



## *Echinococcus* species in wildlife

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### ABSTRACT

Transmission of *Echinococcus* spp. in life cycles that involve mainly wildlife is well recognized for those species with small mammals as intermediate hosts (e. g. *E. multilocularis*), as well as for *E. felidis* and the ‘northern’ genotypes of *E. canadensis* (G8 and G10). In contrast, the remaining taxa of *E. granulosus* sensu lato are best known for their domestic life cycles, and the numerous wild mammal species (mainly ungulates) that have been recorded with cystic echinococcosis in the past were mainly considered a result of spill-over from the dog-livestock transmission system. This view was challenged with the advent of molecular characterization, allowing discrimination of the metacestodes, although the contribution of wild mammals to various *Echinococcus* life cycles has remained uncertain for scarcity of wildlife studies. Numerous records of cysts in wild ungulates date back to the 20th century, but cannot with certainty be allocated to the *Echinococcus* species and genotypes that are recognized today. This means that our current knowledge is largely restricted to studies of the past two decades that kept adding gradually to our concepts of transmission in various geographic regions. In particular, new insights were gathered in the past years on *E. granulosus* s.l. in wildlife of sub-Saharan Africa, but also on transmission patterns of *E. multilocularis* in previously neglected regions, e. g. North America. Here, an update is provided on the current state of knowledge on wild mammals as hosts for all *Echinococcus* species, listing >150 species of wild hosts with references, as well as estimates on their epidemiological impact and our current gaps of knowledge.

### 1. General remarks

All species of the genus *Echinococcus* (Cestoda: Taeniidae) are transmitted in two-host life cycles that involve exclusively mammals. *Echinococcus* species with ‘silvatic’ life cycles exploit natural predator-prey relationships between their carnivorous definitive hosts (almost exclusively Canidae or Felidae), harbouring intestinal worms, and their mainly herbivorous intermediate hosts, harbouring metacestodes in tissue of internal organs, which have to be ingested by the definitive hosts to complete the life cycle (Thompson, 2017). The exclusive – at least predominant – host role of wild mammals in silvatic life cycles puts them apart from domestic life cycles or ‘semi-silvatic’ life cycles (combining wild and domesticated hosts), where domestic animals are important hosts and where human behaviour and economic practices play a crucial part e. g. by facilitating the infection route of metacestodes from livestock hosts to domestic dogs as definitive hosts (Eckert and Deplazes, 2004).

Taking a conservative approach, nine species of *Echinococcus* are

currently recognized, at least two of them with complex intraspecific genetic structures that may in future lead to a split-off of additional species (Table 1) (Vuitton et al., 2020). Some of them are important agents of human diseases (echinococcoses). These can differ substantially in terms of clinical/pathological features and are therefore subdivided into ‘neotropical echinococcosis (NE)’, caused by *E. oligarthra* and *E. vogeli*, ‘alveolar echinococcosis (AE)’ caused by *E. multilocularis*, and ‘cystic echinococcosis (CE)’ caused by *E. granulosus* sensu stricto, *E. equinus*, *E. ortleppi*, and *E. canadensis* (Kern et al., 2017). Two additional species are not (yet?) known to cause human disease (*E. shiquicus*, *E. felidis*) (Romig et al., 2017).

Transmission ecology is highly variable among different *Echinococcus* species and major genotypes. For some taxa only wild mammals are known as host species; their life cycles are clearly independent from domestic animals, although, as we live in the Anthropocene, hardly any ‘wild’ parasite life cycle will not be influenced by human activities to some extent. In case of *E. multilocularis*, which is essentially a wildlife parasite, anthropogenic alteration of landscapes is likely to be a key

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**Table 1**  
Principal and secondary life cycles of the *Echinococcus* species and their disease in human.

Taxon	Principal <sup>a</sup> life cycle	Secondary life cycle/additional host species	Human disease
<i>E. oligarthra</i>	silvatic		NE
<i>E. vogeli</i>	silvatic	domestic dogs	NE
<i>E. multilocularis</i>	silvatic	domestic dogs	AE
<i>E. shiquicus</i>	silvatic		–
<i>E. granulosus</i> s.s. G1, G3	domestic	silvatic cycle (Australia), numerous records from wild DH and IH	CE
<i>E. granulosus</i> s.s. G-Omo	unknown		CE
<i>E. felidis</i>	silvatic		–
<i>E. equinus</i>	domestic	silvatic (southern Africa)	CE
<i>E. ortleppi</i>	domestic	records from wild DH and IH	CE
<i>E. canadensis</i> G6, G7a, G7b, Gmon	domestic	records from wild DH and IH	CE
<i>E. canadensis</i> G8	silvatic		CE
<i>E. canadensis</i> G10	silvatic	semi-silvatic (dog – moose, wolf - reindeer)	CE

DH - definitive host; IH - intermediate host.

NE - neotropical echinococcosis; AE - alveolar echinococcosis; CE - cystic echinococcosis.

<sup>a</sup> We avoid the term 'primary' for domestic life cycles, as they had eventually descended from ancestral silvatic life cycles.

factor to facilitate its spread across large parts of Europe (Romig et al., 2006; Cenni et al., 2023). In contrast, some *Echinococcus* taxa are almost exclusively known from domestic animals and depend on human practices for transmission, while for some species (and to a regionally different extent) a complex interaction between wild and domestic hosts is evident. Examples are *E. multilocularis* on the Tibetan plateau, where both domestic dogs and wild foxes feed on the same pool of intermediate hosts (Vaniscotte et al., 2011), *E. granulosus* s.s. in parts of Australia, where a secondary silvatic cycle between dingoes and macropod marsupials spills over to sheep via contamination of pastures with dingo faeces (Jenkins, 2006), or different *Echinococcus* spp. in sub-Saharan Africa, where contamination of wild herbivore pastures by domestic dogs and predation of livestock by wild carnivores may cause spill-over of *Echinococcus* in both directions (Kagendo et al., 2014; Aschenborn et al., 2023a). In most such cases of life cycle overlap, insufficient data do not allow the identification of the principal transmission routes and the epidemiologically crucial host species, which leads to numerous open questions. To which extent does the involvement of wild hosts stabilize, or contribute to, the 'domestic' transmission? Are domestic dogs or wild carnivores the more important infection sources for humans or for livestock? For obvious reasons, gaps of knowledge are most evident for the wild host species. In case of small mammals, there are often insufficient data on population sizes, geographic distribution and even taxonomic identity. In case of wild carnivores and large herbivores, sampling can be difficult due to protection status, hunting practices and other restrictions, which limits research to opportunistic surveys that usually do not yield reliable data on infection frequency. The identification of *Echinococcus* species, in particular concerning the agents of CE, largely rests on molecular typing, which limits the available data for retrospective analyses to surveys done in the last two decades. Older records from wildlife abound, particularly from Africa (Deplazes et al., 2017), but are difficult to interpret, as the causative *Echinococcus* species could not be differentiated at the time and conserved specimens for re-examination are rare. For such reasons data resources for *Echinococcus* in domestic animals are far more comprehensive than those for wildlife even in the same geographic areas, which is likely to cause an underestimate of the contribution of wildlife on *Echinococcus* spp. life cycles at least in regions where wildlife still coexists with livestock.

Looking at phylogenetics of *Echinococcus* gene sequences, it was calculated that branching of the major species and genotypic clades took place at >>1 mya (Knapp et al., 2011; Massolo et al., 2022). This is also true for those taxa that are today associated with domestic transmission, such as *E. ortleppi* or *E. granulosus* s.s. This means that their origin predates the domestication of livestock by far, and that all present-day *Echinococcus* taxa must have initially evolved as wildlife parasites subsequently to be inherited by the domesticated descendants of wild herbivores and canids. Thus, the intermediate host predilections we observe today are probably rooted in distinct silvatic life cycles of the past,

where e. g. *E. granulosus* s.s. may have evolved in a wolf – wild sheep cycle, and *E. ortleppi* in a wolf – aurochs cycle. As the wild ungulate species became either extinct or numerically insignificant later on, the parasites survived in the respective descendant livestock species with the domestic dog as a substitute for the wolf. Despite these apparently preserved host adaptations, there is evidence for efficient and rapid fine tuning of the parasites to locally prevailing hosts and changing transmission conditions (possibly via gene regulation), exemplified by rapid maturation of cysts in domestic pigs as response to early pig slaughter (Bruzinskaite et al., 2009), extremely delayed cyst maturation in regions where livestock is kept to old age (Yang et al., 2009b), or shift to development of large lung cysts in response to hunting behaviour of 'new' wild definitive hosts (Barnes et al., 2011).

Recognizing the origin of all extant *Echinococcus* species under silvatic conditions can provide us with a fresh appraisal of some morphological and physiological characteristics, whose adaptive purpose is unexplained in the domestic setting. Most obvious is the size and structure of the metacestodes of the CE-causing taxa. It is well recognized, that the large size that can be attained by cystic metacestodes, is the principal reason for host morbidity and mortality both in animals and humans (Kern et al., 2017). However, the cysts mainly contain fluid with only a small proportion of parasitic germinal tissue or protoscolex present (Thompson, 2017). The service of this structure for the parasite appears enigmatic. It is not necessary for protoscolex development, as *E. multilocularis*, whose 'cysts' have been miniaturized in response to the small body size of its rodent hosts (Woolsey et al., 2015), is able to develop approx. 20,000 protoscolexes per gram (= <1 ml) of metacestode (that contains only little fluid and appears like solid tissue in the mature stage) (Martini et al., 2022). This compares to a mean number of only 12,603 protoscolexes in cysts of *E. granulosus* sensu lato with an average content of 8.8 ml in the oldest age group of sheep, that harbours cysts with the highest fertility (Torgerson et al., 2009). Reducing fitness of livestock by unnecessarily large cyst size does not serve any apparent advantage for the parasite. However, this can be different under (ancestral) silvatic conditions. There, the mature cyst is destined to be ingested by a carnivorous predator, and any mechanism that facilitates predation success on infected intermediate hosts benefits the parasite. It has been shown in North America that moose infected with the wildlife forms of *E. canadensis* (G8, G10) are overrepresented in the prey of wolves as compared to uninfected moose (Messier et al., 1989; Joly and Messier, 2004). This can be explained by the reduction of respiratory capacity caused by large lung cysts of these parasites, acting on the prey's stamina while being chased or during fighting-off attacking wolves (Joly and Messier, 2004). A similar effect has been described in Australia, where *E. granulosus* sensu stricto, previously transmitted domestically between dogs and sheep (and mainly producing liver cysts), has switched to a silvatic transmission involving dingoes and macropod marsupials (Jenkins and Macpherson, 2003). Unlike in sheep,

it often produces large, rapidly growing lung cysts in the macropod intermediate hosts, which presumably decrease their hosts' ability to escape predation (Barnes et al., 2011). However, the sole purpose of cystic metacestodes as agents of fitness reduction is likely an oversimplification and is only plausible, when chase predators (e.g. wolves) are involved. Recently, a 'bridge effect' hypothesis was brought forward in an attempt to explain the successful global spread of some species of *E. granulosis* sensu lato, the agents of CE, and their colonization of highly diverse ecosystems including extremely arid areas, vs. the rather narrow set of ecological parameters in moist-temperate to cold climates, which is apparently necessary for the life cycle of *E. multilocularis* (Massolo et al., 2022). Especially in hot and dry climates, where infection of intermediate hosts via eggs from the environment is likely to be limited to short periods of moist conditions enabling the survival of eggs, the long-lived cystic metacestodes in equally long-lived large herbivores are crucial for the survival of the parasite by 'bridging' the long periods of hot and dry conditions which are detrimental to egg survival and may last for many months, sometimes years (Massolo et al., 2022). Under this scenario, it is obvious that reducing the host's fitness is a disadvantage for the parasite, and selection should favour small, fertile and persisting cysts. Preliminary data support this for wild herbivores of Africa, but data are still insufficient for a conclusion (Aschenborn et al., 2023a). An alternative (or complementary) explanation for the excessive production of cyst fluid by metacestodes may be the feeding behaviour of wild carnivores after the kill of their large-bodied prey. Protoscoleces are sensitive to desiccation, heating and freezing, and both in very cold and in hot climates survival time after the host's death will be short. Carcasses of large herbivores may take days to be devoured by the predators, so it is crucial for the parasite to be ingested preferentially. The first parts of the carcass fed on e. g. by wolves or large cats are internal organs like liver and lungs, and precisely there most *Echinococcus* cysts are located (Wade and Bowns, 1989; Stahler et al., 2006). Moreover, anecdotal observations on dogs fed with different organs of slaughtered goats, including *Echinococcus* cysts, indicate that the latter are more attractive for carnivores than other parts of the carcass (Zeyhle, Macpherson and Romig, personal observation). This needs confirmation, but it is intriguing that cysticerci or coenuri of *Taenia hydatigena* and *Taenia multiceps* with almost identical transmission patterns also develop into

large, bladder-like structures filled with fluid (Sweatman and Plummer, 1957). One remaining function of the cyst fluid may be to spill brood capsules over an extended area of the carcass after rupture of the cyst during the feeding process. Predators of large ungulates are often cooperative hunters, and spread of infective stages away from the initial cyst site would enable more members of the group to be infected by a single cyst. In summary, we may hypothesize that selection pressure on the morphology of metacestodes acts differently in varying predator-prey systems, and that the principal structure of a fluid-filled cyst, whose development, size and organ location can be modified to different, even contradictory requirements, is a putative key factor in the success and global spread of *Echinococcus* spp. under greatly divergent geographic and climatic conditions. In conclusion of this aspect, the study of *Echinococcus* in wildlife can provide us with hypothetical explanations for pathogenic features of the parasites in livestock.

