How to Cite: Suleimanova K.U., Zhabykpayeva A.G., Šarkūnas M., Balabayev B.K., Kubekova B.Zh. (2026). Modern studies on the biodiversity of *Sarcocystis* and their role in ecosystems. *Fundamental and Experimental Biology. 2026, 31, 2(122), 23-41.* https://doi.org/10.31489/2026FEB2/23-41

Review

https://doi.org/10.31489/2026FEB2/23-41

UDC 576.895.1:578.087.1:616-036.22 Received: 31.10.2025 | Accepted: 21.02.2026 | Published online: 30 June 2026

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Modern studies on the biodiversity of *Sarcocystis* and their role in ecosystems

The review summarizes current data on the biodiversity of parasites of the genus *Sarcocystis* and their significance for ecosystems, veterinary medicine, and public health. Sarcocystoses are considered diseases of pronounced veterinary and zoonotic importance, as they lead to reduced productivity in farm animals, deterioration of meat quality, and may cause pathological effects in humans. Information on the taxonomic and geographic diversity of representatives of the genus, the specificity of intermediate and definitive hosts, as well as the influence of environmental factors on parasite circulation has been analyzed. It is noted that the actual species diversity of *Sarcocystis* significantly exceeds the number of morphologically described forms, which is associated with the active implementation of molecular genetic identification methods. Modern diagnostic approaches are reviewed, including morphological and histological studies, as well as molecular methods using markers such as 18S rRNA, cox1, and ITS-1, which make it possible to clarify taxonomic boundaries, identify cryptic species, and analyze phylogenetic relationships. The need to integrate classical parasitological and molecular methods to improve diagnostic accuracy, enhance monitoring, and develop preventive measures is emphasized. It is concluded that an interdisciplinary approach combining parasitology, epizootology, ecology, and molecular biology is essential, as it provides a deeper understanding of the evolutionary relationships between parasite and host and forms a scientific basis for the effective control and prevention of zoonotic sarcocystosis.

Keywords: Sarcocystis, biodiversity, ecology, parasites, morphology, molecular identification, zoonoses, bioindicators.

Introduction

Sarcocystosis is one of the most widespread protozoan infections affecting domestic and wild animals, as well as humans. The causative agents belong to the genus *Sarcocystis* (phylum *Apicomplexa*), which is characterized by a complex life cycle involving obligatory alternation of intermediate and definitive hosts [1–3]. The disease has both veterinary and zoonotic significance, as certain species, such as *S. hominis* and *S. suihominis*, are capable of infecting humans [4–7]. In recent decades, the study of sarcocystosis has acquired an interdisciplinary character, encompassing parasitology, molecular biology, epizootology, and ecology.

The relevance of studying the biodiversity of *Sarcocystis* is determined by its high prevalence, its significant role in animal population dynamics, and its potential use as a bioindicator of ecosystem health. Modern research approaches make it possible not only to refine the taxonomic structure of the genus but also to reveal new aspects of the impact of these parasites on the biosphere [8].

Recent advances in molecular characterization have revolutionized the identification of *Sarcocystis* species, overcoming the limitations of traditional morphological methods. Although morphological features, such as cyst wall structure, have historically been used for diagnosis, they often fail to reliably differentiate closely related species [9, 10]. Molecular genetic methods employing markers such as 18S rRNA, 28S rRNA, ITS-1, and mitochondrial cytochrome c oxidase subunit I (cox1) have become essential for taxonomic identification [11]. The cox1 gene has emerged as a particularly promising DNA barcode marker, demonstrating superior efficiency in discriminating closely related species compared to ssrRNA genes, with intraspecific sequence identity of 98.5–100 % and interspecific identity of 58–92 % [12]. These molecular diagnostic approaches have proven to be more time- and cost-effective than electron microscopy and have helped overcome the limited sensitivity of serological methods [10]. Phylogenetic analyses using these markers

have shown that some previously recognized species may represent distinct taxa with specific host ranges [7].

The aim of this review study is to analyze diagnostic methods, systematize and evaluate current approaches to the identification of the genus *Sarcocystis* in animals and humans, and determine their role in understanding the biodiversity and eco-epidemiological significance of these parasites.

This review provides a scientific basis for further investigation of sarcocystosis as a complex biological phenomenon integrating morphological, molecular-genetic, ecological, and veterinary-medical aspects. The data summarized in the review highlight directions for improving diagnostics through the combined use of classical and molecular methods, as well as for developing approaches to the prevention and control of zoonotic forms of the disease.

Experimental

Review method. This review was conducted based on a structured analysis of the scientific literature related to protozoa of the genus *Sarcocystis* Lankester, 1882. Relevant publications were identified through the academic databases Web of Science, Scopus, and RINC, including articles published. The literature search was performed using the following keywords: *Sarcocystis*, biodiversity, molecular identification, parasite ecology, and zoonotic infections. Particular attention was given to studies reporting the application of molecular genetic methods (18S rRNA, cox1, ITS-1, and other markers), as well as to data concerning the role of sarcocysts in biocenoses.

Literature sources. The present review is based on the analysis of 62 scientific sources, including a limited number of studies conducted in Kazakhstan, as well as publications devoted to the investigation of sarcocystosis in countries of the Eurasian region. The genus *Sarcocystis* is characterized by exceptional biodiversity and a complex system of host–parasite interactions, which determines the sustained scientific interest and ongoing research activity in this field. Current evidence indicates that the actual number of species considerably exceeds the number of forms described on the basis of morphological characteristics [7]. This discrepancy is largely explained by the broad specificity of definitive hosts and, conversely, the relatively narrow specificity of intermediate hosts, which together create a rich mosaic of species diversity.

Results and Discussion

The genus *Sarcocystis* is characterized by an exceptionally high level of biodiversity and represents one of the most species-rich groups of protozoan parasites among apicomplexan organisms. Members of this genus are obligate intracellular parasites infecting mammals, birds, and reptiles worldwide. Some *Sarcocystis* species have pronounced pathogenic and zoonotic significance for both animals and humans [2, 13].

