Echinococcus canadensis transmission in the North

Oksanen, Antti

2015-10-30

Oksanen , A & Lavikainen , A 2015 , ' Echinococcus canadensis transmission in the North ' , Veterinary Parasitology , vol. 213 , no. 3-4 , pp. 182-186 . https://doi.org/10.1016/j.vetpar.2015.07.033

http://hdl.handle.net/10138/203417
https://doi.org/10.1016/j.vetpar.2015.07.033

Veterinary Parasitology 213 (2015) 182–186

Contents lists available at ScienceDirect

Veterinary Parasitology

journal homepage: www.elsevier.com/locate/vetpar

Echinococcus canadensis transmission in the North

Antti Oksanen[a,*], Antti Lavikainen[b]

[a] Finnish Food Safety Authority Evira (FINPAR), Elektroniikkatie 3, FI-90590 Oulu, Finland
[b] Department of Bacteriology and Immunology (FINPAR), Haartman Institute, P.O. Box 21, FI-00014 University of Helsinki, Finland

ARTICLE INFO

Keywords:
Cystic echinococcosis
Wolf
Reindeer herding dog
Reindeer
Elk/moose
Chest radiography

ABSTRACT

The *Echinococcus granulosus* complex (EG) is the causative agent of cystic echinococcosis (CE). Northern cervid *Echinococcus* was previously suggested to be the ancestor of the entire EG. During the last century, it was regarded to have three (or four) different, but often overlapping, transmission cycles in the circumpolar North: the original wolf–wild cervid (reindeer or elk)-cycle; the semi-synanthropic cycle involving sled and hunting dogs and wild cervids; and the synanthropic cycle involving herding dogs and semi-domesticated reindeer. Human infections mainly derived from the latter two cycles. In Fennoscandia, the synanthropic cycle has been eliminated during the last 50 years due to changes in reindeer husbandry methods; machinery making herding dogs largely redundant. Typical to human CE in the North has been the relatively benign nature of the disease compared with CE caused by *E. granulosus* sensu stricto. The metacestodes in humans and in the natural cervid hosts predominantly appear in the lungs. The causative agents have been identified as EG mitochondrial genotypes G8 and G10, now together with G6 (camel), G7 (pig) and G9 genotypes constituting the *Echinococcus canadensis* species. Based on recent findings in reindeer in Yakutia, G6 might also be recognised among cervid genotypes. The geographical distribution of both G8 and G10 is circumpolar, with G10 currently apparently more prevalent both in the Palearctic and Nearctic. Because of the disappearance of the working dog, *E. canadensis* in Fennoscandia is again highly dependent on the wolf, as it was before domestication of the dog. Pet and sled dogs, if their number further increases, may to a minor part participate in the life cycle. Human CE in the North was mostly diagnosed by mass chest tuberculosis radiography campaigns, which have been discontinued.

1. Introduction

Rausch (2003) gave a comprehensive review on cystic echinococcosis (CE) in the Arctic and sub-Arctic. In this article, we attempt to concentrate mostly on contemporary developments, based mainly on new molecular research. In addition, we wish to remind of several views presented by Rausch (1952) already half a century before the aforementioned review.

Echinococcus cestodes causing CE were obviously present already during part of the Pleistocene (2.6 million to 11,700 years ago) (Nakao et al., 2013b), before domestication of animals. Then, their life cycle involved wild canids as definitive hosts and wild ungulates as intermediate hosts. It was previously suggested that the northern wolf (*Canis lupus*)–wild cervid cycle is the mother of all CE cycles caused by the *Echinococcus granulosus* sensu lato complex (EG) (Rausch, 1986; Thompson and Lymbery, 1990). Current molecular phylogeny does not, however, support the hypothesis (Nakao et al., 2013a,b), but indicates that the species *Echinococcus canadensis* involved in the wolf-cervid life cycle, well-known both in the Palearctic (Eurasia) and Nearctic (North America) ecozones, is the most lately derived clade of EG. Recent molecular phylogenies further support the obvious assumption that the wolf-cervid life cycle is ancestral to the domestic cycles caused by the *E. canadensis* mitochondrial genotypes G6 and G7, with G10 as the direct ancestor (Nakao et al., 2013b). In Yakutia, Siberia, three genotypes of *E. canadensis*, G6, G8 and G10 were found in wolves and/or cervids, suggesting that they occur in similar life cycles (Konyaev et al., 2013). The number of G6 isolates from cervids is so far small, but its finding also in the wolf, together with the absence of camels from the region very much support the wolf-cervid life cycle of G6. The genotypic diversity of *E. canadensis* in Yakutia might indicate that this region is the cradle of the species.