Records of *Echinococcus* in wildlife have been reviewed previously (e. g. Carmena and Cardona, 2014; Deplazes et al., 2017; Romig et al., 2017), but numerous studies have since provided novel information on almost all *Echinococcus* species. Given the difficulties to obtain samples from wild mammals, some of these articles describe findings from restricted localities, others are case reports, but all contribute to our understanding on the ecology of these parasites and deserve to be presented in a broader context. The current update is therefore intended to provide background information for researchers interested in the subject and, by describing the extensive gaps of knowledge, to encourage additional studies and to emphasize the value to publish even minor findings. In the following sections we provide a summarized account as to which extent wild mammals are involved in the life cycles of different *Echinococcus* taxa, give an overview on recent advances in research and describe missing information. Records of individual host species are provided in table form. When multiple references exist for a particular species or region, an exemplary reference or a review article is cited. Host species, from which only immature worms or infertile metacestodes are reported, are omitted in the tables awaiting proof of host competence. However, in many cases the references do not provide this information, so these records are included. Animals, whose host competence only rests on experimental infections, or animals kept in zoos or similar institutions outside their natural range, are also omitted

**Table 2**  
Host records of *Echinococcus oligarthra*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Felidae:</b>		
<i>Herpailurus yagouaroundi</i> (Jaguarundi)	Panama, Colombia, Brazil	Rausch and D'Alessandro, 2002; Schwantes et al. (2021)
<i>Leopardus pardalis</i> (Ocelot)	Colombia, Argentina	Rausch and D'Alessandro, 2002; Arrabal et al. (2017)
<i>Leopardus colocolo</i> (Colocolo)	Argentina	Rausch and D'Alessandro, 2002
<i>Leopardus geoffroyi</i> (Geoffroy's Cat)	Argentina	Rausch and D'Alessandro, 2002
<i>Lynx rufus</i> (Bobcat)	Mexico	Salinas-Lopez et al. (1996)
<i>Panthera onca</i> (Jaguar)	Panama	Rausch and D'Alessandro, 2002
<i>Puma concolor</i> (Puma)	Costa Rica, Panama, Colombia, Brazil, Argentina	Rausch and D'Alessandro, 2002; Arrabal et al. (2017)
<b>Intermediate host species</b>		
<b>Rodentia (Caviomorpha)</b>		
<i>Cuniculus paca</i> (Lowland Paca)	Colombia	D'Alessandro et al. (1981)
<i>Dasyprocta azarae</i> (Azara's Agouti)	Argentina	Arrabal et al. (2017)
<i>Dasyprocta fuliginosa</i> (Black Agouti)	Colombia	Rausch and D'Alessandro, 2002
<i>Dasyprocta leporina</i> (Common Red-rumped Agouti)	Brazil, Venezuela	Rausch and D'Alessandro, 2002
<i>Dasyprocta punctata</i> (Central American Agouti)	Panama	Rausch and D'Alessandro, 2002
<i>Dasyprocta</i> sp.	Brazil	Rausch and D'Alessandro, 2002
<i>Proechimys guyannensis</i> (Guyenne Spiny-rat)	Colombia	D'Alessandro et al. (1981)
<i>Proechimys semispinosus</i> (Tomes's Spiny-rat)	Panama, Colombia	Rausch and D'Alessandro, 2002
<i>Proechimys</i> sp.	Colombia	D'Alessandro et al. (1981)
<b>Lagomorpha:</b>		
<i>Sylvilagus floridanus</i> (Eastern Cottontail)	Venezuela	Meléndez et al. (1984)
<b>Marsupialia</b>		
<i>Didelphis marsupialis</i> (Northern Black-eared Opossum)	Colombia	Thatcher (1972)

from the lists. Host species are grouped according to taxonomic positions and nomenclature is updated.

## 2. Species accounts

### 2.1. *Echinococcus oligartha*

The known area of distribution of *E. oligartha* extends from southern Argentina through tropical South and Central America to northern Mexico (D'Alessandro and Rausch, 2008). All host records of *E. oligartha* originate from wild mammals with the exception of some human infections (do Carmo Pereira Soares et al., 2013) and the report of a few incompletely developed worms from a domestic dog (D'Alessandro et al., 1981). There is no doubt that this is an original wildlife parasite, although its life cycle is only known in sketches and from small parts of its vast geographic range. Only felids are known as competent definitive hosts. Six out of ten Central/South American wild cat species are on record as hosts, ranging in size from jaguar (*Panthera onca*) to small *Leopardus* species, in addition a bobcat (*Lynx rufus*) was found infected in Mexico (Table 2). Most likely, all felids are competent hosts, which would indicate a variety of different life cycle patterns across the huge distribution area. Various species of large rodents (paca – *Cuniculus paca*, agoutis – *Dasyprocta* spp., spiny-rats – *Proechimys* spp.) were found infected with metacestodes in a number of smaller studies between Panama and northern Argentina. Unfortunately, there is only one large-scale survey available, where a life cycle was proposed between puma (*Puma concolor*) and ocelot (*Leopardus pardalis*) as definitive hosts and large rodents (pacas, spiny rats) as intermediate hosts in Colombia. More recently, puma, ocelot and a species of agouti (*Dasyprocta azarae*) were found infected in northernmost Argentina; as agoutis are preferred prey of ocelots, a respective life cycle has been proposed (Arrabal et al., 2017). However, this cycle cannot be representative for the entire range of *E. oligartha* as these rodent genera do not occur in the northern and southern parts of the parasite's recognized range, so there are extensive gaps of knowledge on the transmission ecology of the species. Moreover, genetic analyses of (few) isolates have shown genetic distances that match or even exceed those between other recognized species of *Echinococcus*, an indication of hidden taxa within *E. oligartha* (do Carmo Pereira Soares et al., 2013; Arrabal et al., 2017; Schwantes et al., 2021).

### 2.2. *Echinococcus vogeli*

The geographic range of this parasite has been assumed to be identical to that of the only wild definitive host that was ever found infected, the bush dog (*Speothos venaticus*), stretching from Panama to Paraguay and eastern Argentina (DeMatteo and Loiselle, 2008). However, the assumed key role of the bush dog rests on precisely two records: the first from an animal imported from Ecuador to a US zoo in 1970 (that had prompted the description of the species and had led to infection of a

large variety of captive primates in that zoo – Howard and Gendron, 1980; O'Grady et al., 1982; Rausch, 1995; Rausch and Bernstein, 1972), and the second from one bush dog hunted in eastern Brazil in 2007 (do Carmo Pereira Soares et al., 2014). More data exist on intermediate hosts, which seem to be largely identical with those of *E. oligartha* (pacas and agoutis) (Table 3). Evidence of a bush-dog - paca life cycle derives from a study in eastern Colombia, where 22 % of 325 examined pacas were found infected and where bush dogs were known to be present (although no record of an infected bush dog could be obtained). Young animals of the long-lived pacas were not infected, which led to the conclusion that infection events are rare (D'Alessandro et al., 1981). In addition to large rodents, armadillos (*Dasyus novemcinctus*) were found with metacestodes in eastern Brazil, but their contribution to the life cycle is not known. Most probably, life cycles of *E. vogeli* exist that involve other canids and rodents, which would explain human cases from outside the bush dog's range (D'Alessandro and Rausch, 2008). This assumption is supported by infection experiments, which yielded fertile metacestodes in a range of smaller rodent species (Rausch and D'Alessandro, 1999).

In contrast to the sympatric *E. oligartha*, there are substantial numbers of human NE patients infected with *E. vogeli*. This is usually explained by domestic dogs acquiring infection by feeding on viscera of hunted pacas, contaminating the environment in rural settlements. This hypothesis appears convincing, but is only supported by one record of adult *E. vogeli* in a domestic dog in Colombia (D'Alessandro et al., 1981) and molecular identification in dog faeces in northern Brazil (das Neves et al., 2017).

In conclusion, the silvatic life cycle of *E. vogeli* is almost unknown in most parts of its vast distribution range and the possible importance of domestic dogs for human infection needs to be confirmed.

### 2.3. *Echinococcus multilocularis*

The geographic range of this wildlife parasite covers the largest part of the temperate to arctic regions of the northern hemisphere in Eurasia and North America. Unsurprisingly, there is some genetic structuring apparent across this vast range, although the integrity of the species as such is not in doubt. Except for one divergent genotype that has so far only been found in Mongolia (Nakao et al., 2009; Konyaev et al., 2013), all examined isolates are closely related and have been grouped into 'Asian', 'European' and 'North American' clusters (Umhang et al., 2021b). It is known, however, that the 'North American' cluster is probably widespread in the circumpolar region (e. g. in the North of Russia), variants of the 'Asian' cluster also occur in eastern Europe and Alaska, and most of the recently examined *E. multilocularis* isolates from North America actually belong to the European cluster (Santa et al., 2023; Santoro et al., 2024). This leads to questions on possible anthropogenic translocations (Santa et al., 2021; Hayashi et al., 2023) as well as the correlation of genetic variants with host predilections and

**Table 3**  
Host records of *Echinococcus vogeli*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<i>Speothos venaticus</i> (Bush Dog)	Ecuador, Brazil	Rausch and Bernstein (1972); do Carmo Pereira Soares et al., 2014
<b>Intermediate host species</b>		
<b>Rodents (Caviomorpha)</b>		
<i>Cuniculus paca</i> (Lowland Paca)	Colombia, Peru, Brazil, Suriname, Bolivia, Argentina	D'Alessandro et al. (1981); Santos et al. (2012); Vizcaychipi et al. (2013); Mayor et al. (2015)
<i>Dasyprocta leporina</i> (Common Red-rumped Agouti)	Venezuela	D'Alessandro et al. (1981)
<i>Dasyprocta</i> sp.	Brazil	Rausch and D'Alessandro, 2002
<b>Armadillos:</b>		
<i>Dasyus novemcinctus</i> (Nine-banded Armadillo)	Brazil	Santos et al. (2012)

pathogenicity to humans. Current data are still insufficient to draw conclusions, although there is evidence for adaptations of locally prevailing parasite variants to different host species.

Naturally, a large number of different hosts have been identified across the range of *E. multilocularis* spanning three continents. Throughout, *E. multilocularis* is adapted to life cycles between rodents (and few other mammals of small body size) and their canid predators. The most evident adaptation of the metacestodes to small-bodied mammals is their morphology consisting of miniaturized cysts ('alveoles'), that are almost devoid of cyst fluid in the mature stage and produce the maximum number of protoscoleces in the limited available space leading to the appearance of a firm tumour-like structure growing in the liver. Almost all wild canid species living in a given area of the parasite's range have been identified as competent definitive hosts (Table 4), although their relative contributions to the parasite's life cycle may differ considerably due to different population densities and behaviour. Carnivores other than canids do not seem to play a significant – if any – role anywhere, although cats can acquire the parasite, albeit with (usually) low worm burden, retarded worm development and limited egg production (Kapel et al., 2006). The marginal role of felids is supported by a recent report of an infected lynx (*Lynx lynx*) in Turkey, where only a small proportion of worms were gravid and those contained only few eggs (Avcioğlu et al., 2018). Domestic dogs, which are competent definitive hosts, may contribute significantly to the life cycle in urban areas of Europe (Deplazes et al., 2004) and some pastoral areas of central Asia (Vaniscotte et al., 2011; Giraudoux et al., 2013), but there is hardly any evidence, that life cycles can be sustained by domestic dogs without the presence of wild canids.