The combination of an obligatory two-host life cycle, high ecological plasticity, and varying degrees of host specificity contributes to the formation of a complex and mosaic biodiversity structure within this genus. Sarcocystosis is a parasitic disease caused by intracellular protozoan parasites of the genus *Sarcocystis* (phylum *Apicomplexa*, order *Coccidiida*, family *Sarcocystidae*), which is characterized by a complex and, in many aspects, still incompletely resolved taxonomy. The life cycle of these parasites involves an obligate alternation between an intermediate host, typically a herbivorous or omnivorous animal, and a definitive host, usually a carnivorous or omnivorous species [14]. Currently, more than 220 species of *Sarcocystis* have been described, although the complete life cycle has been established only for a limited number of species associated with specific host pairs [2, 15].

Numerous *Sarcocystis* species have been recorded in cattle, each exhibiting distinctive life-cycle characteristics and host associations. The most common and well-studied species include *Sarcocystis cruzi* Hasselmann, 1923 (syn. *S. bovicanis*), with canids as definitive hosts, and *Sarcocystis bovifelis* Hu, Liu, Li, Zhang, Chen, 2017, with felids serving as definitive hosts. In addition, *Sarcocystis hominis* Railliet, 1891 and *Sarcocystis heydorni* Dubey, Fayer, Rosenthal, 2002 have been identified in cattle and are considered zoonotic, as humans may act as definitive hosts following the consumption of infected meat [15]. The presence of these species underscores the importance of sarcocystosis in veterinary sanitary control and food safety systems. Other reported species include *Sarcocystis hirsuta* Railliet, 1886, *Sarcocystis bovifelis*, *Sarcocystis bovini* Blanchard, 1885 and others, reflecting the complex species structure of sarcocysts in this animal group [16].

Sheep and goats are also hosts to multiple Sarcocystis species *Sarcocystis*. *tenella* Railliet, 1886 and *Sarcocystis arieticanis* Heydorn, 1975, whereas in goats *Sarcocystis capracanis* Heydorn, 1975 and *Sarcocystis moulei* Levine, 1986 are commonly identified [17]. These species exhibit a high degree of host

specificity and participate in life cycles involving carnivores, such as dogs and cats, as definitive hosts [18]. In contrast to bovine sarcocysts, the zoonotic potential of *Sarcocystis* species identified in sheep and goats is considered limited [19]. Nevertheless, the high prevalence of infection and pronounced tissue localization of sarcocysts make these species important targets for veterinary surveillance and population monitoring in small ruminants.

Recent molecular-genetic studies have demonstrated that even in sheep and goats, whose *Sarcocystis* species composition is considered relatively well characterized, the existence of cryptic species remains likely. This finding highlights the necessity of applying integrative approaches to clarify the true biodiversity of sarcocysts in small ruminants.

Pigs and wild boars serve as intermediate hosts for species such as *Sarcocystis miescheriana* Miescher, 1843 and *Sarcocystis suihominis* Railliet & Lucet, 1891, with the latter regarded as zoonotic because humans may act as definitive hosts after consuming insufficiently cooked pork. Molecular studies have confirmed the presence of these species in the musculature of domestic pigs and wild boars, emphasizing the importance of veterinary sanitary inspection of meat products [20].

Horses serve as intermediate hosts for a relatively limited number of *Sarcocystis* species, in contrast to cattle and small ruminants, which exhibit greater species diversity. The best known and most widespread species associated with horses is *Sarcocystis bertrami* Doflein, 1901 (syn. *S. fayeri*), for which dogs and other canids serve as definitive hosts [20]. Epizootiologically, equine sarcocystosis is closely linked to the presence of dogs, which play a key role in maintaining parasite circulation. Contamination of feed and water with sporocysts shed by definitive hosts is considered the primary route of infection in both agricultural and private farming systems. Although infections are typically subclinical, clinical manifestations, including muscle weakness, reduced performance, and inflammatory changes, may occasionally occur, which is particularly relevant for sport and breeding horses. Specific *Sarcocystis* species have also been described in camels, llamas, and other herbivores, reflecting the parasite's broad adaptive capacity across ecosystems and host networks [21].

A considerable diversity of *Sarcocystis* species has been reported in birds, and for several species the complete life cycle has been elucidated or widespread occurrence documented. Examples include *Sarcocystis falcatula* Stiles, 1893, *Sarcocystis calchasi* Olias, Gruber, Hafez, Heydorn & Mehlhorn, 2009, *Sarcocystis halieti* Prakas, Butkauskas, 2012, and *Sarcocystis wobeseri* Prakas, Butkauskas, Švažas & Juozaitytė-Ngugu, 2014, which infect various avian intermediate hosts, while raptors and other carnivorous species serve as definitive hosts [22]. Studies demonstrate a high species richness of *Sarcocystis* in the musculature of gulls and other birds, as well as substantial intraspecific genetic variability, underscoring the complexity of parasite biodiversity in avifauna.

From an ecological perspective, birds play a crucial role in the dissemination of *Sarcocystis* across large geographic areas, including migratory routes, thereby contributing to parasite circulation in diverse ecosystems. Migration facilitates the transfer of genetically distinct *Sarcocystis* lineages between regions and promotes the formation of complex spatial population structures.

In addition to mammals and birds, *Sarcocystis* species have been recorded in reptiles and other vertebrate groups, further expanding the taxonomic range of this parasite within global fauna [23].

In humans, zoonotic species *Sarcocystis hominis* Railliet & Lucet, 1891 and *Sarcocystis suihominis* Railliet & Lucet, 1891 have been documented, with humans acting as definitive hosts after consuming infected beef or pork, respectively [13]. Clinical manifestations of intestinal sarcocystosis in humans are generally rare and associated with foodborne transmission; however, confirmed cases of muscular sarcocystosis, in which humans serve as intermediate hosts, have been reported only sporadically due to both low detection rates and diagnostic challenges. Current evidence suggests the possible involvement of additional, incompletely characterized *Sarcocystis* species, highlighting the need for further molecular investigations.

The high species diversity of *Sarcocystis* and the complexity of host–parasite interactions make this genus an attractive subject for epizootiological, taxonomic, and molecular studies. In particular, molecular approaches, including analyses of ITS1, cox1, and other genetic markers, have facilitated the detection of hidden species diversity, refinement of phylogenetic relationships, and clarification of host specificity patterns within *Sarcocystis spp.*

A summary of the principal *Sarcocystis* species, their hosts, morphological characteristics, and diagnostic methods is presented in Table 1.