Sweatman and Williams (1963) proposed, based on morphology, geographical origin and host specificity, that two distinct subspecies of EG occur in cervids in North America: *E. granulosus canadensis*, introduced from Scandinavia with semi-domesticated reindeer, *Rangifer t. tarandus*, and indigenous *E. granulosus borealis* associated with moose, *Alces alces*. It has been speculated that these

* Corresponding author.
E-mail address: antti.oksanen@evira.fi (A. Oksanen).

http://dx.doi.org/10.1016/j.vetpar.2015.07.033
0304-4017/

subspecies might correspond to genotypes G10 and G8, respectively (Lavikainen et al., 2003), and should even be raised to species level (Lymbery et al., 2014). Sympatric occurrence of G8 and G10 does not support subspecific ranking, and the genotypes cannot be distinguished by ecological criteria (Nakao et al., 2013a,b). Furthermore, evidence of adult morphology linking G8 and G10 to '*borealis*' and '*canadensis*' has not been presented in published studies. Level of difference in mitochondrial DNA alone is insufficient to justify recognition of G8 and G10 as distinct species (Nakao et al., 2013b). In addition, according to limited available nuclear DNA data, they are indistinguishable (Saarma et al., 2009). Thus, in the present review, G8 and G10 are treated as a single species, *E. canadensis*, as was suggested in terms of priority by Thompson et al. (2006) based on cervid intermediate hosts of these genotypes. In addition, closely related genotypes G6 and G7 (and the dubious G9) are included (Thompson et al., 2006; Nakao et al., 2007; Nakao et al., 2013a), since their exclusion would lead to paraphyly of *E. canadensis*. It is probable that discussion on the taxonomy of *E. canadensis* will continue.

2. *Echinococcus canadensis* as a cause of human infection

The data on properly confirmed human infection by *E. canadensis* is still meagre, but increasing. Apparently, only one case of human infection by G8 has been reported hitherto (McManus et al., 2002). Both G6 and G10 have been identified from human infection in Siberia (Konyaev et al., 2012, 2013) and Mongolia (Jabbar et al., 2011). Globally, the G6 genotype is regarded as the second most common cause of human CE, only preceded by *E. granulosus* sensu stricto (G1) (Alvarez Rojas et al., 2014). However, at many locations where G1 and G6 coexist, diagnosed human infections are predominantly caused by G1 (Alvarez Rojas et al., 2014). The southern G6 human infections are not associated with life cycles involving cervids.

Human infections caused by *E. canadensis*, either identified by PCR, such as those by G6 in Africa, Asia or South America, or highly suspected by epidemiological knowledge to be caused by G8 or G10 in Alaska, Canada, Fennoscandia, and Russia have often been less pathogenic than those caused by G1. Another clear difference has been the predominance of pulmonary cysts instead of hepatic (Wilson et al., 1968; Eckert and Thompson, 1997; Castrodale et al., 2002; Bessonov, 2002; Guarnera et al., 2004; Lavikainen, 2005). Also in the natural intermediate hosts, infection has been located predominantly in the lungs (e.g., Hellesnes, 1935; Rausch, 1952, 2003; Finnish Food Safety Authority Evira, unpublished data from reindeer meat inspection).

The genotype G7, despite being closely related to G6, so much so that many authors have identified the parasite only as genotype G6/G7 (e.g., Mogoye et al., 2013), is an exception from the other *E. canadensis* genotypes. It is well-known from central and eastern Europe, and in Austria it has been found to be the major cause of autochthonous human CE (Schneider et al., 2010) causing predominantly liver infections in humans.

3. *Echinococcus canadensis* in bovids and other non-cervid intermediate hosts

There are reports on hydatid infections in cattle in Northern Norway in the early 20th century (Hellesnes, 1935), and these used to be considered to have been caused by the parasite circulating between reindeer herding dogs and reindeer (Hellesnes, 1935).