Despite the vast endemic area and the large number of recorded host species, there are few regions with detailed information on the epidemiology of this parasite. The most comprehensive information is available for central Europe, based on research that commenced in the 1950s, when the general life cycle of *E. multilocularis* was discovered (Vogel, 1955). Most important host species are the red fox (*Vulpes vulpes*) and various species of arvicoline rodents. While the key role of red foxes for the life cycle is unchallenged (based on population densities and prevalence), other definitive hosts may contribute additionally in some areas. This is the case for the invasive raccoon dog (*Nyctereutes procyonoides*), that is now well established mainly in eastern and central Europe. It is susceptible to the parasite (Kapel et al., 2006) and can be infected at high prevalence (Bagrade et al., 2016; Romig et al., 2017). However, its capacity to spread infection may be limited due to its defaecation behaviour in 'latrines' and hibernation periods in some areas, which limits the distribution of eggs in habitats of intermediate hosts; defaecation of definitive hosts in vole habitats is likely to be crucial for parasite transmission and is performed effectively by red foxes (lit. in Simoncini and Massolo, 2023). Hypothetically, the recent findings of genetic variants of *E. multilocularis* in Poland, that belong to the 'Asian' genetic cluster, have been linked to the East Asian origin of the European raccoon dog populations (Santoro et al., 2024). Golden jackals (*Canis aureus*), previously restricted to remnant populations in southeastern Europe, are currently expanding their range and are becoming established in central Europe. They are susceptible to infection with *E. multilocularis* and are regarded as an established component of its life cycle in Hungary and Serbia; concerning transmission ecology, golden jackals may in future play a similar part in Europe as coyotes (*Canis latrans*) in North America (see below) (Balog et al., 2021; Miljević et al., 2021; Frey et al., 2022). Additional definitive hosts are domestic dogs in urbanized areas, but it is questionable if the life cycle of *E. multilocularis* anywhere in Europe could be maintained in the absence of foxes. The role of individual intermediate host species (mainly Arvicolinae) is more difficult to estimate. Even in well-researched Europe, prevalence data from rodents are sporadic (Oksanen et al., 2016) and relative population densities are largely unknown and are likely to diverge considerably according to habitat type and geography. Yet, areas of high *E. multilocularis* endemicity, where prevalence in foxes may

exceed 50% (EFSA, 2015), largely coincide with the distribution area of the common vole (*Microtus arvalis*), a principal prey species of red foxes. In central Europe, common voles can reach extremely high population densities on meadows and pastures, which are rarely part of natural landscapes and depend on human agricultural activities. Thus, although the parasite's life cycle clearly depends on wild mammal hosts and can be categorized as 'silvatic', it is the anthropogenic alteration of the environment which provides the conditions for the highly endemic status of *E. multilocularis* in Europe (Romig et al., 2006). Where common voles are absent (e. g. on the British Isles, in Fennoscandia and most of the Mediterranean region), the parasite seems to be either absent, rare or localized. Yet, the example of Sweden demonstrates, that outside of the common vole's range other rodents are able to maintain the life cycle. In this particular case, the field vole (*Microtus agrestis*) and water vole (*Arvicola amphibius*) were found infected. Both are known to be competent hosts, but lower population size, restriction to less widespread habitats and decreased availability for foxes (e. g. due to fossorial habits of *Arvicola* spp.) are the (hypothetical) reasons for the extremely low prevalence of *E. multilocularis* in foxes in Sweden and its limitation to few circumscribed locations in the south of the country (Miller et al., 2016). An apparent paradox is the generally low prevalence of *E. multilocularis* in voles (usually  $\ll 5\%$ ), even in *M. arvalis* in highly endemic areas (Hanosset et al., 2008; Oksanen et al., 2016), except for microfoci of intense transmission (Burlet et al., 2011; Beerli et al., 2017). This low prevalence, however, is compensated by high population densities and the large numbers of voles preyed on by foxes in typical vole habitats (Beerli et al., 2017). The intermediate host species that exhibits by far the highest prevalence of *E. multilocularis* in Europe is the muskrat (*Ondatra zibethicus*), an invasive species from North America that is by now well established in Europe and temperate regions of Asia. While muskrats were found infected in central Europe at prevalences of up to 39% (Romig et al., 1999), a significant contribution of this large-bodied arvicoline rodent to the life cycle is debatable due to its much lower population density and restriction to wetland habitats (Martini et al., 2022). During the 1990s, the frequency of *E. multilocularis* had increased drastically in central Europe both in terms of prevalence and population sizes of host animals, probably linked to the eradication of fox rabies (Romig, 2002). In the wake of this development, the life cycle also became established in urban environments, particularly the suburban parts of towns and cities, where vole habitats can be found (Deplazes et al., 2004). Prevalence of *E. multilocularis* is generally lower there compared to rural areas, which is more than compensated by the far higher population densities of foxes due to anthropogenic food supply that carries the animals through the winter period (Contesse et al., 2004). In addition, this 'urban' life cycle also involves domestic dogs that acquire infection through feeding on voles e. g. in parks. Prevalence in dogs is extremely low in Europe, but a significant contribution of dogs to the life cycle in human settlements cannot be excluded due to their large numbers (Toews et al., 2021). Further, dogs appear to be an important risk factor for human infection by shedding eggs in the vicinity of humans, and possibly by contaminating their fur with fox faeces (Schmidberger et al., 2022).

By far the largest number of host species has been reported from the Asian endemicity range, stretching from the Caucasus through central Asia to northern Japan (Table 4). Available information on life cycles shows a considerable plasticity of the parasite to exploit local host species and predator-prey systems for its transmission. Examples are life cycles, that include two fox species and greater gerbils (*Rhombomys opimus*) in Kazakhstan, Tibetan foxes (*Vulpes ferrilata*), pikas (*Ochotona curzoniae*) and several vole species on the Tibetan plateau, or foxes and marmots in Kyrgyzstan. Even a life cycle between wild cats (*Felis lybica*) and muskrats (*Ondatra zibethicus*) has been suggested in wetlands of southern Kazakhstan, although this needs to be verified as cats were found to be unsuitable hosts elsewhere (Kapel et al., 2006). Many other host records from Asia (often old and difficult to access) also need confirmation, since diagnostic criteria and fertility status of the

**Table 4**  
Host records of *Echinococcus multilocularis*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Canis aureus</i> (Golden Jackal)	Hungary, Serbia, Croatia, Slovenia, Switzerland, 'Uzbekistan, and Turkmenistan', Iran	Shaikenov, 2006; Beiromvand et al., 2011; Szell et al., 2013; Sindičić et al., 2018; Miljević et al., 2021; Bandelj et al., 2022; Frey et al., 2022
<i>Canis latrans</i> (Coyote)	USA, Canada	Massolo et al. (2014)
<i>Canis lupus</i> (Wolf)	Latvia, Slovakia, France, Germany, Italy, Russia, Turkey, Georgia, Azerbaijan, Iran, Uzbekistan, China, Mongolia, Canada, USA	Rausch, 1995; Massolo et al., 2014; Deplazes et al., 2017; Lesniak et al., 2017; Romig et al., 2017; Andreyanov, 2020; Brandell et al., 2022; Safarov et al., 2023; Umhang et al., 2023; Akyuz et al., 2024
<i>Nyctereutes procyonoides</i> (Raccoon Dog)	Denmark, Germany, Austria, Poland, Slovakia, Lithuania, Latvia, Estonia, Russia, Japan	Hurníková et al., 2009; Bagrade et al., 2016; Deplazes et al., 2017; Duscher et al., 2017; Romig et al., 2017; Petersen et al., 2018; Pilarczyk et al., 2022
<i>Urocyon cinereoargenteus</i> (Northern Grey Fox)	USA	Vusse et al. (1978)
<i>Vulpes corsac</i> (Corsac Fox)	Kazakhstan, Uzbekistan, Turkmenistan, Tadjikistan, China	Rausch, 1967; Shaikenov, 2006; Tang et al., 2006; Safarov et al., 2023
<i>Vulpes ferrilata</i> (Tibetan Fox)	China	Jiang et al. (2012)
<i>Vulpes lagopus</i> (Arctic Fox)	Russia, Alaska, Svalbard Archipelago, Canada	Rausch, 1995; Shaikenov, 2006; Gesy et al., 2014; Deplazes et al., 2017; Romig et al., 2017
<i>Vulpes vulpes</i> (Red Fox)	throughout Europe, Asia and North America	Deplazes et al., 2017; Romig et al., 2017
<b>Felidae</b>		
<i>Felis lybica</i> (African Wildcat)	Kazakhstan, Uzbekistan	Rausch, 1995; Safarov et al., 2023
<i>Felis silvestris</i> (European Wildcat)	France, Germany, Luxembourg	Steeb, 2015; Umhang et al., 2015
<i>Lynx lynx</i> (Eurasian Lynx)	Russia, Turkey	Avcioglu et al., 2018; Pomamarev et al., 2011
<b>Intermediate host species</b>		
<b>Rodentia:</b>		
<b>- Myocastoridae:</b>		
<i>Myocastor coypus</i> (Coypu)	France, Germany, Slovenia	Umhang et al., 2013; Romig et al., 2017; Krizman et al., 2022
<b>- Sciuridae:</b>		
<i>Marmota baibacina</i> (Grey Marmot)	Kazakhstan, Kyrgyzstan	Shaikenov and Torgerson, 2002; Abdyjaparov and Kuttubaev, 2004
<i>Marmota bobak</i> (Bobak Marmot)	Russia, Kazakhstan	Shaikenov and Torgerson (2002)
<i>Marmota caudata</i> (Long-tailed Marmot)	Kazakhstan	Abdyjaparov and Kuttubaev (2004)
<i>Marmota marmota</i> (Alpine Marmot)	France	Callait (2003)
<i>Sciurus vulgaris</i> (Eurasian Red Squirrel)	Russia	Rausch (1995)
<i>Spermophilus alashanicus</i> (Alashan Ground Squirrel)	China	Li et al. (1985)
<i>Spermophilus dauricus</i> (Daurian Ground Squirrel)	China	Wang et al. (2008)
<i>Spermophilus erythrogenys</i> (Red-cheeked Ground Squirrel)	China	Wang et al. (2008)
<i>Spermophilus pygmaeus</i> (Little Ground Squirrel)	Kazakhstan	Shaikenov and Torgerson (2002)
<i>Spermophilus relictus</i> (Relict Ground Squirrel)	Kyrgyzstan	Abdyjaparov and Kuttubaev (2004)
<i>Tamias striatus</i> (Eastern Chipmunk)	Canada	French et al. (2018)
<i>Uroditellus undulatus</i> (Long-tailed Ground Squirrel)	Russia	Rausch (1995)
<b>- Gliridae:</b>		
<i>Dryomys nitedula</i> (Eurasian Forest Dormouse)	Kyrgyzstan	Abdyjaparov and Kuttubaev (2004)
<b>- Castoridae:</b>		
<i>Castor fiber</i> (Eurasian Beaver)	Germany, Switzerland, Austria	Janovsky et al., 2002; Campbell-Palmer et al., 2015; Posautz et al., 2015
<b>- Spalacidae:</b>		
<i>Eospalax fontanieri</i> (Fontanier's Zokor)	China	Zhao et al. (2009)
<i>Myospalax myospalax</i> (Altai Zokor)	Kazakhstan	Shaikenov and Torgerson (2002)
<b>- Cricetidae (Arvicolinae):</b>		
<i>Alexandromys limnophilus</i> (Lacustrine Vole)	China	Giraudoux et al. (2013)
<i>Alexandromys middendorffii</i> (Middendorff's Vole)	Russia	Rausch (1995)
<i>Alexandromys oeconomus</i> (Root Vole)	Russia, Kazakhstan, Alaska	Rausch, 1995; Bessonov, 1998; Shaikenov and Torgerson, 2002
<i>Alticola argentatus</i> (Silver Mountain Vole)	Kyrgyzstan	Abdyjaparov and Kuttubaev (2004)
<i>Alticola olchonensis</i> (Lake Baikal Mountain Vole)	Russia	Konyaev et al. (2013)
<i>Alticola strelzowi</i> (Strelzow's Mountain Vole)	Russia	Konyaev et al. (2013)
<i>Arvicola</i> spp. (Water Voles)	France, Germany, Switzerland, Sweden, Romania; Russia; Kazakhstan, China	Rausch, 1995; Shaikenov and Torgerson, 2002; Sikó Barabási et al., 2011; Deplazes et al., 2017; Romig et al., 2017
<i>Chionomys nivalis</i> (European Snow Vole)	Bulgaria, Romania	Genov et al., 1980; Sikó Barabási et al., 2011
<i>Chionomys roberti</i> (Robert's Snow Vole)	Georgia	Rausch, 1995
<i>Clethrionomys gapperi</i> (Southern Red-backed Vole)	Canada	Liccioli et al. (2013)

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Table 4 (continued)