Table 1

Main Sarcocystis species in animals, their morphological characteristics, significance, and diagnostic methods

Intermediate host	*Sarcocystis* species	Cyst morphology / wall structure	Significance	Diagnostic methods
Cattle	*S. cruzi*, *S. hirsuta*, *S. hominis*	Thin-walled (*S. cruzi*); thick-walled with finger-like protrusions (*S. hirsuta*)	Animal pathology, human infection risk	Histology, PCR (cox1, 18S rRNA), sequencing
Sheep	*S. tenella*, *S. arieticanis*	Differences in wall thickness	Economic losses, reduced meat quality	Light microscopy, PCR identification
Goats	*S. capracanis*, *S. moulei*	Differences in cyst wall capsule	Pathology, reduced productivity	Microscopy, molecular markers (ITS-1)
Pigs	*S. miescheriana*, *S. suihominis*	*S. suihominis* — thick-walled cysts, zoonotic importance	Human health risk (*S. suihominis*)	Histology, PCR, immunohistochemistry
Domestic birds (ducks, geese)	*Sarcocystis rileyi* Stiles, 1893, *Sarcocystis wobeseri* Prakas, Butkauskas, Švažas & Juozaitytė-Ngugu, 2014	Ducks — multiple cysts in muscles (*S. rileyi*); geese — thin-walled (*S. wobeseri*)	Mass infections in wild and domestic birds	Morphology, PCR (cox1), molecular phylogeny
Wild birds	*Sarcocystis halieti* Prakas & Butkauskas, 2012, *Sarcocystis columbae* Blanchard, 1885	High morphological diversity, narrow host specificity	Important role in biocenoses	PCR, sequencing, marker comparison (18S, ITS-1)
Humans (intermediate host)	*S. hominis*, *S. suihominis*	Thick-walled cysts in muscles	Zoonotic hazard, foodborne infections	Biopsy, histology, molecular methods

The data presented in Table 1 summarize the species diversity of Sarcocystis, their host specificity, and diagnostic approaches, highlighting the complexity of host–parasite relationships and providing a basis for analyzing the role of these parasites in ecosystem functioning [11].

Life cycle

Parasites of the genus Sarcocystis require a two-host life cycle with distinct developmental stages occurring in definitive and intermediate hosts, including both sexual and asexual reproduction. In intermediate hosts, only asexual stages of the parasite are present. However, in humans the life cycle may vary: they can act as definitive hosts for certain species, such as Sarcocystis hominis (associated with beef consumption) and S. suihominis (associated with pork consumption), resulting in intestinal infection (Fig. 1), or as intermediate hosts for other species, for example S. nesbitti.

Sarcocystis nesbitti has been identified in humans and non-human primates serving as intermediate hosts, while snakes are presumed to act as definitive hosts. However, this identification is based primarily on phylogenetic comparisons with related species in which snakes were confirmed definitive hosts, and definitive evidence of the complete life cycle has not yet been fully established [6].

In the typical life cycle, definitive hosts become infected by ingesting tissues of intermediate hosts containing mature sarcocysts. Sexual development of the parasite occurs in the intestinal epithelium of the definitive host, resulting in the formation of oocysts that sporulate and release sporocysts, which are shed with feces into the environment. Intermediate hosts acquire infection through ingestion of food or water contaminated with sporocysts. Following invasion, sporozoites undergo a series of asexual developmental stages, including merogony within vascular endothelial cells, before forming tissue cysts (sarcocysts) primarily in skeletal muscles, myocardium, and occasionally in other organs.

The ecological success of Sarcocystis is largely attributed to this obligate predator–prey transmission pattern, which facilitates efficient circulation of the parasite within food webs. This life-cycle strategy con-

tributes to the widespread distribution of Sarcocystis species and their ability to persist across diverse ecosystems and host communities.

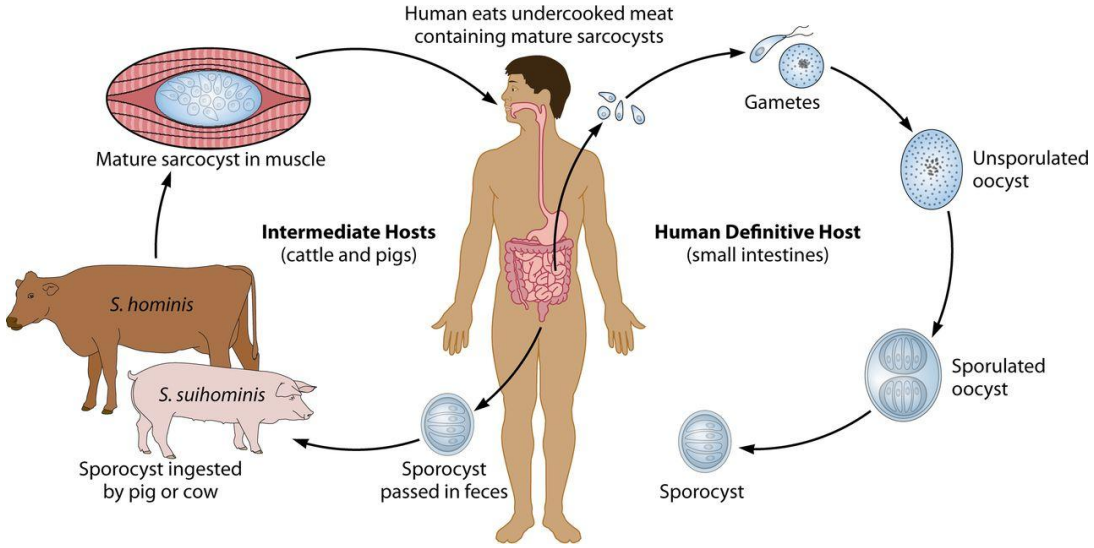

Figure 1. Life cycle of *Sarcocystis* **(**Fayer R., 2015**)**

In bovines, the biological life cycle involves carnivores, such as dogs, acting as definitive hosts, while cattle serve as intermediate hosts [24]. The cycle includes three key stages: schizogony (asexual reproduction in intermediate hosts), and gametogony and sporogony (sexual stages occurring in definitive hosts) [25].

