brianti, E., Cabras, P.A., Boi, R., Pipia, A.P., Giannelli, A., et al. (2014). *Angiostrongylus chabaudi* Biocca, 1957: a new parasite for domestic cats? *Parasit Vectors*. 7, 588.  
<https://doi.org/10.1186/s13071-014-0588-1>  
PMid:25515026 PMCID:PMC4308007
59. Eleni, C., Di Cesare, A., Cavicchio, P., Tonnichchia, M.C., Meoli, R., di Regalbano, A.F., Paoletti, B., et al. (2016). Fatal *Angiostrongylus dujardini* infection in callitrichid monkeys and suricates in an Italian zoological garden. *Parasitol Int*. 65(4): 333-335.  
<https://doi.org/10.1016/j.parint.2016.04.005>  
PMid:27094227
60. Magi, M., Guardone, L., Dell'Omodarme, M., Prati, M., Mignone, W., Torracca, B., Monni, G., Macchioni, F. (2009). *Angiostrongylus vasorum* in red foxes (*Vulpes vulpes*) and badgers (*Meles meles*) from Central and Northern Italy. *Hystrix It J Mamm*. 20(2): 121-126.
61. Bagraade, G., Kirjusina, M., Vismanis, K., Ozoliņš, J. (2009). Helminth parasites of the wolf *Canis lupus* from Latvia. *J Helminthol*. 83(1): 63-68.  
<https://doi.org/10.1017/S0022149X08123860>  
PMid:19138449
62. Bružinskaitė-Schmidhalter, R., Šarkūnas, M., Malakauskas, A., Mathis, A., Torgerson, P.R., Deplazes, P. (2012). Helminths of red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*) in Lithuania. *Parasitol*. 139(1): 120-127.  
<https://doi.org/10.1017/S0031182011001715>  
PMid:21996514
63. Nugaraitė, D., Mažeika, V., Paulauskas, A. (2019). Helminths of Mustelids with Overlapping Ecological Niches: Eurasian Otter *Lutra lutra* (Linnaeus, 1758), American Mink *Neovison vison* Schreber, 1777, and European Polecat *Mustela putorius* Linnaeus, 1758. *Helminthologia*. 56(1): 66-74.  
<https://doi.org/10.2478/helm-2018-0035>  
PMid:31662675 PMCID:PMC6662030
64. Steeb, S. (2015). Postmortem examinations of the European wildcat (*Felis silvestris silvestris* Schreber, 1777). [Postmortale Untersuchungen an der Europäischen Wildkatze (*Felis silvestris silvestris* SCHREBER, 1777).] PhD thesis, Justus Liebig Universität, Fachbereich Veterinärmedizin, Gießen, VVB Laufersweiler Verlag Gießen, p. 230. [In German]
65. Chihai, O., Nistoreanu, V., Larion, A., Tălămbuță, N., Rusu, Ș., Zamornea, M., Melnic, G. (2023). Transmissible parasitic zoonoses of the species *Vulpes vulpes* (Linnaeus, 1758). *Natural sciences*. In: The dialogue of generations, September, 14-15 (p. 86), Chisinau, Republic of Moldova
66. Chihai, O., Nistoreanu, V., Larion, A., Rusu, Ș., Tălămbuță, N., Zamornea, M., Melnic, G., Kolodrevski, O. (2022). Epidemiological characteristics of the parasite fauna in *Apodemus uralensis* (Pallas, 1771) from various biotopes of the Republic of Moldova. [Caracteristica epidemiologică a parazitofaunei la *Apodemus uralensis* (Pallas, 1771) din diverse biotopuri ale Republicii Moldova.] *Studia Universitatis Moldaviae (Seria Științe Reale și ale Naturii)*, 156(6): 81-86. [In Romanian]

67. Lempereur, L., Nijse, R., Losson, B., Marechal, F., De Volder, A., Schoormans, A., Martinelle, L., et al. (2020). Coprological survey of endoparasite infections in owned dogs and owners' perceptions of endoparasite control in Belgium and the Netherlands. *Vet Parasitol Reg Stud Reports*. 22, 100450. <https://doi.org/10.1016/j.vprsr.2020.100450> PMID:33308762
68. Franssen, F., Nijse, R., Mulder, J., Cremers, H., Dam, C., Takumi, K., van der Giessen, J. (2014). Increase in number of helminth species from Dutch red foxes over a 35-year period. *Parasit Vectors*. 7, 166. <https://doi.org/10.1186/1756-3305-7-166> PMID:24708710 PMCid:PMC3978201
69. Robbestad, J., Jiménez-Meléndez, A., Robertson, L.J., Vatne, L.I., Hauback, M.N., Nerhagen, S. (2024). First case of autochthonous *Angiostrongylus vasorum* infection in a Norwegian dog. *Acta Vet Scand*. 66(1): 41. <https://doi.org/10.1186/s13028-024-00765-7> PMID:39223595 PMCid:PMC11367999
70. Hamnes, I.S., Enemark, H.L., Henriksen, K., Madslie, K., Er, C. (2019). The surveillance programme for *Angiostrongylus vasorum* in red foxes (*Vulpes vulpes*) Norway 2019. Norwegian Veterinary Institute 2020 - Annual Report. 1-7.