Host species	area	Reference (exempl.)
<i>Clethrionomys glareolus</i> (Bank Vole)	Belgium, France, Switzerland, Germany, Czech Republic, Romania, Latvia, Russia	Rausch, 1995; Sikó Barabási et al., 2011; Deplazes et al., 2017; Romig et al., 2017; Kokolova et al., 2021
<i>Clethrionomys rutilus</i> (Northern Red-backed Vole)	Russia, Japan, Alaska	Rausch, 1995; Shaikenov and Torgerson, 2002; Romig et al., 2017
<i>Craseomys rex</i> (Hokkaido Red-backed Vole)	Japan	Takahashi and Nakata (1995)
<i>Craseomys rufocanus</i> (Grey Red-backed Vole)	Russia, Japan	Rausch (1995)
<i>Dicrostonyx torquatus</i> (Palearctic Collared Lemming)	Russia	Bessonov (1998)
<i>Ellobius talpinus</i> (Northern Mole Vole)	Kyrgyzstan	Rausch (1995)
<i>Ellobius tancrei</i> (Eastern Mole Vole)	Kyrgyzstan, China	Afonso et al. (2015); Guo et al. (2021)
<i>Lagurus lagurus</i> (Steppe Vole)	Russia, Kazakhstan	Shaikenov and Torgerson (2002)
<i>Lasiopodomys brandtii</i> (Brandt's Vole)	China	Tang (1988)
<i>Lasiopodomys gregalis</i> (Narrow-headed Vole)	Russia, Kazakhstan, Kyrgyzstan, China	Rausch (1995); Bessonov, 1998; Shaikenov and Torgerson (2002); Abdyjaparov and Kuttubaev (2004); Fu et al. (2021)
<i>Lemmus lemmus</i> (Norway Brown Lemming)	Russia	Peklo, 2014, EFSA, 2015
<i>Lemmus sibiricus</i> (Siberian Brown Lemming)	Russia	Rausch (1995); Bessonov, 1998
<i>Microtus agrestis</i> (Short-tailed Field Vole)	Sweden, France, Russia	Abuladze (1964); Shaikenov, 2006; Miller et al. (2016); Umhang et al. (2016)
<i>Microtus arvalis</i> (incl. <i>obscurus</i> ) (Common Vole)	Central Europe to central Asia	Deplazes et al. (2017); Romig et al. (2017)
<i>Microtus guentheri</i> (Levant Vole)	Turkey	Gürler et al. (2023)
<i>Microtus hartingi</i> (Harting's Vole)	Turkey	Gürler et al. (2023)
<i>Microtus ilaeus</i> (Tian Shan Vole)	China	Wang et al. (2008)
<i>Microtus irani</i> (Iranian Vole)	Turkey	Gürler et al. (2023)
<i>Microtus juldaschi</i> (Juniper Vole)	Kyrgyzstan	Abdyjaparov and Kuttubaev (2004)
<i>Microtus mystacinus</i> (syn. <i>M. levis</i> , <i>M. rossiaemeridionalis</i> ) (East European Vole)	Svalbard Archipelago, Turkey	Henttonen et al. (2001); Gürler et al. (2023)
<i>Microtus pennsylvanicus</i> (Meadow Vole)	USA, Canada	Massolo et al. (2014)
<i>Microtus socialis</i> (Social Vole)	Russia, Georgia	Rausch (1995)
<i>Microtus subterraneus</i> (Common Pine Vole)	France	Delattre et al. (1990)
<i>Microtus transcasicus</i> (Transcaspian Vole)	Iran	Beiromvand et al. (2013)
<i>Neodon fuscus</i> (Smoky Mountain Vole)	China	Giraudoux et al. (2013); Wang et al. (2018)
<i>Neodon irene</i> (Irene Mountain Vole)	China	Giraudoux et al. (2013)
<i>Neodon leucurus</i> (Blyth's Mountain Vole)	China	Giraudoux et al. (2013)
<i>Ondatra zibethicus</i> (Muskrat)	France, Switzerland, Germany, Luxembourg, Belgium, Netherlands, Russia, Kazakhstan, Kyrgyzstan, Uzbekistan, USA, Canada	Rausch (1995); Abdyjaparov and Kuttubaev (2004); Shaikenov, 2006; Oksanen et al. (2016); Romig et al. (2017); Martini et al. (2022); Thiele et al. (2023); Trudeau et al. (2023)
<b>Cricetidae (Cricetinae):</b>		
<i>Cricetulus barabensis</i> (Striped Dwarf Hamster)	Russia	Abuladze (1964)
<i>Cricetulus kamensis</i> (Tibetan Dwarf Hamster)	China	Giraudoux et al. (2013)
<i>Cricetulus migratorius</i> (Grey Dwarf Hamster)	Turkey, Kazakhstan, Kyrgyzstan	Shaikenov and Torgerson (2002); Abdyjaparov and Kuttubaev (2004); Gürler et al. (2023)
<b>- Cricetidae (Neotominae):</b>		
<i>Peromyscus maniculatus</i> (North American Deermouse)	USA, Canada	Massolo et al. (2014)
<b>- Muridae (Gerbillinae)</b>		
<i>Meriones libycus</i> (Libyan Jird)	Kazakhstan	Shaikenov and Torgerson (2002)
<i>Meriones meridianus</i> (Midday Jird)	Uzbekistan	Shaikenov (2006)
<i>Meriones persicus</i> (Persian Jird)	Azerbaijan	Aslanova and Fataliyev (2022)
<i>Meriones unguiculatus</i> (Mongolian Jird)	Russia, China	Rausch (1995); Wang et al. (2008)
<i>Rhombomys opimus</i> (Great Gerbil)	Russia, Kazakhstan, Uzbekistan, China	Rausch (1995); Shaikenov and Torgerson (2002); Shaikenov, 2006; Fu et al., (2021)
<b>- Muridae (Murinae)</b>		
<i>Apodemus agrarius</i> (Striped Field Mouse)	Belarus, Romania, Russia, Kazakhstan	Rausch (1995); Shaikenov and Torgerson (2002); Sikó Barabási et al., 2011
<i>Apodemus argenteus</i> (Small Japanese Field Mouse)	Japan	Tsukada et al. (2002)
<i>Apodemus sylvaticus/uralensis</i> (Long-tailed Field Mouse)	Russia, Azerbaijan, Kazakhstan, Kyrgyzstan, China	Rausch (1995); Shaikenov and Torgerson (2002); Abdyjaparov and Kuttubaev (2004); Pliyeva and Uspenskii (2006); Guo et al. (2021); Aslanova and Fataliyev (2022)t
<i>Apodemus witherbyi</i> (Steppe Field Mouse)	Iran	Beiromvand et al. (2013)
<i>Mus macedonicus</i> (Macedonian Mouse)	Turkey	Gürler et al. (2023)
<i>Mus musculus</i> (House Mouse)	France, Russia, Azerbaijan, Kyrgyzstan, Iran, China, Japan, USA	Leiby and Kritsky (1972); Takahashi et al. (1986); Petavy et al. (1990); Abdyjaparov and Kuttubaev (2004); Wang et al. (2008); Beiromvand et al. (2013); Aslanova and Fataliyev (2022)
<i>Nesokia indica</i> (Short-tailed Bandicoot Rat)	Iran	Rausch (1967)
<i>Rattus norvegicus</i> (Brown Rat)	Japan	Okamoto et al. (1992)
<b>- Dipodidae:</b>		

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Table 4 (continued)

Host species	area	Reference (exempl.)
<i>Pygeretmus pumilio</i> (Dwarf Fat-tailed Jerboa)	Kazakhstan	Shaikenov and Torgerson (2002)
<i>Scarturus elater</i> (Small Five-toed Jerboa)	Azerbaijan, Kazakhstan	Rausch (1995); Shaikenov and Torgerson (2002)
<b>Lagomorpha:</b>		
<i>Lepus europaeus</i> (European Hare)	Switzerland	Chaignat et al. (2015)
<i>Lepus oiostolus</i> (Woolly Hare)	China	Xiao et al. (2004)
<i>Ochotona curzoniae</i> (Plateau Pika)	China	Giraudoux et al. (2013)
<i>Ochotona dauurica</i> (Daurian Pika)	Russia, China	Rausch (1995); Zhao et al. (2009)
<i>Ochotona pallasii</i> (Pallas's Pika)	Russia	Rausch (1995)
<i>Ochotona rufescens</i> (Afghan Pika)	Iran	Beiromvand et al. (2013)
<i>Ochotona</i> sp.	Kyrgyzstan	Rausch (1995) (as <i>O. roylei</i> )
<b>Eulipotyphla ('insectivores'):</b>		
<i>Crociodura suaveolens</i> (syn. <i>C. gmelini</i> ) (Lesser White-toothed Shrew)	Iran	Beiromvand et al. (2013)
<i>Sorex unguiculatus</i> (Long-clawed Shrew)	Japan	Takahashi and Uruguchi (1994)
<i>Sorex jacksoni</i> (Saint Lawrence Island Shrew)	Alaska	Obayashi et al. (1971)
<i>Talpa altaica</i> (Altai Mole)	Russia	Rausch (1995)

<sup>a</sup> Nomenclature of rodent hosts was updated following Wilson et al. (2016), 2017, except for the re-establishment of *Clethrionomys* (see Kryštufek et al., 2020).

metacestodes were rarely reported. Even identification of rodent species can be unreliable: the authors of a recent study from western China claim that the vole species *Neodon fuscus* (syn. *Lasiopodomys fuscus*) had been misidentified in previous surveys on the Tibetan highlands (Wang et al., 2018). The presence of *E. multilocularis* in Japan is largely restricted to the northern island of Hokkaido, where the parasite had apparently been introduced on multiple occasions in the 20th century together with translocated or immigrated red foxes from the Kurile Islands (Inukai et al., 1955; Ito et al., 2003; Hayashi et al., 2023). Today's *E. multilocularis* population in Japan shows genetic affinities both to variants known from the arctic St. Lawrence Island in the Bering Strait and from western China (Hayashi et al., 2023). This has been explained by a convoluted cascade of anthropogenic wildlife translocations, involving the transfer of voles (*Clethrionomys rutilus*) to Bering Island off Kamchatka (to increase numbers of arctic foxes (*Vulpes lagopus*) for fur harvesting), translocation of arctic foxes ('blue foxes') for the same purpose from Bering Island to the Kurile Islands northeast of Japan, translocation of voles and lemmings from unclear sources to the Kurile Islands to feed those foxes, introduction of red foxes from Sakhalin and Canada to the Kurile Islands, and translocation of red foxes (for fur harvesting and controlling vole damage) from the Kurile Islands to Rebun Island off Hokkaido, which obviously caused a serious outbreak of human AE infections there one decade after fox introduction in the 1920s. The genetic affinity of most Japanese *E. multilocularis* isolates to those from St. Lawrence Island may be due to the origin of some translocated voles there (Yamashita, 1973), although other sources are in contradiction (Rausch and Schiller, 1954). As *E. multilocularis* on St. Lawrence and Bering Islands was assumed to have originated in Siberia - and was for that reason named '*E. sibiricensis*' (Rausch and Schiller, 1954) -, those variants may be widespread on the East Asian mainland and hence ended up in Japan. In addition to purposeful translocations of wildlife, a natural dispersion via foxes that had been observed on drifting sea ice from the north to Hokkaido cannot be excluded (Inukai et al., 1955; Ito et al., 2003; Hayashi et al., 2023). In recent years, some stray domestic dogs were found infected in a circumscribed area of the Japanese mainland Honshu, but it is still unclear if a life cycle is established there (Tsukada et al., 2023). In contrast to Europe, the life cycle on Hokkaido does not depend on agricultural landscapes, as there are no grassland-adapted rodents in northern Japan. Rather, it is maintained by woodland-associated rodents, predominantly the grey red-backed vole (*Craseomys rufocanus*) (Takahashi et al., 2005). The main habitat of this species is the bamboo undergrowth of forests and woodland, which provides food and shelter even under snow cover in winter, thus maintaining high population densities all year round which seems to be favourable for intense transmission. In the city of Sapporo, Hokkaido, there is a well established population of urbanized red foxes,

which were shown to be frequent hosts of *E. multilocularis*; infection is likely acquired in the more densely vegetated areas at the urban fringe, where populations of suitable rodent hosts are found (Tsukada et al., 2000; Kato et al., 2017). In addition to the silvatic life cycles mentioned from various parts of Asia, there are multiple reports of the involvement of domestic dogs, creating complex transmission patterns which are poorly understood. On the Tibetan plateau, unrestricted domestic dogs are frequently infected due to feeding on wild intermediate hosts, thus interacting with an already complex silvatic cycle that involves two fox species, probably wolves, and various species of rodents and pikas. Infected dogs are likely the principal reason for the large number of human AE cases, but it is unclear, if the life cycle of the parasite could be maintained without the involvement of wild canids. A peculiar semi-silvatic transmission pattern is reported from Ningxia, China, where wild canids are absent. Intermediate hosts are Fontanier's zokors (*Eospalax fontanieri*), strictly fossorial rodents which are commonly trapped as agricultural pests and fed to dogs. Thus, only human activities provide the link between the intermediate and definitive hosts, as the zokors would otherwise be unavailable to dogs due to their life underground (Giraudoux et al., 2013).

Despite the wide spread of *E. multilocularis* in the northern USA and Canada, few epidemiological data are available for North America south of the arctic. In addition to red foxes, coyotes (*Canis latrans*) were shown to be important definitive hosts, particularly in the western part of North America (Table 4). Only four rodent species (three voles and a deer-mouse) have been recorded as hosts, of which the meadow vole (*Microtus pennsylvanicus*) seems to be most important due to its role as preferred prey species for the wild canids and its host competence (Liccioli et al., 2014, 2015). The ecological niche of the meadow vole (moister areas with dense vegetation) suggests a lesser dependence on human-altered landscapes than its European counterpart, the common vole, although a recent study detected a negative correlation between the spatial proportion of natural forest cover and prevalence of *E. multilocularis* in coyotes in eastern Canada (Kotwa et al., 2020). There is a surprisingly large number of records from wolves (*Canis lupus*) in southwestern Canada, a species previously thought to be little at risk of infection due to its preference of larger prey (Schurer et al., 2014). Generally, the host range, frequency and precise geographical distribution of *E. multilocularis* in temperate North America are not well understood; there seems to be some recent geographical spread, as >20 % of red foxes and coyotes were found infected in southern Ontario, Canada, a region previously thought to be free of the parasite (Kotwa et al., 2019). It has been shown, that coyotes have established urbanized populations in the Canadian city of Calgary and seem to maintain the parasite's life cycle in suburban areas with high human populations. Prevalence in these 'urban' coyotes was, locally, as high as 84 % (Liccioli



et al., 2014); like in Europe, this urban life cycle also spills over to domestic dogs (Massolo et al., 2014). While the main intermediate host is assumed to be the meadow vole, muskrats caught within the city of Calgary were recently found infected at high prevalence (22/93) (Trudeau et al., 2023), which is in contrast to older surveys from rural areas of the USA where *E. multilocularis* prevalence was extremely low (Romig et al., 2017). Although muskrats seem to be a relatively rare prey of coyotes (Liccioli et al., 2014), high prevalence and large numbers of protozoetes in muskrats can lead on occasion to massive infections in individual coyotes (Martini et al., 2022; Trudeau et al., 2023). Whether this high frequency of the parasite in Calgary reflects a general increase of *E. multilocularis* prevalence in North America, is a consequence of high host population densities in urban areas, or is due to a novel strain of the parasite is in need for further studies. Unexpectedly, most recent records of *E. multilocularis* in North America could be genetically assigned to the European rather than the North American cluster of variants (Jenkins et al., 2012; Santa et al., 2023). It has been hypothesized that this is due to an accidental introduction in the past, possibly with foxes from Europe (Kamler and Ballard, 2002). Should this be the case, questions arise on the reason for the rapid spread of these variants across the continent and a possible change of the epidemiology of this parasite in North America and its impact on public health.