After ingestion of sporocysts or oocysts shed in the feces of definitive hosts, digestive enzymes and bile salts in cattle disrupt the sporocyst wall, releasing four motile sporozoites. These penetrate the intestinal wall and disseminate throughout the body, initially localizing within endothelial cells of small arteries. This is followed by a series of successive cycles of asexual multiplication (merogony or schizogony), the number and timing of which vary depending on the species. During early cycles, crescent-shaped merozoites are formed, structurally similar to sporozoites. Subsequent generations are detected in arterioles, capillaries, and veins of various organs. The final stage of merogony results in the invasion of motile, crescent-shaped merozoites into skeletal, cardiac, and smooth muscle cells, and less frequently into nervous tissue, where sarcocyst formation begins [6].

At early stages within muscle cells, a metrocyte (mother cell) develops, undergoing repeated divisions that ensure cyst growth and formation of a protective wall isolating the parasite from surrounding tissues. As maturation progresses, metrocytes differentiate into bradyzoites (cystozoites), and the sarcocyst becomes infective to the definitive host. Maturation may require two months or longer, and sarcocysts can persist in host tissues for years. They vary considerably in size, shape, and ultrastructural characteristics of the cyst wall, including thickness and the presence of peripheral protrusions (cytophaneres), which have important taxonomic value. Internal structures may include septa dividing the cyst cavity into compartments. Sarcocysts are most commonly localized in skeletal muscles, myocardium, diaphragm, tongue, and esophagus, and more rarely in structures of the central nervous system [13].

This life-cycle pattern is largely universal for the genus and reflects the typical endogenous development characteristic primarily of vascular species (e.g., *S. cruzi*, *S. tenella*), although localization and timing of schizogony may vary among other representatives of the genus [6].

The sexual phase of the *Sarcocystis* life cycle occurs in the definitive host following ingestion of meat containing mature sarcocysts. Digestive processes disrupt the cyst wall, releasing bradyzoites that invade epithelial cells of the small intestinal villi. Here they differentiate into gamonts: microgamonts (male forms) and macrogamonts (female forms). Multiple divisions of microgamonts produce motile microgametes, one of which fertilizes a macrogamont to form an oocyst. Sporulation occurs within the intestine, resulting in the formation of two sporocysts, each containing four sporozoites. Oocysts, or more commonly liberated sporocysts, are excreted with feces into the environment. Sporocysts of most species are morphologically similar, oval in shape, approximately 10 × 15 μm in size, and contain four sporozoites and residual granules. In zoonotic species such as *S. hominis* and *S. suihominis*, sporocysts are immediately infective upon excre-

tion. The sexual phase of the life cycle is the most conserved developmental stage among representatives of the genus *Sarcocystis* and proceeds according to a similar pattern in most species [6].

Distribution of sarcocystosis

The distribution of parasites, including *Sarcocystis*, is closely associated with climatic conditions and anthropogenic landscape transformation. Because the life cycle of *Sarcocystis* depends on interactions between intermediate and definitive hosts and their contact with environmental reservoirs such as feed and water sources, climate change—including rising temperatures and extreme weather events—may alter epidemiological patterns and transmission pathways. Studies of other complex parasitic systems indicate that climatic shifts contribute to range expansion and increase contact opportunities among host species, potentially facilitating the wider spread of zoonotic infections [26].

Anthropogenic factors, such as land-use changes, agricultural intensification, urbanization, and ecosystem disturbance, further enhance interactions between wild and domestic species, thereby promoting parasite transmission and the emergence of epizootic and zoonotic foci. Evidence suggests that habitat alteration and biodiversity loss may increase parasite transmission among host populations and represent risk factors for the emergence of new outbreaks [26].

Agricultural practices, including livestock management, sanitary conditions, and interactions between carnivorous and herbivorous animals, also significantly influence the epidemiology of *Sarcocystis* transmission, determining the degree of parasite circulation within populations and the risk of zoonotic outbreaks through food chains [27].

Globally, *Sarcocystis* species occur from temperate to tropical regions, with distribution patterns largely determined by host ranges and migratory movements (Table 2). For example, *S. rileyi* is widely distributed among northern waterfowl in North America and Northern Europe, whereas *S. cruzi* and *S. hominis* predominate among domestic ruminants in Asia and South America. These geographic patterns reflect host ecology and may even serve as indicators of wildlife migration routes [14, 28, 29].

Table 2

Global distribution and prevalence of sarcocystosis in domestic and wild animals

Host species	Region / Country	Prevalence (%)	Dominant / identified species	Notes on distribution & epidemiology	References
Cattle	Global (21 countries, meta-analysis)	62.7 %	*S. cruzi* (76.4 %), *S. hominis* (30.2 %), *S. hirsuta* (8.7 %)	Cosmopolitan; higher in extensive systems; zoonotic relevance (S. hominis)	[6, 14]
Cattle	Asia (various countries)	50–90 %	*S. cruzi predominant*	High prevalence in warm-temperate zones; linked to dog–cattle cycle	[30]
Cattle	Kazakhstan (Kostanay, North)	up to 77.4 % (cox1 PCR)	*S. cruzi*, *S. bovifelis*, *S. dehongensis*	Molecular confirmation; high carcass infection rate	[31, 32]
Sheep	China	33.85 %	*S. tenella*, *S. arieticanis*	Associated with production losses	[33]
Sheep	Kazakhstan (East)	~18 % (macrocysts)	*Sarcocystis* spp.	Macroscopic cysts; need for monitoring	[34]
Pigs	Europe, Asia, Americas	15–45 %	*S. miescheriana*, *S. suihominis*	Influenced by management system	[35]
Horses	Europe, Central Asia	>50 % (regional data)	*Sarcocystis* spp.	Muscle alterations; meat inspection relevance	[36]
Waterfowl (Anseriformes)	North America	Variable; local outbreaks	*S. rileyi*	Mass epizootics; linked to migratory flyways	[14]
Waterfowl	Northern Europe	Local epizootics	*S. rileyi*	Expanding range; climate-linked spread	[14]
Passerines & raptors	Europe, Asia	Not population-based; multiple species	>40 avian spp.	High host specificity; molecular identification expanding diversity	[23, 25]