71. Llokmani, A., Rapti, D. (2018). Gastrointestinal parasites of shepherd dogs from Tetovo Region Macedonia. *JAFES* 72(1): 109-112. <https://doi.org/10.55302/JAFES187211091>
72. Schnyder, M., Schaper, R., Pantchev, N., Kowalska, D., Szwedko, A., Deplazes, P. (2013). Serological detection of circulating *Angiostrongylus vasorum* antigen-and parasite-specific antibodies in dogs from Poland. *Parasitol Res*. 112(Suppl. 1): 109-117. <https://doi.org/10.1007/s00436-013-3285-7> PMID:23779223
73. Demiaszkiewicz, A.W., Pyziel, A.M., Kuligowska, I., Lachowicz, J., Demiaszkiewicz, A.W., Pyziel, A.M. (2014). The first report of *Angiostrongylus vasorum* (Nematoda; Metastrongyloidea) in Poland, in red foxes (*Vulpes vulpes*). *Acta Parasitol*. 59(4): 758-762. <https://doi.org/10.2478/s11686-014-0290-7>
74. Alho, A.M., Schnyder, M., Schaper, R., Meireles, J., Belo, S., Deplazes, P., de Carvalho, L.M. (2016). Seroprevalence of circulating *Angiostrongylus vasorum* antigen and parasite-specific antibodies in dogs from Portugal. *Parasitol Res*. 115(7): 2567-2572. <https://doi.org/10.1007/s00436-016-5001-x> PMID:27000086 PMCid:PMC4914520
75. Eira, C., Vingada, J., Torres, J., Miquel, J. (2006). The Helminth community of the Red fox, *Vulpes vulpes*, in Dunas de Mira (Portugal) and its effect on host condition. *Wildl Biol Pract*. 2, 26-36. <https://doi.org/10.2461/wbp.2006.2.5>
76. Doby, J.M., Piedade-Guerreiro, J., Drozd, J. (1971). Geographic distribution of *Angiostrongylus* (*Parastrongylus*) *dujardini* Drozd and Doby, 1970, nematode parasite of small wild rodents. Its appearance in Portugal. *An Esc Nacl Saude Publica Med Trop*. 5(1): 59-60.
77. Deak, G., Gillis-Germitsch, N., Ionică, A.M., Mara, A., Păstrav, I.R., Cazan, C.D., Ioniță, M., et al. (2019). The first seroepidemiological survey for *Angiostrongylus vasorum* in domestic dogs from Romania. *Parasit Vectors*. 12(1): 224. <https://doi.org/10.1186/s13071-019-3481-0> PMID:31088513 PMCid:PMC6515677
78. Deak, G., Gherman, C.M., Ionică, A.M., Vezendan, A.D., D'Amico, G., Matei, I.A., Daskalaki, A.A., et al. (2017). *Angiostrongylus vasorum* in Romania: an extensive survey in red foxes, *Vulpes vulpes*. *Parasit Vectors*. 10(1): 330. <https://doi.org/10.1186/s13071-017-2270-x> PMID:28701176 PMCid:PMC5508484
79. Gherman, C.M., Deak, G., Matei, I.A., Ionică, A.M., D'Amico, G., Taulescu, M., Barbu-Tudoran, L., et al. (2016). A rare cardiopulmonary parasite of the European badger, *Meles meles*: first description of the larvae, ultrastructure, pathological changes and molecular identification of *Angiostrongylus daskalovi* Janchev & Genov 1988. *Parasit Vectors*. 9(1): 423. <https://doi.org/10.1186/s13071-016-1718-8> PMID:27485118 PMCid:PMC4969667
80. Gherman, C.M., Ionică, A.M., D'Amico, G., Otranto, D., Mihalca, A.D. (2016). *Angiostrongylus chabaudi* (Biocca, 1957) in wildcat (*Felis silvestris silvestris*, S) from Romania. *Parasitol Res*. 115(6): 2511-2517. <https://doi.org/10.1007/s00436-016-5032-3> PMID:27106235