*Echinococcus multilocularis* is widespread in the circumpolar arctic region, where it is maintained by arctic foxes, with wolves and red foxes as additional definitive hosts in some areas. Most host records and prevalence data originate from older studies in Russia and from two longitudinal surveys on St. Lawrence Island off Alaska and on the Svalbard archipelago, Norway. The arctic region encompasses highly diverse ecosystems, from rocky areas and gravel plains to water-logged tundra. While arctic foxes as definitive hosts are widespread and able to disperse over enormous distances (Fuglei and Tarroux, 2019), there is a large variation in presence, frequency and species composition of rodents. The highly different prevalence figures of *E. multilocularis* reported from arctic foxes (ranging from 0 % to 100 % - (Rausch et al., 1983; Rausch and Fay, 2002) are clearly rooted in the presence and population stability of susceptible rodent species in any given area. Contradictory reports on host competence of different rodents may be caused by different host adaptations of local parasite strains. In arctic North America, presence of *E. multilocularis* has been associated with the root vole (*Alexandromys oeconomus*), while various species of lemmings were considered to be unsuitable hosts. In contrast, the Siberian lemming (*Lemmus sibiricus*) is reported as one of the most commonly infected rodents in the Russian Arctic. In the absence of further epidemiological data and genetic characterization of the parasites, we can only conclude that *E. multilocularis* exploits different host communities in different parts of the arctic region. Detailed data are available for the life cycle on St. Lawrence Island between arctic foxes and root voles, which had spilled over into the domestic dog population, causing in turn an exceptionally large number of human patients (Schantz et al., 1995). The key role of rodents is exemplified by the situation on Svalbard, where – in the absence of any terrestrial small mammal – the parasite life cycle had not existed prior to the accidental introduction and local establishment of the East European vole (*Microtus mystacinus*, syn. *M. levis*) from Russia (Fredga et al., 1990). This had prompted a life cycle

of *E. multilocularis*, which, according to genetic data, had been introduced by migrating arctic foxes rather than by the voles (Knapp et al., 2012; Umhang et al., 2021a).

In conclusion, *E. multilocularis* displays a significant adaptability to different host species in different regions and locations, which led to the colonization of habitats as diverse as arctic tundra, high altitude grassland, bamboo forests or European suburbia. A conspicuous exception are the hot and dry desert areas to the south of its distribution range. This has been hypothetically explained by environmental conditions that are detrimental to egg survival on the ground, inhibiting new infections of intermediate hosts for many months or even years. Given the short life span of adult worms in the canids and the short life span of rodent intermediate hosts, the parasite may die out in both hosts before a new window of transmission opportunity opens (Massolo et al., 2022). This may explain the affinity of *E. multilocularis* to moist and cool conditions (Miterpakova et al., 2006), which enable rodent infections during the largest part of the year. On small spatial scales, cooler temperatures, higher precipitation, soil moisture and presence of surface water have been linked to higher frequency of *E. multilocularis*; wetlands interspersed within arid areas may form microfoci of endemicity (Shaikenov, 2006; Moloj et al., 2023). While a positive effect on egg survival may play some role there, these parameters are also likely to act indirectly by determining presence and frequency of suitable intermediate host species (Simoncini and Massolo, 2023). It has been shown, that, although the overwhelming number of host species are wild mammals, the parasite may depend on (or benefit from) human activities in several ways, e. g. the alteration of landscapes, that impact on host densities (central Europe), accidental introductions of competent host species (voles to Svalbard, muskrats to Eurasia, raccoon dogs to Europe), or even purposeful translocation of accidentally infected wildlife (Davidson et al., 2012). Examples for the latter are the introduction of *E. multilocularis* with infected foxes or the resettlement of infected wild-caught beavers (*Castor fiber*) from endemic areas to other countries (Barlow et al., 2011; Hayashi et al., 2023). Possibly, also the accidental introduction of foreign parasite variants into other endemic areas may have an impact on the epidemiology (North America).

#### 2.4. *Echinococcus shiquicus*

Genetically, the recently described *E. shiquicus* is a sister taxon to *E. multilocularis*. All records so far are from the Tibetan plateau, where its life cycle seems to depend on Tibetan foxes (*V. ferrilata*) as definitive hosts and plateau pikas (*Ochotona curzoniae*) as intermediate hosts (Table 5). The distribution area of both mammals, which form a predator-prey relationship, largely overlap and are essentially limited to elevations above 3500 m (Clark et al., 2008; Qu et al., 2013). Unlike with *E. multilocularis*, adult worms were never found in the sympatric red foxes or domestic dogs, although copro-PCR had demonstrated *E. shiquicus* DNA in faecal matter of dogs (Boufana et al., 2013; Weng et al., 2020). A recent study found Asian badgers (*Meles leucurus*) shedding eggs of *E. shiquicus*, indicating that the definitive host range is wider than previously thought (Fu et al., 2023). However, the epidemiological role of badgers needs to be assessed further, as the species defaecates in ‘latrines’ and may contribute little to the spread of parasite

**Table 5**  
Host records of *Echinococcus shiquicus*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Vulpes ferrilata</i> (Tibetan Fox)	China (Tibetan plateau)	Xiao et al. (2005)
<b>Mustelidae:</b>		
<i>Meles leucurus</i> (Asian Badger)	China (Tibetan plateau)	Fu et al. (2023)
<b>Intermediate host species</b>		
<b>Lagomorpha:</b>		
<i>Ochotona curzoniae</i> (Plateau Pika)	China (Tibetan plateau)	Xiao et al. (2005); Zhu et al. (2020)

eggs over the intermediate hosts' habitats (see the role of raccoon dogs in the transmission of *E. multilocularis*). In addition to pikas, *E. shiquicus* DNA could be demonstrated in 'lesions' or organ tissue of three sympatric vole species and a hamster, but fertile metacestodes were only present in *O. curzoniae* in that study (Wang et al., 2018). Unless the host competence of these other species can be proven, we are left with an extremely simple wildlife cycle, essentially involving only two species of mammals. Typical metacestodes are fluid-filled cysts of approximately 10 mm diameter that develop in liver or lungs (Xiao et al., 2005; Fan et al., 2016). This morphology is very distinct from *E. multilocularis* metacestodes and may be an adaptation to the much larger body size of pikas compared to voles.

## 2.5. *Echinococcus granulosus sensu stricto* (G1/3)

This is mainly a livestock-associated parasite, which is present across the globe due to accidental transfer together with the hosts. It is well adapted to sheep, although it shows a low host specificity and may produce fertile infections in a range of other domestic animals such as pigs, cattle, camels and horses. The highest level of genetic variation can be observed in western Asia, where the domestication process of important livestock species and, hypothetically, the transition from a silvatic to a domestic life cycle had taken place (Yanagida et al., 2012). The adaptation of *E. granulosus* s.s. to sheep as intermediate hosts suggests, that the ancestral life cycle may have evolved in wolves and wild sheep (*Ovis* spp.) and was maintained subsequently by their domestic descendants. There is no indication that this ancestral cycle is still in existence, as it is uncertain to which degree the various records of the parasite from wild definitive or intermediate hosts are caused by spill-over from domestic transmission which concurs almost everywhere.

Yet, in some regions a silvatic transmission is plausible: there are records of *E. granulosus* s.s. in wolves and wild boar from the same region of Spain (Rojo-Vazquez et al., 2011) and a wildlife cycle has been proposed for Romania, where wild boar and red deer were found infected in wolf habitats (Onac et al., 2013). Besides, a number of wild host species has been recorded from other parts of the palearctic region, e. g. in North Africa and Iran (Table 6), but further epidemiological data on prevalence and host species populations will be needed to conclude on transmission patterns that run independently from domestic hosts.

This is also true for East Africa, where *E. granulosus* s.s. seems to be widespread in lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) in conservation areas of Kenya (Kagendo et al., 2014). All these areas are surrounded and encroached by pastoralists and their livestock. Sheep and cattle are frequently infected with this parasite, and killing of livestock by wild predators in this human-wildlife interface is not unusual. Silvatic transmission cannot be ruled out though, as very few potential wild intermediate hosts have been examined in the past five decades from East Africa. An exception is a survey of 354 wildebeest (*Connochaetes mearnsi*) from the Mara-Serengeti ecosystem of Kenya and Tanzania, which were examined after drowning in the Mara River of Kenya during the annual migration, four of which had viable cysts (Kagendo et al., 2014). There are (almost) no records of *E. granulosus* s.s. from wild mammals in other parts of sub-Saharan Africa, despite the highly endemic status of this parasite in the domestic setting in several regions (Deplazes et al., 2017). The exception is the recent finding of two African wild dogs (*Lycan pictus*) infected with *E. granulosus* s.s. in northern Namibia (Aschenborn et al., 2023a). This is somewhat enigmatic, as *E. granulosus* s.s. has neither been found in other wild mammals during that survey (in contrast to other *Echinococcus* spp.), nor was it present in Namibian livestock during a recent survey (Aschenborn et al., 2022). This paradox might be explained by the fact that African wild dogs travel extremely long distances and the animals may have acquired the infection in an endemicity focus of this parasite yet to be discovered. Generally, the sporadic records in wild hosts of sub-Saharan Africa coincide with the paucity of recent studies. Older surveys, mainly from

the mid-20th century, had resulted in a long list of wild carnivore and ungulate species as hosts of *Echinococcus* spp. (Macpherson and Wachira, 1997; Jenkins and Macpherson, 2003; Hüttner and Romig, 2009; Deplazes et al., 2017). However, records from the pre-molecular era cannot now be allocated to *Echinococcus* species, as voucher specimens appropriately conserved for molecular identification are rarely available.

There are very few reports of wildlife infected with any species of *E. granulosus* s.l. in South America. In the 1970's, frequent infections were reported from culpeos, fox-like indigenous canids (*Lycalopex culpeus*) and introduced European hares (*Lepus europaeus*) in the Neuquén province of Argentina. This was considered a secondary silvatic life cycle that got established by spill-over from the ubiquitous dog-sheep life cycle in the area (Schantz et al., 1972). It is unknown, if such a life cycle still exists there. Recent surveys of thousands of hares and 95 Pampas foxes (*Lycalopex gymnocercus*) in Buenos Aires province further east yielded just one fox harbouring few worms of *E. granulosus* s.s.; the involvement of wild animals in *Echinococcus* transmission there was deemed unimportant (Scioscia et al., 2013, 2016). In the south of Chile, a cyst of *E. granulosus* s.s. was found in a highly endangered species of deer, the South Andean huemul (*Hippocamelus bisulcus*). Due to the rarity of this host and the large number of sheep in the area, this was considered a spill-over infection from the domestic life cycle, either via domestic dogs or culpeos scavenging on sheep or cattle carcasses (Hernández et al., 2019).

There is only one region, Australia, where there is convincing evidence that an initial spill-over from domestic transmission resulted in an independent and sustained secondary silvatic life cycle. *Echinococcus granulosus* s.s. is, apparently, the only *Echinococcus* species that had been introduced (or got established) during the colonization of Australia by Europeans, probably with sheep from southern Europe or northern Africa (Alvarez-Rojas et al., 2016). After being perpetuated for almost two centuries, at high intensity, in the classic dog-sheep cycle (Kumaratilake and Thompson, 1982), domestic transmission strongly declined due to effective control efforts during the late 20th century (Craig et al., 2017). However, at some point of time a switch from domestic to silvatic transmission had occurred, probably linked to transhumant livestock husbandry and facilitated by the presence of dingos (*Canis lupus dingo*) and native macropod marsupials, which were all found highly susceptible to the parasite (Jenkins, 2005). Today, an apparently stable silvatic transmission can be observed in various parts of Australia, whose independence from the domestic cycle is supported by high prevalence in wildlife and only sporadic presence in dogs and livestock (Jenkins, 2021). Dingos, whose ancestors were domestic dogs that had reached Australia together with early human immigrants from southeast Asia, can be considered as wild canids from an ecological perspective and frequently prey on various species of kangaroos and wallabies (Jenkins, 2021) (Fig. 1). This predator-prey system is now the backbone for transmission of *E. granulosus* s.s., although other hosts species (e. g. the invasive red fox or wombats) were occasionally also found infected. Different species of macropods are important as intermediate hosts in Australia (Table 6), e. g. the swamp wallaby (*Wallabia bicolor*) and the eastern grey kangaroo (*Macropus giganteus*) in the southeast, the black-striped wallaby (*Notamacropus dorsalis*) in the north and the western grey kangaroo (*Macropus fuliginosus*) in the west (Jenkins and Macpherson, 2003). In contrast to sheep, the development of cysts in the macropods occurs almost exclusively in the lungs, where they mature rapidly and form large or multiple cysts. Infection causes serious morbidity by reducing respiratory capacity (Barnes et al., 2011), which is likely to facilitate transmission to the definitive host. Further aspects of this peculiar and widespread secondary wildlife cycle are conservation issues due to high mortality of endangered wallaby species after infection (Barnes et al., 2008), and infection risks for humans due to the establishment of dingo populations in urban environments (Allen et al., 2013).