Continuation of Table 2

Host species	Region / Country	Prevalence (%)	Dominant / identified species	Notes on distribution & epidemiology	References
Game fauna (wild mammals)	Lithuania	8 species identified	*S. albifronsi*, *S. wobeseri*, *S. anasi*, *S. cornixi*, others	First European record of S. rileyi in wildlife	[14, 37, 38]
Sika deer	Japan	7 species	*S. japonica*, *S. matsuoae*, *S. gjerdei*, *S. pilosa*, *S. ovalis*	High diversity; molecular taxonomy	[39]
Farmed sika deer	Lithuania	5 species	*S. frondea*, *S. nipponi* + 3 known spp.	Demonstrates spillover between wild and farmed systems	[40]
Deer (general)	Europe, Asia	≥9 spp.	Multiple	Indicator of wildlife biodiversity and molecular detection capacity	[41]
Humans	Europe, Asia, Americas, Africa (sporadic reports worldwide)	Intestinal form: usually low (<10 % in surveyed populations); Muscular form: rare (<100 documented cases worldwide)	*S. hominis*, *S. suihominis*	Occurs globally; intestinal infection acquired through consumption of raw or undercooked beef or pork; often asymptomatic or mild gastrointestinal symptoms; muscular sarcocystosis reported mainly in Southeast Asia and travelers; zoonotic significance	[42, 43]

Sarcocystosis is widely prevalent among livestock worldwide. A global meta-analysis across 21 countries reported a prevalence of 62.7 % in cattle, with *S. cruzi* (76.4 %), *S. hominis* (30.2 %), and *S. hirsuta* (8.7 %) being the most common species [14]. In birds, biodiversity is even greater, with more than 40 described species, many exhibiting strict host specificity [23, 30, 44]. Of particular importance is *S. rileyi*, responsible for mass outbreaks among waterfowl in Europe and North America. Recent molecular studies have also identified new species in passerine and raptorial birds [1, 25].

In sheep, prevalence may reach approximately 33.85 % in certain regions of China, particularly involving *S. tenella* and *S. arieticanis*, emphasizing the importance of infection control to prevent production losses [33]. In pigs, infection rates range from 15 % to 45 % across different production systems, indicating widespread transmission dynamics [35]. Overall, *Sarcocystis* exhibits a cosmopolitan distribution, occurring in nearly all regions where livestock production is practiced. Its prevalence is strongly influenced by ecological and management factors, including the presence of definitive hosts, husbandry systems, sanitary practices, and food sources [33].

Recent studies have documented considerable *Sarcocystis* diversity in wild mammals across different geographic regions. In Lithuania, comprehensive surveys of game fauna identified eight *Sarcocystis* species, including the first European records of *S. rileyi* and newly described species such as *S. albifronsi*, *S. wobeseri*, *S. anasi*, and *S. cornixi* [14, 37-38]. Studies of sika deer in Japan revealed seven species, including three newly described taxa (*S. japonica*, *S. matsuoae*, and *S. gjerdei*), alongside previously known species such as *S. pilosa* and *S. ovalis* [39]. Similarly, investigations of farmed sika deer in Lithuania identified two new species (*S. frondea* and *S. nipponi*) in addition to three previously recognized taxa [40]. These findings demonstrate that deer alone may harbor at least nine distinct *Sarcocystis* species, highlighting the remarkable diversity of these parasites in wild mammalian hosts and the crucial role of molecular methods in their discovery [1, 41].

In Kazakhstan, sarcocystosis is widespread among livestock, as confirmed by both classical and molecular studies. Investigations of cattle in the Kostanay region revealed a high prevalence of sarcocysts consistent with *Sarcocystis bovicanis* (syn. *S. cruzi*) and other species, indicating extensive regional distribution [31]. Molecular analyses based on the cox1 gene demonstrated infection rates reaching approximately 77.4 % of examined carcasses, with three species (*S. cruzi*, *S. bovifelis*, and *S. dehongensis*) identified in northern Kazakhstan [32]. Sarcocystosis has also been confirmed in horses, with studies in northern regions reporting infection in more than half of examined animals, accompanied by notable muscular tissue altera-

tions relevant to meat quality and veterinary surveillance [36]. In sheep from eastern Kazakhstan, macrocysts of *Sarcocystis* spp. were detected in approximately 18 % of examined animals, underscoring the need for continuous monitoring and diagnostic efforts [34].

Human sarcocystosis is reported in many regions of the world, including Europe, Asia, North and South America, and Africa. However, the prevalence of the disease varies significantly depending on the form of infection, sanitary conditions, and dietary habits of the population [6, 14, 42-43]. The intestinal sarcocystosis form is found in Europe, Asia, Africa, North and South America, indicating its global distribution, especially in areas where raw meat is consumed or proper heat treatment is lacking. The muscular form, although rare, is most commonly reported in tropical and subtropical regions, especially in areas where potential definitive hosts (e.g., reptiles) are present, such as Southeast Asia. Cases of muscular sarcocystosis have also been reported in travellers, making the epidemiology of the disease worldwide, but with high-frequency foci in certain climatic and environmental conditions [6].

Clinical signs of sarcocystosis in animals

Sarcocystosis in animals is characterized by a wide spectrum of clinical manifestations, ranging from asymptomatic infections to severe systemic disorders, depending on the stage of invasion, host species, infection intensity, and parasite localization. Many chronic cases remain undetected without laboratory or pathological examination, increasing the significance of subclinical pathology in the epidemiology of the disease.

The intestinal sarcocystosis form occurs in humans as the final host when consuming meat containing mature sarcocysts: Humans serve as the definitive host for Sarcocystis hominis, which is associated with the consumption of raw or undercooked beef, and for Sarcocystis suihominis, which is associated with raw or undercooked pork. This form occurs worldwide, although clinical manifestations are usually mild (nausea, abdominal pain, diarrhoea) and often go unnoticed in standard diagnostics. Intestinal cases have been reported in Europe (e.g., Germany, the Netherlands, Poland), Asia (China, Thailand, Laos), Australia, South America, and other regions, indicating widespread global distribution even with rare detection of the disease. In epidemiological studies of sarcocystosis in developing countries, infections have been recorded even in poor hygienic conditions, for example, in some communities in Australia. The infection can be detected in faeces in the form of sporocysts or oocysts after consumption of contaminated meat, and although most cases remain clinically insignificant, outbreaks and cases with significant symptoms have been reported among volunteers and in conditions of natural infection [6].