81. Simin, S., Spasojević Kosić, L., Kuruca, L., Pavlović, I., Savović, M., Lalošević, V. (2014). Moving the boundaries to the South-East: first record of autochthonous *Angiostrongylus vasorum* infection in a dog in Vojvodina province, northern Serbia. *Parasit Vectors*. 7, 396. <https://doi.org/10.1186/1756-3305-7-396> PMID:25164574 PMCid:PMC4261976
82. Gavrilović, P., Todorović, I., Pavlović, I., Živilj, A. (2018). First report of *Angiostrongylus vasorum* in red foxes (*Vulpes vulpes*) in Serbia. *J Hellenic Vet Med Soc*. 69(4): 1265-1270. <https://doi.org/10.12681/jhvms.19616>
83. Gavrilović, P., Marinković, D., Vidanović, D., Dobrosavljević, I., Gavrilović, A. (2019). Are golden jackals (*Canis aureus*) definitive hosts for *Angiostrongylus vasorum*? *Transbound Emerg Dis*. 66(6): 2305-2310. <https://doi.org/10.1111/tbed.13284> PMID:31254445

84. Carretón, E., Morchón, R., Falcón-Cordón, Y., Matos, J., Costa-Rodríguez, N., Montoya-Alonso, J.A. (2020). First epidemiological survey of *Angiostrongylus vasorum* in domestic dogs from Spain. *Parasit Vectors*. 13, 306.  
<https://doi.org/10.1186/s13071-020-04180-5>  
PMid:32532325 PMCid:PMC7291642
85. Martínez-Rondán, F.J., de Ybáñez, M.R.R., López-Beceiro, A.M., Fidalgo, L.E., Berriatua, E., Lahat, L., Sacristán, I., et al. (2019). Cardiopulmonary nematode infections in wild canids: does the key lie on host-prey-parasite evolution? *Res Vet Sci*. 126, 51-58.  
<https://doi.org/10.1016/j.rvsc.2019.08.008>  
PMid:31437776
86. Torres, J., Miquel, J., Motjé, M. (2001). Helminth parasites of the eurasian badger (*Meles meles* L.) in Spain: a biogeographic approach. *Parasitol Res*. 87(4): 259-263.  
<https://doi.org/10.1007/s004360000316>  
PMid:11355672
87. Gerrikagoitia, X., Barral, M., Juste, R.A. (2010). *Angiostrongylus* species in wild carnivores in the Iberian Peninsula. *Vet Parasitol*. 174(1-2): 175-180.  
<https://doi.org/10.1016/j.vetpar.2010.07.015>  
PMid:20728995
88. Alvarez, F., Iglesias, R., Bos, J., Rey, J., Sanmartin Durán, M.L. (1991). Lung and hearth nematodes in some Spanish mammals. *Wiad Parazytol*. 37(4): 481-490.
89. Delgado-Serra, S., Sola, J., Negre, N., Paredes-Esquivel, C. (2022). *Angiostrongylus cantonensis* nematode invasion pathway, Mallorca, Spain. *Emerg Infect Dis*. 28(6): 1163-1169.  
<https://doi.org/10.3201/eid2806.212344>  
PMid:35608603 PMCid:PMC9155863
90. Grandi, G., Lind, E.O., Schaper, R., Ågren, E., Schnyder, M. (2017) Canine angiostrongylosis in Sweden: a nationwide seroepidemiological survey by enzyme-linked immunosorbent assays and a summary of five-year diagnostic activity (2011-2015). *Acta Vet Scand*. 59(1): 85.  
<https://doi.org/10.1186/s13028-017-0351-7>  
PMid:29258532 PMCid:PMC5735942
91. Lurati, L., Deplazes, P., Hegglin, D., Schnyder, M. (2015). Seroepidemiological survey and spatial analysis of the occurrence of *Angiostrongylus vasorum* in Swiss dogs in relation to biogeographic aspects. *Vet Parasitol*. 212(3-4): 219-226.  
<https://doi.org/10.1016/j.vetpar.2015.08.017>  
PMid:26342624
92. Gillis-Germitsch, N., Manser, M. B., Hilbe, M., Schnyder, M. (2017). Meerkats (*Suricata suricatta*), a new definitive host of the canid nematode *Angiostrongylus vasorum*. *Int J Parasitol Parasites Wildl*. 6(3): 349-353.  