Table 6

Host records of *Echinococcus granulosus* sensu stricto.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Canis aureus</i> (Golden Jackal)	Bulgaria, Iran, Uzbekistan	Breyer et al. (2004); Kim et al. (2020); Zarei et al. (2023)
<i>Canis lupaster</i> (African Wolf)	Tunisia	Lahmar et al. (2009)
<i>Canis lupus</i> (incl. <i>C. l. dingo</i> ) (Wolf)	Spain, Bulgaria, Italy, Turkey, Iran, Kazakhstan, Australia	Jenkins and Macpherson (2003); Breyer et al. (2004); Sobrino et al. (2006); Abdybekova and Torgerson (2012); Gori et al. (2015); Heidari et al. (2019); Akyuz et al. (2024)
<i>Lycalopex gymnocercus</i> (Pampas Fox)	Argentina	Scioscia et al. (2016)
<i>Lycan pictus</i> (African Wild Dog)	Namibia	Aschenborn et al. (2023a)
<i>Vulpes vulpes</i> (Red Fox)	UK, Australia	Thompson and Smyth (1975); Jenkins and Morris (2003)
<b>Hyaenidae:</b>		
<i>Crocuta crocuta</i> (Spotted Hyena)	Kenya	Kagendo et al. (2014)
<b>Felidae:</b>		
<i>Panthera leo</i> (Lion)	Kenya	Kagendo et al. (2014)
<b>Intermediate host species</b>		
<b>Suidae:</b>		
<i>Phacochoerus africanus</i> (Common Warthog)	Uganda	Hüttner et al. (2009)
<i>Sus scrofa</i> (Wild Boar)	Spain, Italy, Greece, Romania, Turkey, Iran, Tunisia	Martin-Hernando et al. (2008); Onac et al. (2013); Boufana et al. (2014); Chaligiannis et al. (2015); Sarkari et al. (2015); Di Paolo et al. (2017); Kesik et al. (2021)
<b>Cervidae:</b>		
<i>Cervus elaphus</i> (Western Red Deer)	Romania	Onac et al. (2013)
<i>Hippocamelus bisulcus</i> (South Andean Huemul)	Chile	Hernández et al., 2019
<b>Bovidae:</b>		
<i>Addax nasomaculatus</i> (Addax)	Tunisia	Boufana et al. (2015)
<i>Connochaetes mearnsi</i> (Serengeti White-bearded Wildebeest)	Kenya, Tanzania	Kagendo et al. (2014)
<i>Ovis gmelini</i> (Anatolian Sheep)	Turkey, Iran	Simsek and Eroksuz (2009); Eslami et al. (2016)
<b>Rodentia, Sciuridae:</b>		
<i>Spermophilus dauricus</i> (Daurian Ground Squirrel)	China	Yang et al. (2009a)
<b>Marsupialia, Macropodidae:</b>		
<i>Macropus fuliginosus</i> (Western Grey Kangaroo)	Australia	Thompson et al. (1988)
<i>Macropus giganteus</i> (Eastern Grey Kangaroo)	Australia	Jenkins and Morris (2003)
<i>Notamacropus dorsalis</i> (Black-striped Wallaby)	Australia	Banks et al. (2006)
<i>Notamacropus parryi</i> (Whip-tailed Wallaby)	Australia	Durie and Riek (1952)
<i>Notamacropus rufogriseus</i> (Red-necked Wallaby)	Australia	Jenkins and Morris (2003)
<i>Onychogalea fraenata</i> (Bridled Nail-tailed Wallaby)	Australia	Spratt and Beveridge (2016)
<i>Osphranter robustus</i> (Common Wallaroo)	Australia	Banks et al. (2006)
<i>Petrogale godmani</i> (Godman's Rock Wallaby)	Australia	Beveridge et al. (1989)
<i>Petrogale mareeba</i> (Mareeba Rock Wallaby)	Australia	Beveridge et al. (1989)
<i>Petrogale penicillata</i> (Brush-tailed Rock Wallaby)	Australia	Barnes et al. (2008)
<i>Petrogale persephone</i> (Proserpine Rock Wallaby)	Australia	Beveridge et al. (1989)
<i>Thylogale stigmatica</i> (Red-legged Pademelon)	Australia	Griffith et al. (2000)
<i>Wallabia bicolor</i> (Swamp Wallaby)	Australia	Jenkins and Morris (2003)
<b>Marsupialia, Vombatidae:</b>		
<i>Vombatus ursinus</i> (Common Wombat)	Australia	Grainger and Jenkins (1996)

## 2.6. *Echinococcus granulosus* s.s. (*G-Omo*)

This variant, which is genetically quite distant from the G1/3 cluster that includes all other haplotypes of *E. granulosus* s.s., is only known from one isolate from a human patient in southern Ethiopia, a local pastoralist, who presented with an unusual subcutaneous cyst (Wassermann et al., 2016). This genotype (which may warrant species status in future) had never been found in any of the large number of livestock and domestic dogs that had been examined in eastern Africa (Romig et al., 2011; Addy et al., 2012; Mbaya et al., 2014; Mulinge et al., 2018),

which had prompted hypotheses on wildlife-related transmission of this taxon. In the absence of any further records, this remains highly speculative.

## 2.7. *Echinococcus felidis*

Genetically, this parasite is a sister taxon of *E. granulosus* s.s., but differs drastically in terms of (known) epidemiology, distribution and host range. So far it has only been recorded from wild mammals of sub-Saharan Africa, where its presence is confirmed for Kenya, Uganda,



**Fig. 1.** Dingos (*Canis lupus dingo*) are the only definitive hosts that are relevant for the secondary silvatic life cycle of *E. granulosus* s.s. in Australia, while a number of different macropod marsupial species act as intermediate hosts (here: *Macropus giganteus*). Photos: T. Romig, Kosciuszko NP, Australia, 2016).

South Africa and Namibia. The taxon had initially been described as *E. felidis* from a lion in South Africa (Ortlepp, 1937), but was subsequently treated as a subspecies or the ‘lion strain’ of *E. granulosus* (lit. in Romig et al., 2015). Later, the name *E. felidis* was proposed for all *Echinococcus* of lions and their prey animals, although a possible involvement of lions in transmission of *E. equinus* had also been discussed before (Macpherson and Wachira, 1997). Now we know that African wild animals can be infected with all species of the *E. granulosus* s.l. complex, and genetic identification is required for differentiation. Thus, in terms of epidemiology of this taxon we are back at the drawing board, and our molecularly confirmed knowledge of the host range of *E. felidis* is based on only few surveys. Apart from the original description from a South African lion, lions and spotted hyenas were found to be commonly infected in conservation areas across Kenya (Kagendo et al., 2014) and in Uganda’s Queen Elizabeth National Park (Hüttner et al., 2008). In a country-wide survey in Namibia, infected lions were only found in a small area in the Zambezi region, while lions from other areas harboured other *Echinococcus* species (Aschenborn et al., 2023a). Apart from some eggs recovered from faeces of a domestic dog in the Masai Mara area of Kenya (Mulinge et al., 2018), no canid was ever found infected. Records of *E. felidis* cysts from intermediate hosts are restricted to warthogs (*Phacochoerus africanus*) in Uganda and Namibia, only from locations where lions were also infected. The only additional confirmed intermediate host for *E. felidis* is hippopotamus (*Hippopotamus*

*amphibius*) in the Kruger National Park in South Africa (Halajian et al., 2017). While the host records from domestic dogs need confirmation and hippopotamus are rarely a prey for lions, we are currently left with a very simple life cycle involving lions and warthogs, supplemented by spotted hyenas (Table 7). This is supported by the absence of *E. felidis* in a large number of wild and domestic ungulates in Namibia (and its frequent presence in both lions and warthogs in a small endemic area) (Aschenborn et al., 2022, 2023a), and its absence in livestock from the vicinity of Kenyan conservation areas endemic for this parasite (Addy et al., 2012; Mbaya et al., 2014). An older study describes *Echinococcus* in lions, warthogs and red river hogs (*Potamochoerus porcus*), but not in any other ungulates, in the Central African Republic; cysts derived from the hogs were not infective for dogs (Graber and Thal, 1980). Although no species confirmation was done at that time, the host range is suggestive for *E. felidis*.

Despite a large number of *Echinococcus* cysts of human origin from eastern Africa, that were genetically characterized in the past, no patient was ever confirmed as infected with *E. felidis* (Romig et al., 2011; Deplazes et al., 2017). However, some diagnostic sequences used in the past are inadequate to discriminate between *E. felidis* and *E. granulosus* s. s. (Hüttner et al., 2009). In addition, the absence of human infection could also be explained by the spatial limitation to wildlife habitats and the rare exposure of humans to the infection sources. Yet, until further evidence arises this is the only species of the *E. granulosus* s.l. cluster

**Table 7**  
Host records of *Echinococcus felidis*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Felidae:</b>		
<i>Panthera leo</i> (Lion)	Uganda, Kenya, South Africa, Namibia, Zambia	Hüttner et al. (2008); Kagendo et al. (2014); Halajian et al. (2017); Aschenborn et al. (2023a); Banda, unpublished
<b>Hyaenidae:</b>		
<i>Crocuta crocuta</i> (Spotted Hyena)	Uganda, Kenya	Hüttner et al. (2008); Kagendo et al. (2014)
<b>Intermediate host species</b>		
<b>Suidae:</b>		
<i>Phacochoerus africanus</i> (Common Warthog)	Uganda, Namibia	Hüttner et al. (2008); Aschenborn et al. (2023a)
<b>Hippopotamidae:</b>		
<i>Hippopotamus amphibius</i> (Hippopotamus)	South Africa	Halajian et al. (2017)

regarded as non-zoonotic.

Considering the evidence, there remains little doubt that *E. felidis* is maintained in a primary silvatic life cycle and is geographically restricted to sub-Saharan Africa.

## 2.8. *Echinococcus equinus*

This species is globally distributed and transmitted in a domestic life cycle between dogs and horses, mules or donkeys (Deplazes et al., 2017; Romig et al., 2017). At the intermediate host level, it is closely adapted to members of the Equidae (which are poor hosts for other *Echinococcus* spp.), although there are some records from other mammals and even few human patients (Denk et al., 2016; Kim et al., 2020; Macin et al., 2021). Apart from one record in a wolf in Turkey (Kilinc et al., 2023), the only involvement of wild mammals in transmission in the wild has been found in southern Africa, where self-maintained silvatic transmission is known from two separate areas of northern Namibia (Table 8). There, lions and black-backed jackals (*Lupulella mesomelas*) were identified as definitive hosts, while plains zebras (*Equus quagga*) carry the metacestodes (Wassermann et al., 2015; Aschenborn et al., 2023a). In the expansive Etosha National Park, *E. equinus* was so far the only *Echinococcus* species found in wildlife, but at high prevalence (Fig. 2). As neither domestic dogs nor any livestock are present in the area, there is no doubt, that the life cycle is self-sustained. While lions prey frequently on zebras, the jackals could acquire the infection by scavenging on remains of lion prey, or on carcasses of zebras that had succumbed to the frequent outbreaks of anthrax in that area. Additionally, zebras were infected with *E. equinus* in the extreme northeast of Namibia, in the Zambezi flood plains. Only few lions exist in this area, but the zebra population there is known to migrate seasonally between Botswana and Namibia, and two of four faecal samples from lions in Botswana were recently found to contain eggs of *E. equinus* (Aschenborn et al., 2023a). This lion-zebra life cycle may be widespread in other wildlife areas of southern Africa: in older studies, zebras were reported to be infected with *Echinococcus* at high prevalence in the Kruger National Park (Young, 1975). Since cysts derived from those zebras were experimentally infective for lions, the parasite was at the time allocated to '*E. granulosis felidis*'. As we now know, lions are also competent hosts for *E. equinus* (as well as for other species of *E. granulosis* s.l.), so determination by host species is no longer valid. An ongoing circulation of *E. equinus* in the Kruger Park was recently supported by the first record of that species (and any other *Echinococcus*) in a white rhinoceros (*Ceratotherium simum*) (Zaffarano et al., 2021). As rhinoceros are certainly not important intermediate hosts of any predator-prey transmitted parasite, the life cycle in Kruger Park is most likely maintained by zebras as well. All zebra records so far are derived from plains zebras (*Equus quagga*), although it is highly likely that Namibian mountain



Fig. 2. Suitable (foreground) and non-suitable (background) intermediate hosts for *Echinococcus* spp. in the Etosha NP, Namibia. In this particular location, 33 of 40 examined plains zebras (*Equus quagga burchellii*) had cysts of *E. equinus* (Wassermann et al., 2015; Aschenborn et al., 2023a), while no *Echinococcus* cyst has ever been found in elephants (*Loxodonta africana*), despite parasitological examinations of >2000 animals from different parts of sub-Saharan Africa (Graber et al., 1969; Young, 1975). Photo: T. Romig, 2012.

zebras (*Equus zebra hartmannae*) are involved as well: five of eleven lions were recently found infected with *E. equinus* in an area of northwestern Namibia, where mountain zebras are the only equid present (Aschenborn et al., 2023a).