The muscular form of sarcocystosis is much less common in humans, but it is more serious in terms of clinical manifestations: Less than 100 reliably confirmed cases of muscular sarcocystosis have been described in the literature, making it a rare but significant disease. Most of these cases are associated with tropical regions, especially in Southeast Asia (e.g., Malaysia), where cases have been repeatedly reported in tourists and local residents. In this form, humans act as intermediate hosts for species other than S. hominis and S. suihominis (e.g., Sarcocystis nesbitti with a possible reptilian definitive host). Infection occurs when sporocysts are ingested, most likely from contaminated food or water, allowing the parasite to develop first in the vascular endothelium and then in muscle tissue. Clinical symptoms of the muscular form include fever, myalgia, headaches, eosinophilia, and weakness, and diagnosis usually requires a muscle biopsy to detect sarcocysts [6, 14].

In cattle, sarcocystosis most often proceeds asymptomatically or with mild clinical signs, particularly during the chronic muscular stage. However, under conditions of high parasite burden or during the acute phase, clinical manifestations may include weakness, anorexia, reduced productivity, and depression. Anemia, emaciation, and progressive cachexia may also develop, especially in young animals [21]. Experimental infections have demonstrated fever, lethargy, tachycardia, and, in some cases, abortion [45]. These manifestations are frequently masked by concurrent infections, complicating diagnosis and leading to underestimation of the clinical impact of sarcocystosis on herd health.

In addition, cattle may develop sarcocystosis-associated inflammatory lesions of skeletal muscles, known as bovine eosinophilic myositis (BEM). Affected animals often appear clinically normal during life, but muscle lesions are detected at slaughter, resulting in carcass condemnation and substantial economic losses due to reduced meat quality and productivity [46].

In small ruminants and carnivorous animals, sarcocystosis is generally asymptomatic or subclinical, particularly in cases of mild to moderate infection. In sheep and goats, severe infections may lead to systemic disturbances, including general weakness, anemia, decreased appetite, and progressive weight loss, while in severe cases neurological disorders and abortions may occur [33-34]. In pigs, heavy parasite loads are asso-

ciated with lameness, generalized weakness, and inflammatory lesions of cardiac and skeletal muscles, such as endocarditis and myocarditis, leading to deterioration in overall condition and reduced productivity [47].

In dogs, sarcocystosis is typically asymptomatic, especially in the intestinal form. However, in young animals with high infection intensity, nonspecific signs such as digestive disturbances, reduced appetite, and growth retardation may occur [48]. The muscular form of sarcocystosis in dogs is considerably less common but may be accompanied by myositis, generalized weakness, and muscle pain, significantly complicating clinical presentation and requiring differential diagnosis from other myopathies [49].

In other host species, including camels, rodents, and birds, sarcocysts often result in subclinical infections but may adversely affect animal health in cases of heavy infestation. Experimental studies in small vertebrates have reported weakness, emaciation, and severe pathological effects on vital organs at high infection intensities [50].

One of the characteristic features of sarcocystosis is its frequently asymptomatic course, particularly during the chronic muscular stage. This latent pathology is largely attributable to the deep localization of sarcocysts within muscle tissue, where they do not initially cause overt pain or clinical symptoms. Nevertheless, parasites may produce toxic metabolites, such as sarcocystin, which exert both mechanical and toxic effects on host tissues, ultimately leading to metabolic disturbances and reduced animal productivity [51].

Chronic infection may also be associated with mild myositis, destruction of muscle fibers, and lymphohistiocytic infiltration, changes that are often detectable only through histological examination, even when animals appear clinically healthy [51].

Such subclinical forms present a significant epizootiological challenge, as infected animals may serve as reservoirs for parasite transmission, maintaining infection cycles and increasing the risk of zoonotic spread while remaining undetected in livestock production systems and slaughter facilities.

Diagnostic approaches to sarcocystosis

Diagnosis of sarcocystosis in livestock represents a complex task requiring the integration of morphological, microscopic, serological, and molecular methods, as no single approach provides sufficient sensitivity and specificity when used in isolation. Diagnostic challenges arise from the wide host range, variable clinical manifestations, and morphological similarities among *Sarcocystis* species. In modern practice, complementary methods are applied to improve diagnostic accuracy and informativeness in both animal and human investigations.

Macroscopic, microscopic, and histological methods

Macroscopic examination is based on visual inspection of muscle tissues and internal organs for cysts visible to the naked eye (macrocysts). These cysts may reach several millimeters in size and are most commonly detected in striated muscles, the diaphragm, and myocardium during necropsy or postmortem meat inspection. Although macroscopic evaluation remains a fundamental step in diagnostic assessment, it frequently fails to detect smaller microscopic cysts.

Microscopic examination includes light microscopy and the tissue compression method, in which muscle samples are pressed between glass slides and examined under magnification to detect sarcocysts. This method allows visualization of characteristic banana-shaped bradyzoites within cysts; however, it does not reliably determine species identity without additional diagnostic techniques [34].

Histological methods involve tissue fixation, paraffin embedding, sectioning, and staining (e.g., hematoxylin–eosin, Mallory's stain). Histology enables visualization of cyst wall structure, localization within muscle fibers, inflammatory responses, and parasite morphology at the cellular level. Nevertheless, morphologically similar cyst wall structures among closely related *Sarcocystis* species often prevent accurate species identification, particularly in the absence of electron microscopy.

Serological tests (ELISA, IFAT)

Serological methods aim to detect circulating antibodies against *Sarcocystis* antigens in live animals and humans. The most widely used techniques include:

ELISA (enzyme-linked immunosorbent assay)—enables detection of specific antibodies in serum samples. ELISA has demonstrated higher sensitivity compared with visual and microscopic methods alone, significantly increasing detection rates in cattle by identifying antibodies even in cases of subclinical microscopic infection [52].

IFAT (indirect fluorescent antibody test)—visualizes antigen–antibody binding using fluorescent labeling. Comparative studies indicate that IFAT exhibits sensitivity comparable to ELISA in detecting antibodies against *Sarcocystis* spp.; however, it requires specialized fluorescence microscopy for result interpretation [53].

Serological methods have several limitations, including potential cross-reactivity with antigens of other apicomplexan parasites, poor correlation between antibody titers and infection severity or stage, and the inability to determine species identity [53].

Modern molecular methods

Molecular techniques provide high sensitivity and specificity, enabling not only parasite detection but also accurate species identification.