<https://doi.org/10.1016/j.ijppaw.2017.10.002>  
PMid:29379713 PMCid:PMC5779638
93. Varodi, E.I., Malega, A.M., Kuzmin, Y., Korniyushin, V.V. (2017). Helminths of wild predatory mammals of Ukraine. nematodes. *Vestnik Zoologii*. 51(3): 187-202.  
<https://doi.org/10.1515/vzoo-2017-0026>
94. Schnyder, M., Schaper, R., Bilbrough, G., Morgan, E.R., Deplazes, P. (2013). Seroepidemiological survey for canine angiostrongylosis in dogs from Germany and the UK using combined detection of *Angiostrongylus vasorum* antigen and specific antibodies. *Parasitol*. 140(11): 1442-1450.  
<https://doi.org/10.1017/S0031182013001091>  
PMid:23965824 PMCid:PMC3762218
95. Taylor, C.S., Gato, R.G., Learmount, J., Aziz, N.A., Montgomery, C., Rose, H., Coulthwaite, C.L., et al. (2015). Increased prevalence and geographic spread of the cardiopulmonary nematode *Angiostrongylus vasorum* in fox populations in Great Britain. *Parasitol*. 142(9): 1190-1195.  
<https://doi.org/10.1017/S0031182015000463>  
PMid:26027539
96. Anderson, R.C. (1987). Keys to genera of the superfamily Metastrongyloidea. In: D.I. Gibson, A. Jones, R.A. Bray (Eds.), *Keys to the nematode parasites of vertebrates: archival volume (40)*. CABI Publishing
97. Ubelaker, J.E. (1986). Systematics of species referred to the genus *Angiostrongylus*. *J Parasitol*. 72(2): 237-244.  
<https://doi.org/10.2307/3281599>  
PMid:3525794
98. Rosen, L., Ash, L.R., Wallace, G.D. (1970). Life history of the canine lungworm *Angiostrongylus vasorum* (Baillet). *Am J Vet Res*. 31(1): 131-143.  
<https://doi.org/10.2460/ajvr.1970.31.01.131>  
PMid:5414275
99. Guilhon, J., Cens, B. (1973). *Angiostrongylus vasorum* (Baillet, 1866). Etude biologique et morphologique. *Ann Parasitol Hum Comp*. 48(4): 567-596.  
<https://doi.org/10.1051/parasite/1973484567>  
PMid:4791829
100. Costa, J.O., De Araujo Costa, H.M., Guimaraes, M.P. (2003). Redescription of *Angiostrongylus vasorum* (Baillet, 1866) and systematic revision of species assigned to the genera *Angiostrongylus* Kamensky, 1905 and *Angiocaulus* Schulz, 1951. *Revue Méd Vét*. 154(1): 9-16.
101. Souza, J.G., Simões, R.O., Thiengo, S.A., Lima, W.S., Mota, E.M., Rodrigues-Silva, R., Lanfredi, R.M., Maldonado Jr, A. (2009). A new metastrongilid species (Nematoda: Metastrongylidae): A lungworm from *Akodon montensis* (Rodentia: Sigmodontinae) in Brazil. *J Parasitol*. 95(6): 1507-1511.  
<https://doi.org/10.1645/GE-2013.1>  
PMid:19566346

102. del Rosario Robles, M., Navone, G.T., Kinsella, J.M. (2008). A new angiostrongylid (Nematoda) species from the pulmonary arteries of *Akodon azarac* (Rodentia: Cricetidae) in Argentina. *J Parasitol.* 94(2): 515-519.  
<https://doi.org/10.1645/GE-1340.1>  
PMid:18564753
103. Vieira, F.M., Muniz-Pereira, L.C., de Souza Lima, S., Neto, A.H., Guimarães, E.V., Luque, J.L. (2013). A new metastrongyloidean species (Nematoda) parasitizing pulmonary arteries of *Puma* (*Herpailurus*) *yagouaroundi* (É. Geoffroy, 1803) (Carnivora: Felidae) from Brazil. *J Parasitol.* 99(2): 327-331.  
<https://doi.org/10.1645/GE-3171.1>  
PMid:23016945
104. Vieira, F.M., Muniz-Pereira, L.C., Souza-Lima, S.D., Rocha, B.M., Luque, J.L. (2017). Parasitic nematodes of three species of wild carnivore mammals from Atlantic forest in the state of Minas Gerais, Brazil. *Rev Mex Biodiv.* 88(4): 801-806.  