The question remains, whether this silvatic life cycle is the remnant of a formerly widespread cycle between wild predators and equids (which became extinct elsewhere for lack of wild equids) or whether it is the result of a host switch from a domestic life cycle. There is no conclusive evidence, but genetic variants found in Namibian zebra were identical to horse isolates from Europe (Wassermann et al., 2015), which suggests an introduction with domestic horses during the European settlement of southern Africa (Mitchell, 2022). Also, *E. equinus* is conspicuously absent in wild carnivores of eastern Africa (no zebras were ever surveyed for *Echinococcus* there), which would be difficult to explain for an original wildlife parasite in the presence of all necessary hosts. A spill-over from domestic transmission to wildlife in eastern Africa is prevented by the general absence (or extreme rarity) of the parasite in most areas: a recent survey of >5000 donkeys from Kenya, Uganda, Tanzania and Ethiopia found *E. equinus* almost exclusively in animals from a circumscribed area in Ethiopia (Mulinge et al., 2023).

Table 8

Host records of *Echinococcus equinus*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Felidae:</b>		
<i>Panthera leo</i> (Lion)	Namibia, Botswana	Aschenborn et al. (2023a)
<b>Canidae:</b>		
<i>Canis lupus</i> (Wolf)	Turkey	Kilinc et al. (2023)
<i>Lupulella mesomelas</i> (Black-backed Jackal)	Namibia	Wassermann et al. (2015)
<b>Intermediate host species</b>		
<b>Equidae:</b>		
<i>Equus quagga</i> (Plains Zebra)	Namibia, Botswana	Wassermann et al. (2015); Aschenborn et al. (2023a)
<b>Rhinocerotidae:</b>		
<i>Ceratotherium simum</i> (White Rhinoceros)	South Africa	Zaffarano et al., 2021

**Table 9**  
Host records of *Echinococcus ortleppi*.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Canis lupus</i> (Wolf)	Italy, Poland	Massolo et al. (2018); Karamon et al. (2021)
<i>Lupulella mesomelas</i> (Black-backed Jackal)	Namibia	Aschenborn et al. (2023a)
<b>Intermediate host species</b>		
<b>Suidae:</b>		
<i>Sus scrofa</i> (Wild Boar)	Portugal	Mateus et al. (2021)
<b>Bovidae:</b>		
<i>Oryx gazella</i> (Southern Oryx)	Namibia	Aschenborn et al. (2023a)

### 2.9. *Echinococcus ortleppi*

In contrast to other species of the *E. granulosus* s.l. complex, *E. ortleppi* is adapted to cattle and closely related hosts, where it produces a high proportion of fertile cysts. It is a typical livestock parasite, which, like cattle, is globally distributed. Unlike *E. granulosus* s.s. with a similar distribution pattern, there are few records of spill-over to wildlife (Table 9). Apart from isolated records of *E. ortleppi* cysts in captive mammals - e. g. in monkeys in Vietnam, where they caused lethal infections (Plesker et al., 2009; Thanh et al., 2020) -, records from wildlife are restricted to Europe and southwestern Africa. In Italy, close to the border of France, wolves were found to shed *E. ortleppi* eggs in their faeces, but it is yet unknown if the infection is acquired via wild ungulates or as a spill-over from domestic transmission (Massolo et al., 2018). Likewise, the infection sources of a wolf in Poland (Karamon et al., 2021) and a wild boar in Portugal (Mateus et al., 2021) are entirely unclear, as *E. ortleppi* is either unreported or very rare there even in domestic animals. In contrast, *E. ortleppi* was found to be widespread, albeit infrequent, in cattle throughout Namibia and in western Zambia (Banda et al., 2020; Aschenborn et al., 2022). During a concurrent wildlife survey (Aschenborn et al., 2023a), it was also detected at a prevalence of 4/58 in oryx antelopes (*Oryx gazella*), but not in any other wild ungulate, in the central Namibian cattle farming region. In the same area, 2/40 necropsied black-backed jackals were also infected with *E. ortleppi*. It is suggestive that the infection of cattle, oryx and jackals is interlinked (e. g. by jackals feeding on cattle or oryx carcasses and spreading the infection on the farms), but conclusions require further data (Aschenborn et al., 2023a). The only other location in Namibia, where *E. ortleppi* was detected in wildlife, was the desert town of Oranjemund, far from any livestock area; there, two of only four

examined oryx were infected. The proposed life cycle of *E. ortleppi* (and *E. canadensis*, see below) is rather peculiar: oryx, naturally occurring at low population densities in the surrounding Namib desert, are attracted to irrigated parts of Oranjemund town, like parks and sports grounds, that are covered with grass and other vegetation. The permanent presence of large numbers leads to an overload of soil-transmitted helminths, and carcasses of succumbed oryx are rather frequently seen in the periphery of town. This leads to scavenging opportunities for domestic dogs and jackals and forms the basis for effective transmission of *Echinococcus* (Aschenborn et al., 2023b). There is a note on an *E. ortleppi* cyst of unknown fertility from an unreported species of zebra from Namibia, which, however, needs confirmation and is therefore not included in Table 9 (Obwaller et al., 2004).

In conclusion, southwestern Africa is the only region, where substantial involvement of wildlife in transmission of *E. ortleppi* has been discovered. Even there, the presence of this parasite is linked to cattle farming or other human activities, and there is no evidence for an independent silvatic life cycle.

### 2.10. *Echinococcus canadensis* G6/7

Members of the closely related genotypic cluster G6/7, here provisionally retained under *E. canadensis*, are spread globally in domestic life cycles (Romig et al., 2017) and are the second most important cause of human CE after *E. granulosus* s.s. (Alvarez-Rojas et al., 2014). The cluster can be subdivided based on the mitochondrial genome into various subgroups which are largely allopatric (Addy et al., 2017; Laurimäe et al., 2018). The haplotypic cluster G6 mainly affects dogs and camels in northern Africa and the Middle East, G7a is mainly present in Europe and the Americas in a dog-pig cycle, G7b seems to be restricted to the

**Table 10**  
Host records of *Echinococcus canadensis* G6/7.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Canis lupus</i> (Wolf)	Portugal, Turkey, Russia, Mongolia	Guerra et al., 2013; Ito et al., 2013; Nakao et al., 2013; Kilinc et al., 2023
<i>Lupulella mesomelas</i> (Black-backed Jackal)	Namibia	Aschenborn et al. (2023a)
<i>Lycan pictus</i> (African Wild Dog)	Namibia	Aschenborn et al. (2023a)
<b>Felidae:</b>		
<i>Acinonyx jubatus</i> (Cheetah)	Namibia	Aschenborn et al. (2023a)
<i>Panthera leo</i> (Lion)	Namibia	Aschenborn et al. (2023a)
<b>Intermediate host species</b>		
<b>Suidae:</b>		
<i>Sus scrofa</i> (Wild Boar)	Spain, Italy, Corsica, Bosnia and Herzegovina, Serbia, Romania, Ukraine, Germany	Dinkel et al., 2006; Kedra et al., 2000; Mwambete et al., 2004; Onac et al., 2013; Umhang et al., 2014; Addy et al., 2017; Sgroi et al., 2019; Pavia et al., 2020; Hodzić et al., 2022
<b>Bovidae:</b>		
<i>Oryx gazella</i> (Southern Oryx)	Namibia	Aschenborn et al. (2023b)



**Fig. 3.** Black-backed jackals (*Lupulella mesomelas*) are specialized scavengers of large herbivore carcasses, e. g. at kills of large predators, and are frequent in wildlife areas in eastern and southern Africa. In Namibia they are definitive hosts for *E. equinus*, *E. ortleppi* and *E. canadensis* G6/7. By feeding on cysts left over by the predators and scavenging on carcasses of ungulates that had died from other causes, they may contribute significantly to the parasites' transmission in wildlife areas and even assume the role of principal definitive hosts on livestock or game farmland, where large predators are absent. Photo: T. Romig, Etosha NP, Namibia, 2012.



**Fig. 4.** Cheetahs (*Acinonyx jubatus*) were only recently recognized as competent hosts of *Echinococcus*. In the central Namibian farming area, they contribute to a possible silvatic transmission of *E. canadensis* G6/7, that also involves jackals and oryx antelopes. Exemplifying the interface of domestic and silvatic life cycles, this photo shows two cheetahs having killed a calf of Maasai cattle inside Amboseli National Park in Kenya. Photo: T. Romig, 2023.

Mediterranean part of Europe, occurring in domestic pigs and wild boar, and Gmon, phylogenetically located between G6 and G7, is only known from Mongolia (Deplazes et al., 2017; Romig et al., 2017; Laurimäe et al., 2018, 2019). Despite camels and pigs being typical hosts, *E. canadensis* G6/7 shows low host specificity at the intermediate host level and fertile cysts have been found in a variety of other ungulates (Romig et al., 2017). Concerning wildlife, G6/7 is known from wild boar in various European countries, and wolves were found infected in Portugal, Turkey and Mongolia (Table 10). The recent recovery and expansion of wolf populations has led to coexistence with wild boars in large parts of Europe and western Asia, and conditions for a silvatic cycle appear to be present. Yet, there is no solid evidence for a G6/7 life cycle anywhere in Europe, that runs independently from domestic hosts. This is also true for Mongolia, where wolves may acquire infection as

spill-over from domestic transmission (Ito et al., 2013) or for Yakutia (Russia), where G6 is present in (domesticated?) reindeer alongside G10 (Konyaev et al., 2013). The largest number of wild host species was recently recorded in Namibia, where lions, cheetahs (being the first record of any *Echinococcus* in this species), wild dogs, jackals and oryx antelopes were found infected, and where the parasite was present throughout the country (Aschenborn et al., 2023a) (Table 10; Figs. 3 and 4). This frequency of G6/7 in wildlife is in contrast to its extreme rarity in Namibian livestock (Aschenborn et al., 2022), rendering frequent spill-over from domestic transmission to wildlife unlikely. Out of 13 ungulate species examined in Namibia, only oryx antelopes were found infected. This, however, is most certainly due to the small sample sizes for most species, and the parasite was found in lions and wild dogs in the extreme northeast of Namibia, where there are no oryx antelopes. As described for *E. ortleppi* (see above), a 'semi-silvatic' transmission mode (i. e. involving both wildlife and domestic animals) exists in the desert town of Oranjemund, where oryx antelopes, black-backed jackals and domestic dogs were sharing this parasite (Aschenborn et al., 2023b). Interestingly, cysts from Namibian oryx were infected with the same haplotype of *E. canadensis* G6/7 as domestic sheep in southern Namibia, suggesting some interlink between livestock and wildlife transmission at least in this area (Aschenborn et al., 2022). The genetic variants present in Namibia are most closely related to G6/7 isolates from pigs on Corsica (conforming to the clade G7b sensu Laurimäe et al., 2018) and show no close affinity to the camel or goat-transmitted G6 cluster from northern and eastern Africa, nor to pig isolates from Cabo Verde (Addy et al., 2017; Baptista et al., 2023). Again, this raises the question on the origin of this unexpectedly widespread presence of G6/7 in southwestern African wildlife. Like *E. equinus*, it was absent from numerous samples of wild carnivores in East Africa (Hüttner et al., 2009; Kagendo et al., 2014) and has to date never been found in wild animals of any other African country (though, based on parasite geography and host species, old reports of cysts from scimitar-horned oryx (*Oryx dammah*) in Chad may refer to this species (Graber et al., 1969). This is rather indicative for an early introduction with European livestock to southern Africa and subsequent successful host switch (or niche-fitting), but conclusions on this require further data from other countries in southern Africa.