PCR (polymerase chain reaction)—a fundamental method for amplifying specific *Sarcocystis* DNA regions, commonly targeting 18S rRNA or cox1 genes. PCR can detect parasite DNA even at low infection intensities and in tissue samples such as meat or muscle biopsies [54-55].

PCR–RFLP (restriction fragment length polymorphism)—extends PCR by incorporating enzymatic digestion of amplified fragments to detect species-specific genetic variations, making it useful for epidemiological studies and species differentiation [56].

LAMP (loop-mediated isothermal amplification)—an alternative molecular technique characterized by high sensitivity and rapid visual detection without the need for thermal cycling. In *Sarcocystis* diagnostics, LAMP has demonstrated greater sensitivity than conventional PCR for detecting *S. tenella* and *S. gigantea* infections in sheep [57].

NGS (next-generation sequencing)—enables parallel sequencing of multiple genetic regions, facilitating comprehensive genetic analysis, discovery of novel species, and construction of phylogenetic relationships. Although highly informative, NGS requires advanced laboratory infrastructure and bioinformatic processing.

Each diagnostic approach possesses specific strengths and limitations, and their combined application is considered the most effective strategy for accurate detection and identification of *Sarcocystis* infections. A comparative overview of sensitivity and specificity among these methods is presented in Table 3.

Table 3

Comparison of sensitivity and specificity of diagnostic methods for sarcocystosis

Method	Sensitivity	Specificity	Limitations
Macroscopy	Low for microcysts	Moderate	Does not detect microscopic cysts
Microscopy	Moderate	Moderate	Depends on operator experience
Histology	Moderate–high	Moderate	Not always species-specific
ELISA	High relative to visual methods	Moderate	Antibodies may persist
IFAT	High	Moderate	Requires a fluorescence microscope
PCR	High	High	Requires specific primers
PCR–RFLP	High	Very high	Requires restriction enzymes
LAMP	Very high	High	Relatively new method, requires standardization
NGS	Very high	Very high	Expensive; complex data processing

Molecular methods, particularly PCR–RFLP and LAMP, demonstrate higher sensitivity and greater ability to detect low-intensity infections compared with traditional morphological and serological approaches and are therefore preferred for epidemiological studies [58].

To improve diagnostic accuracy for sarcocystosis, the combined use of multiple methods has proven especially effective. The combination of morphological examination and ELISA—visual and microscopic inspection of muscle tissues for preliminary detection supplemented by ELISA to identify seropositive animals—significantly increases detection rates compared with the use of a single method alone [53].

Similarly, the integration of microscopy and PCR–RFLP enhances diagnostic precision: microscopic detection of cysts followed by molecular species identification improves the accuracy of species determination and supports epidemiological investigations, as demonstrated in studies of cardiac muscle infections in cattle [56].

The combined use of PCR and LAMP also provides advantages; LAMP can serve as a rapid screening tool, while PCR can be used to confirm results, ensuring high sensitivity while reducing time and costs.

Research on the genus Sarcocystis continues to evolve, encompassing novel molecular approaches, genomics, the development of preventive and therapeutic measures, and the application of parasites in environmental monitoring. These directions are closely linked to veterinary medicine, epidemiology, food safety, and the One Health framework, which integrates animal, human, and environmental health.

Future perspectives in sarcocystosis research

One of the key challenges in modern parasitology is the expansion of molecular marker sets for accurate identification of Sarcocystis species and assessment of their phylogenetic relationships. Traditionally, 18S rRNA regions and the mitochondrial cox1 gene have been widely used and have demonstrated high sensitivity and specificity in taxonomic identification [59-60]. However, distinguishing closely related lineages and assessing intraspecific diversity requires the development of additional genetic markers, including microsatellite loci, SNP panels, and mitochondrial genomes. These approaches will facilitate clarification of transmission pathways, infection sources, and evolutionary patterns of the parasite.

The emergence of whole-genome sequencing (WGS) and comparative genomic analyses among Sarcocystis species offers new opportunities for investigating molecular structure, adaptive mechanisms, and genetic resilience of the parasite. Genomic approaches enable the identification of genes involved in invasiveness, virulence, and survival across diverse host species, thereby significantly expanding understanding of Sarcocystis biology at the molecular level [61].

Recent studies indicate that parasites, including Sarcocystis, can serve as bioindicators of ecosystem health. Environmental sampling—of water, soil, and feed—combined with molecular detection methods allows identification of sporocysts and zoonotic species without direct tissue sampling from animals. Pilot studies have reported detection of Sarcocystis in water, hay, and soil, emphasizing the importance of environmental monitoring for assessing infection risks in animals and humans [38, 59]. Such approaches enable early detection of contamination of pastures and water sources with infective sporocysts, often long before clinical cases become apparent, making environmental surveillance a critical component of epizootic and zoonotic prevention systems.

Future research perspectives in sarcocystosis can be summarized into several strategic directions:

- Expansion of molecular marker sets for accurate taxonomy, assessment of genetic diversity, and epidemiological investigations of Sarcocystis.
- Application of genomics and WGS to identify genetic determinants of virulence and adaptation, enabling more precise tracking of parasite evolution and spread.
- Development of vaccines and targeted therapeutic agents based on molecular antigens and immunogenic structures of the parasite.
- Implementation of environmental monitoring using molecular methods in natural substrates (water, soil, and feed) to prevent epizootic outbreaks and assess the impact of anthropogenic changes on transmission cycles of Sarcocystis.

These research directions contribute to a deeper understanding of Sarcocystis biology, improved disease control in livestock populations, and reduction of zoonotic transmission risks, ultimately enhancing veterinary and public health safety.

Conclusion

Sarcocystosis remains one of the most widespread protozoan infections of veterinary and medical significance. Pathogens of the genus *Sarcocystis* are characterized by high ecological plasticity, a complex life cycle, and broad host specificity. To date, dozens of species have been identified that infect domestic and wild animals as well as humans. Climate change, urbanization, and the intensification of livestock production contribute to the transformation of parasite life cycles and the expansion of the geographic ranges of certain species, thereby increasing the epizootic and potential zoonotic significance of sarcocystoses.