<https://doi.org/10.1016/j.rmb.2017.10.033>
105. Almeida, L.R.D., Souza, J.G.R.D., Santos, H.A., Torres, E.J.L., Vilela, R.D.V., Cruz, O. M.S., Rodrigues, L., et al. (2020). *Angiostrongylus minasensis* n. sp.: new species found parasitizing coatis (*Nasua nasua*) in an urban protected area in Brazil. *Rev Bras Parasitol Vet.* 29(1): 018119.  
<https://doi.org/10.1590/s1984-29612019103>  
PMid:32049148
106. Tajima, F. (1993). Statistical analysis of DNA polymorphism. *Jpn J Genet.* 68(6): 567-595.  
<https://doi.org/10.1266/ggs.68.567>
107. Buckingham, L.J., Ashby, B. (2022). Coevolutionary theory of hosts and parasites. *J Evol Biol.* 35(2): 205-224.  
<https://doi.org/10.1111/jeb.13981>  
PMid:35030276 PMCid:PMC9305583
108. Jefferies, R., Shaw, S.E., Viney, M., Morgan, E.R. (2009). *Angiostrongylus vasorum* from South America and Europe represent distinct lineages. *Parasitol.* 136(1): 107-115.  
<https://doi.org/10.1017/S0031182008005258>  
PMid:19126274
109. Jefferies, R., Shaw, S.E., Willeßen, J.L., Viney, M., Morgan, E.R. (2010). Elucidating the spread of the emerging canid nematode *Angiostrongylus vasorum* between Palaearctic and Nearctic ecozones. *Infect Genet Evol.* 10(4): 561-568.  
<https://doi.org/10.1016/j.meegid.2010.01.013>  
PMid:20139034
110. Blouin, M.S. (2002). Molecular prospecting for cryptic species of nematodes: mitochondrial DNA versus internal transcribed spacer. *Int J Parasitol.* 32(5): 527-531.  
[https://doi.org/10.1016/S0020-7519\(01\)00357-5](https://doi.org/10.1016/S0020-7519(01)00357-5)  
PMid:11943225
111. Lange, M.K., Penagos-Tabares, F., Vélez, J., Gutiérrez, J., Hirzmann, J., Chaparro-Gutiérrez, J.J., Piedrahita, D., et al. (2018). Regional report on *Angiostrongylus vasorum* in Colombia: Genetic similarity to European lineage. *Vet Parasitol Reg Stud Reports.* 13, 21-23.  
<https://doi.org/10.1016/j.vprsr.2018.03.004>  
PMid:31014876
112. Mejías-Alpízar, M.J., Porras-Silesky, C., Rodríguez, E.J., Quesada, J., Alfaro-Segura, M.P., Robleto-Quesada, J., Gutiérrez, R., Rojas, A. (2024). Mitochondrial and ribosomal markers in the identification of nematodes of clinical and veterinary importance. *Parasit Vectors.* 17, 77.  
<https://doi.org/10.1186/s13071-023-06113-4>  
PMid:38378676 PMCid:PMC10880205
113. Blanch-Lázaro, B., Mitton, Z., Tudor, C., Hindle, J., Martineau, H., Fox, M., Blake, D.P. (2018). Genetic diversity and population structure of *Angiostrongylus vasorum* parasites within and between local urban foxes (*Vulpes Vulpes*). *Vet Parasitol.* 262, 42-46.  
<https://doi.org/10.1016/j.vetpar.2018.09.008>  
PMid:30389010
114. Tayyrov, A., Schnetzler, M., Gillis-Germitsch, N., Schnyder, M. (2021). Genetic diversity of the cardiopulmonary canid nematode *Angiostrongylus vasorum* within and between rural and urban fox populations. *Infect Genet Evol.* 87, 104618.  
<https://doi.org/10.1016/j.meegid.2020.104618>  
PMid:33188914
115. Trontelj, P., Fišer, C. (2009). Perspectives: cryptic species diversity should not be trivialised. *Syst Biodiver* 7(1): 1-3.  
<https://doi.org/10.1017/S1477200008002909>
116. Magurran, A.E. (1998). Population differentiation without speciation. *Phil Trans R Soc Lond B.* 353(1366): 275-286.  
<https://doi.org/10.1098/rstb.1998.0209>  
PMCid:PMC1692201