### 2.11. *Echinococcus canadensis* G8 and G10

The taxa of *E. granulosus* s. l. that are maintained in silvatic life cycles in the northern parts of North America and Eurasia were earlier described as the 'northern form' of *E. granulosus* (Rausch, 2003). In reference to their main intermediate hosts, they were later termed the 'cervid strain(s)' (Thompson and Lymbery, 1990; Romig et al., 2015). Molecular evidence shows, that they are divided in two widely separated genetic clusters, named G8 and G10, without any known intermediate mitochondrial haplotypes (Yanagida et al., 2017; Laurimäe et al., 2023). Soon it was realized that initial attempts of geographical separation as 'American' and 'Eurasian' cervid strain had no factual basis, so we are left without any vernacular names for these clusters. Despite the almost complete overlap in geographical spread and host range, genetic distances are so substantial between the two clusters, that, should it be considered convenient to split the G6/7 cluster off from *E. canadensis*, it would be difficult to justify keeping both G8 and G10 under the same species name (Nakao et al., 2015). The presence of both genotypes in both North America and Eurasia has led to hypotheses on anthropogenic translocations through domestic reindeer (Rausch, 2003; Thompson et al., 2006). Despite the general geographical overlap of both genotypes, at least in Eurasia there seems to be a tendency of G10 to be associated with extremely cold climates: in two recent molecular studies, all of 69 samples (wolf, moose, reindeer, elk) from Fennoscandia, the Arkhangelsk region of Russia and the Republic of Sakha (Yakutia, eastern Russia) were G10, while 14 of 15 samples (wolf, moose, roe deer) from Europe south and southeast of the Baltic Sea were G8 (Laurimäe et al., 2023; Wassermann et al., 2023). Further data are

**Table 11**  
Host records of *Echinococcus canadensis* G8.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Canis latrans</i> (Coyote)	Canada, USA	Garrett et al., 2023; Santa et al., 2023
<i>Canis lupus</i> (Wolf)	Canada, USA, Latvia, Estonia, Poland, Russia (Yakutia)	Nakao et al., 2013; Schurer et al., 2014; Cerda and Ballweber, 2018; Laurimäe et al., 2023
<b>Intermediate host species</b>		
<b>Cervidae:</b>		
<i>Alces alces</i> (Moose)	Canada, USA, Estonia, Russia (Yakutia)	Nakao et al., 2013; Priest et al., 2021; Laurimäe et al., 2023
<i>Capreolus capreolus</i> (Western Roe Deer)	Estonia	Laurimäe et al. (2023)
<i>Cervus canadensis</i> (Wapiti)	Canada, USA	Thompson et al., 2006; Cerda and Ballweber, 2018
<i>Odocoileus hemionus</i> (Mule Deer)	USA	Cerda and Ballweber (2018)
<b>Bovidae:</b>		
<i>Ovibos moschatus</i> (Muskox)	Canada	Schurer et al. (2013)

**Table 12**  
Host records of *Echinococcus canadensis* G10.

Host species	area	Reference (exempl.)
<b>Definitive host species</b>		
<b>Canidae:</b>		
<i>Canis latrans</i> (Coyote)	Canada, USA	Santa et al., 2018; Schurer et al., 2018
<i>Canis lupus</i> (Wolf)	Canada, USA, Finland, Estonia, 'eastern Europe', Russia (Yakutia), Mongolia	Moks et al., 2006; Thompson et al., 2006; Ito et al., 2013; Nakao et al., 2013; Oksanen and Lavikainen, 2015; Cerda and Ballweber, 2018
<b>Intermediate host species</b>		
<b>Cervidae:</b>		
<i>Alces alces</i> (Moose)	Canada, USA, Finland, Estonia, Russia (Arkhangelsk and Yakutia)	Thompson et al., 2006; Nakao et al., 2013; Laurimäe et al., 2023
<i>Cervus canadensis</i> (Wapiti)	Canada, USA, Russia (Yakutia)	Thompson et al., 2006; Cerda and Ballweber, 2018; Wassermann et al., 2023
<i>Odocoileus hemionus</i> (Mule Deer)	USA	Cerda and Ballweber (2018)
<i>Rangifer tarandus</i> (Reindeer)	Canada, USA	Schurer et al., 2013; Yanagida et al., 2017

needed for North America, but in western Canadian wolves, G10 was found much more frequently than G8 (Schurer et al., 2016). If this is due to a specific adaptation of G10 to low temperatures of any kind or caused by chance dispersal routes or translocations of domestic reindeer (Scotter, 1970) remains to be studied.

A recent survey found a far higher genetic diversity of G10 in northeastern Asia (Yakutia) compared to Europe or North America, which is suggestive for an origin of G10 in that region and subsequent spread elsewhere (Wassermann et al., 2023). However, more genetic data will have to be gathered from the entire holarctic region to enable a reconstruction of the biogeography of *E. canadensis*.

Silvatic transmission of both G8 and G10 is centred in the taiga zone of North America and Eurasia, with the principal hosts wolf and moose (*Alces alces*). Other cervids (e. g. elk (*Cervus canadensis*)) and even muskox (*Ovibos moschatus*) were also found infected (Tables 11 and 12), but in contrast to high frequency and high cyst fertility in moose, cyst prevalence and protoscolex production were reported to be much reduced in the other species (Schurer et al., 2013). Despite the wide distribution of wolves, stable presence and high population density of intermediate hosts seem to be important for the life cycle and might explain the absence of the parasite e. g. in the high arctic of North America, where ungulates (reindeer) are only seasonally present (Joly and Messier, 2004; Jenkins et al., 2013). On the other hand, coyotes and, possibly, domestic dogs can assume the definitive host role where wolves are absent, e. g. in eastern North America, as shown by the presence of G8 in Maine (USA) and G10 on Newfoundland (Canada) (Lichtenwalner et al., 2014; Malone et al., 2023). Infection with

*Echinococcus* cysts was shown to increase vulnerability of moose to predation (Joly and Messier, 2004).

While it is undisputed that both genotypes are mainly transmitted in primary silvatic life cycles, spill-over into domestic animals have also been described. Dogs of indigenous communities in North America were found to shed eggs of *E. canadensis* G10 (Himsworth et al., 2010), apparently acquiring the infection via offal from hunted cervids in a semi-silvatic transmission mode (Rausch, 2003; Oksanen and Lavikainen, 2015). The reverse situation is reported from eastern Finland, where wolves act as a latent infection source for (semi-) domesticated reindeer (Hirvelä-Koski et al., 2003; Lavikainen et al., 2003, 2006). Formerly, a domestic life cycle had occurred between dogs and herded reindeer in northern Fennoscandia, correlating with high CE incidence in the human population. Active control and the replacement of sled dogs by snow mobiles had led to a gradual demise of this transmission towards the end of the 20th century (Oksanen and Lavikainen, 2015). The recent report of a fertile G10 cyst from a domestic yak on the eastern end of the Tibetan plateau is the southernmost record so far. As wolves and cervids are present in the area, this may also be a spill-over from silvatic transmission, but a definitive host role of domestic dogs (as in the concurrent dog-yak cycle of *E. granulosus* s.s.) cannot be ruled out (Wu et al., 2018).

### 3. Biodiversity, conservation and control

Parasites of wild animals are integral parts of their ecosystems in terms of species numbers, biomass and impact on fitness and population



densities of their hosts (Carlson et al., 2020). Extinction of a parasitic species is as important as extinction of any free-living organism. Host-specific parasites and those with complex life cycles are at particular danger of extermination by depletion of host populations, and the loss of e. g. lions in their natural ecosystems would most likely also mean the loss of a species of *Echinococcus* (*E. felidis*) as well as several other parasites.

Therefore, the same ethical considerations apply to the ‘treatment’ of wildlife against their parasites as to the destruction of any other species. However, although the value of parasites by contributing to biodiversity and ecosystem functions is undisputed for those that occur exclusively in wild animals, conflict is inevitable when a wildlife parasite also infects livestock or even humans. In case of *Echinococcus*, this mainly concerns *E. multilocularis*, which causes severe morbidity and mortality in humans (Kern et al., 2017). Unlike other *Echinococcus* species, which are important as human pathogens, the life cycle of *E. multilocularis* is essentially silvatic almost everywhere, and any control efforts would necessarily target wildlife. Several field trials have been carried out to assess the feasibility of regional elimination by ‘deworming’ wild foxes with anthelmintic baits (Craig et al., 2017). In this case, there is no serious doubt, that the loss of human suffering outweighs the loss of parasite biodiversity, but it has been shown, that anthelmintic treatment of foxes with praziquantel also eliminates a number of other, non-zoonotic cestode species (Romig et al., 2007). Such ‘collateral damage’ has at least to be assessed when establishing parasite control in wildlife, and elimination programs should be applied sensibly e. g. by targeting areas of human-wildlife interface only.

Host mortality caused by *Echinococcus* can also concern conservation efforts. As other invasive organisms that cause disturbance in ecosystems, introduced parasites may lead to severe mortality in unadapted host species with poor defence mechanisms against the new pathogen. This is the case with *E. granulosus* s.s., which had been translocated accidentally with livestock from Europe to Australia. While it grows slowly and causes little morbidity and hardly any mortality in sheep (Torgerson et al., 2009), it progresses rapidly into large lung cysts in Australian macropod marsupials, leading to the death of the hosts by reduction of lung capacity (Barnes et al., 2011). This may impact on remnant populations of endangered species, e. g. the brush-tailed rock wallaby (*Petrogale penicillata*), where a study found 20 % of adult animals infected with rapidly progressing disease (Barnes et al., 2008). Susceptibility of non-adapted hosts to lethal infections are also known for *E. multilocularis*. While humans (and numerous herbivorous mammals occurring in the parasite’s natural range) are reasonably resistant to infection (Kern et al., 2017), this is not the case for non-human primates, which rapidly succumb to the disease (Tappe et al., 2007; Wenker et al., 2019).

Concerning the complex and not fully understood ecological situation of CE in sub-Saharan Africa, available data do not support a significant role of wildlife as quantitatively important reservoirs for livestock infection. The domestically transmitted *Echinococcus* species are generally far more abundant in livestock (and dogs) as in sympatric wild mammals, and in the absence of effective control programmes against livestock infection a problem of spill-back of the parasites from wildlife into controlled domestic transmission cycles (as can be observed in Australia) does not arise. Moreover, the original wildlife parasite *E. felidis* does not seem to infect ruminants, and domestic pigs (which may be susceptible) are not kept in or near wild ecosystems. Vice versa, the impact of domestically transmitted *Echinococcus* on wildlife is less clear. It was shown that *E. ortleppi* and *E. canadensis* G6/7 – together with other parasites – can cause severe morbidity and mortality in wild oryx antelopes under certain conditions (Aschenborn et al., 2023b), but the limited data available on the pathology of *Echinococcus* spp. cysts in wild ungulates prevents any conclusions. Unlike in many other regions of the world, large wild mammals in Africa are increasingly restricted to conservation areas, many of which are severely encroached by humans and their livestock at least seasonally (Kagendo et al., 2014). There is no

doubt of a significant infection pressure by livestock pathogens, and the impact of CE on fragile wild ungulate populations is in need of monitoring.

#### 4. Gaps of knowledge

As described above, the level of knowledge on wildlife involvement in life cycles differs widely among the species of *Echinococcus* as well as among different regions. The extremes are exemplified by *E. multilocularis* in Europe, where numerous recent studies have provided data on the involvement and relative contributions of various host species and environmental factors on the parasite’s frequency (lit. in Romig et al., 2017; Simoncini and Massolo, 2023), and by *E. oligarthra*, where only few studies have ever been done, and where genetic data of (few) isolates even suggest the existence of cryptic species. For all *Echinococcus* spp. with principal transmission in domestic life cycles, the relevance of the long list of infected wild animal species is often unclear due to a lack of prevalence data, geographic spread, and even the fertility status of metacestodes or development stage of adult worms and, therefore, uncertainties on host competence.

Underlying reasons for this lack of data are diagnostic difficulties, in particular with the *E. granulosus* s.l. complex, whose resolution into cryptic species and genotypes (with distinct life cycles) necessitates molecular discrimination. Thus, the wealth of older data from the pre-molecular era is now difficult to assess and surveys have to be repeated. In general, parasite isolates from wildlife are difficult to obtain, as many of the larger host species are endangered and legally protected – especially in the ‘global south’ – so any studies have to rely on opportunistic sampling, which is time consuming and expensive. These contingencies call for careful and responsible handling and storage of isolates, to keep voucher specimens and other archived material available for future studies. Likewise, we should encourage the additional collection and sharing of parasite material which is not in the immediate focus of any particular study.

Research on wildlife echinococcosis does not only contribute data on the parasites’ life cycles and biogeography, it also adds to our understanding of eco-epidemiological processes. The study of trophically transmitted parasites adds a level of complexity on the study of predator-prey relationships, exemplified by the unexpectedly high prevalence of *E. multilocularis* in wolves, indicating a more frequent predation of wolves on small mammals that previously thought (Schurer et al., 2014). Genetic analyses will continue to contribute to our understanding of the historical spread of livestock and their parasites in the context of European settlements of other continents (e. g. the origin of *E. granulosus* s. s. in Australia and South America – Alvarez Rojas et al., 2016, 2017) as well as the consequences of intentional or accidental translocations of wildlife (Henttonen et al., 2001; Davidson et al., 2016). Despite the limited data available so far, new genetic information on wildlife echinococcosis in southern Africa has already raised fundamental questions on the parasites’ potential to switch hosts and fit into new ecological niches and transmission systems. In conclusion: for some *Echinococcus* species the primary nature of a wildlife cycle is beyond reasonable doubt, as for *E. felidis*, *E. canadensis* G8 and G10 and all *Echinococcus* species outside the *E. granulosus* sensu lato cluster, in other cases the secondary establishment of a life cycle involving wildlife is well documented, e. g. with *E. granulosus* s.s. in Australia. However, for some transmission cycles, mainly from southern Africa, it is still premature to conclude if these are ancient wildlife parasites or the result of recent host switches that followed the anthropogenic introduction together with livestock.

#### Declaration of competing interest

We declare no conflict of interest.

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