From an ecological perspective, sarcocysts represent an important component of biocenoses and can be considered bioindicators of ecosystem health. Their study has not only fundamental but also applied importance—from assessing the epizootological situation in livestock production to predicting risks of zoonotic infections. The analysis of contemporary research on the biodiversity of parasites of the genus *Sarcocystis* has shown that these apicomplexan protozoa should be regarded not only as causative agents of invasive diseases in animals but also as functionally significant elements of ecosystems. The species diversity of *Sarcocystis*, their strict trophic associations with definitive and intermediate hosts, and the high sensitivity of

parasite systems to environmental changes make them important participants in ecosystem processes and indicators of biocenotic status.

Morphological characteristics of sarcocysts have limited diagnostic value and require confirmation using molecular genetic methods. The use of 18S rRNA, ITS-1 markers, and the cox1 gene has enabled clarification of species identity and the establishment of phylogenetic relationships within the genus. Modern studies convincingly demonstrate that the actual biodiversity of *Sarcocystis* is significantly greater than previously defined taxonomic frameworks.

Future research perspectives are associated with the integration of morphological, molecular, and ecological approaches. This will allow a deeper understanding of evolutionary relationships between parasites and their hosts, mechanisms of adaptation, and the role of sarcozoans in regulating animal population dynamics. Interdisciplinary studies combining parasitological, genetic, and ecological methods open new opportunities for assessing biodiversity and the epidemiological potential of sarcocysts.

Thus, the present publication contributes to the formation of an integrative perspective on *Sarcocystis* as a component of ecosystems, uniting data from parasitology, ecology, and molecular biology. The presented syntheses emphasize the value of using *Sarcocystis* as model organisms for studying the stability of parasitic systems and as bioindicators of environmental change. The conclusions obtained may be applied in the development of environmental monitoring programs, assessment of epizootic risks, and planning of further fundamental and applied research within the framework of the "One Health" concept.

Author Contributions

The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript. CRediT: **Suleimanova K.U. —** conceptualization, data curation, investigation; **Suleimanova K.U., Zhabykpayeva A.G.** — data curation, formal analysis, supervision, writing draft, editing; **Balabayev B.K., Kubekova B. Zh.** — investigation, writing draft, editing, preparation of table; **Šarkūnas M**. — formal analysis, editing.

Conflict of Interest

The authors declare no conflict of interest.

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Sarcocystis биоалуантүрлілігін және олардың экожүйелердегі рөлін зерттеудің заманауи бағыттары

Шолуда *Sarcocystis* туысына жататын паразиттердің биоалуантүрлілігі және олардың экожүйелер, ветеринария және қоғамдық денсаулық үшін маңызы туралы заманауи деректер жинақталған. Саркоцистоздар айқын ветеринариялық және зооноздық мәні бар аурулар ретінде қарастырылады, өйткені олар ауыл шаруашылығы жануарларының өнімділігінің төмендеуіне, ет өнімдерінің сапасының нашарлауына әкеледі және адамда патологиялық өзгерістер туындатуы мүмкін. Туыс өкілдерінің таксономиялық және географиялық әртүрлілігі, аралық және түпкілікті иелерінің ерекшеліктері, сондай-ақ паразиттің айналымына экологиялық факторлардың әсері туралы мәліметтер талданды. *Sarcocystis*-тің нақты түрлік алуантүрлілігі морфологиялық тұрғыдан сипатталған формалар санынан едәуір жоғары екені атап өтілді, бұл молекулалық-генетикалық сәйкестендіру әдістерінің белсенді енгізілуімен байланысты. Заманауи диагностикалық тәсілдер қарастырылды, оның ішінде морфологиялық және гистологиялық зерттеулер, сондай-ақ 18S рРНҚ, cox1 және ITS-1 маркерлерін қолданатын молекулалық әдістер, олар таксономиялық шекараларды нақтылауға, криптикалық түрлерді анықтауға және филогенетикалық байланыстарды талдауға мүмкіндік береді. Диагностиканың дәлдігін арттыру, мониторингті жетілдіру және профилактикалық шараларды әзірлеу үшін классикалық паразитологиялық және молекулалық әдістерді біріктірудің қажеттілігі атап көрсетілді. Паразитологияны, эпизоотологияны, экологияны және молекулалық биологияны біріктіретін пәнаралық тәсілдің орындылығы туралы қорытынды жасалды, бұл паразит пен иесінің эволюциялық өзара қатынастарын тереңірек түсінуге мүмкіндік береді және зооноздық саркоцистозды тиімді бақылау мен алдын алудың ғылыми негізін қалыптастырады.

Кілт сөздер: Sarcocystis, биоалуантүрлілік, экология, паразиттер, морфология, молекулалық идентификация, зооноздар, биоиндикаторлар.

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Современные исследования биоразнообразия *Sarcocystis* и их роли в экосистемах

В обзоре обобщены современные данные о биоразнообразии паразитов рода *Sarcocystis* и их значении для экосистем, ветеринарии и общественного здоровья. Саркоцистозы рассматриваются как заболевания с выраженной ветеринарной и зоонозной значимостью, поскольку они приводят к снижению продуктивности сельскохозяйственных животных, ухудшению качества мясной продукции и могут вызывать патологические изменения у человека. Проанализированы сведения о таксономическом и географическом разнообразии представителей рода, специфике промежуточных и окончательных хозяев, а также о влиянии экологических факторов на циркуляцию паразита. Отмечено, что реальное видовое разнообразие *Sarcocystis* существенно превышает число морфологически описанных форм, что связано с активным внедрением молекулярно-генетических методов идентификации. Рассмотрены современные диагностические подходы, включающие морфологические и гистологические исследования, а также молекулярные методы с использованием маркеров 18S рРНК, *cox1* и ITS-1, позволяющих уточнять таксономические границы, выявлять криптические виды и анализировать филогенетические связи. Подчёркнута необходимость интеграции классических паразитологических и молекулярных мето-

дов для повышения точности диагностики, совершенствования мониторинга и разработки профилактических мероприятий. Сделан вывод о целесообразности междисциплинарного подхода, объединяющего паразитологию, эпизоотологию, экологию и молекулярную биологию, что обеспечивает более глубокое понимание эволюционных взаимоотношений паразита и хозяина, а также формирует научную основу для эффективного контроля и профилактики зоонозного саркоцистоза.

Ключевые слова: *Sarcocystis*, биоразнообразие, экология, паразиты, морфология, молекулярная идентификация, зоонозы, биоиндикаторы.

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