Without molecular evidence, the reindeer parasite genotype is now assumed probably to have been that currently known to cycle between wolf and cervids (semi-domesticated reindeer and European elk, the same species as the American moose) in northeastern Finland, i.e., *E. canadensis* G10 (Hirvelä-Koski et al., 2003; Lavikainen et al., 2003, 2006). It is not possible to confirm that there was G10 in cattle; it may even be doubtful if the early reports were really on hydatid cysts, because e.g., *Taenia hydatigena* causing fluid-filled cysts, as its name implies, is known to exist in the region (Hellesnes, 1935), and infects cattle (Taylor et al., 2007). Actually, the information by Hellesnes (1935) and its subsequent referrers about EG in Western Finnmark in 1903 may be inaccurate, as the original report (Anon., 1905) states that District Veterinarian Harald Olsen from Vadsø informs "In Western Finnmark it was told that often during slaughter, in lung and liver of cow and reindeer, up to egg size clear fluid-filled cysts were seen, that no doubt originate from dogs much troubled by cestodes, the species of which I don't know." The reference to the dogs troubled by cestodes indicates that Olsen was more probably thinking of *Taenia* species easily visible e.g., in necropsy than of *Echinococcus*.

As far as we know, apart from one muskox (*Ovibos moschatus*) from Quebec, Canada, infected with G8 (Schurer et al., 2013), only cervids and humans have been confirmed by PCR as intermediate hosts of *E. canadensis* G8 and G10, even though the genotypes coexist with domestic cattle, sheep, goats and swine in North America, Fennoscandia, Estonia, and Russia. They also exist in same habitats as wild sheep and goats in North America and wild sheep in Siberia. One mountain goat, *Oreamnos americanus*, was found to be infected with two pulmonary cysts in southeastern Alaska (Rausch and Williamson, 1959), but the number of animals examined is unknown. Furthermore, Sweatman and Williams (1963) reported single cases of hepatic infections in the American bison (*Bison bison*) and domestic pig in Alberta, Canada. They did not speculate on the closer identity of the parasite.

The *E. canadensis* genotypes G6 ("camel strain") and G7 ("pig strain"), on the other hand, have developed a wider intermediate host spectrum, which may also have enabled them to spread wider due to worldwide introduction of domestic hosts; while G8 and G10 are limited to the North (with 50–55 N as an approximate southern border of distribution), G6 is known to be present in the Middle East, Central/East Asia, Africa and South America, and G7 in Europe, the Mediterranean countries, sub-Saharan Africa and South America (Cardona and Carmena, 2013; Alvarez Rojas et al., 2014).

4. Northern *E. canadensis* life cycles

Until some decades ago, there were three (or four) different, but often overlapping, transmission cycles of *E. canadensis* in the circumpolar North (Rausch, 2003): the original wolf–wild cervid (reindeer or elk) cycle; the semi-synanthropic cycle involving hunting and sled dogs and wild cervids; and the synanthropic cycle involving herding dogs and semi-domesticated reindeer. Human infections mainly derived from the cycles involving dogs.

4.1. Wolf–wild cervid cycles

Before domestication of animals enabled synanthropic life cycles, wolves hunted and consumed both wild reindeer (called caribou in America) and elk/moose, which are intermediate hosts of *E. canadensis* and present in both the Palearctic and Nearctic. Reindeer live in the tundra and taiga and elk predominantly in the taiga zone. Also American elk or wapiti (*Cervus canadensis*) and white-tailed deer (*Odocoileus virginianus*) in the taiga have commonly been found infected by EG (e.g., Sweatman and Williams, 1963). All 12 hydatid cysts recently examined from Riding Mountain National Park, Manitoba, proved to be *E. canadensis* G10 (Schurer et al., 2013).

In Canada, a positive correlation has been shown between moose and wolf density, as well as between moose density and prevalence and intensity of hydatid infection (Messier et al., 1989).

Also, there is indication that hydatid infection makes moose more vulnerable to predation (Rau and Caron, 1979; Joly and Messier, 2004). While this has only been studied in Canada, similar mechanisms may apply also elsewhere—or may not, as parasite-host-environment interactions often are more complex than is apparent. Rausch (1952) argued against pathogenic effects of infection; he had examined a considerable number of infected moose, and concluded that if infected animals were in poorer physical condition, it was most likely because of their higher age when compared with uninfected ones.

4.2. Semi-synanthropic cycle

The next life cycle in the North was enabled by the domestication of wolves to dogs. This process probably started gradually about 35,000 years ago (Galibert et al., 2011). Dogs used in the hunt of wild cervids were given offal, including lungs, and thus they continued the life cycle of *E. canadensis*. Subsistence hunt was, and still is (e.g., Titus et al., 2009), important especially for indigenous people in Alaska and Canada, where semi-domesticated reindeer husbandry did not develop before the import of reindeer in 1892 to compensate for the disappearance of wild caribou (Finstad et al., 2006). In northern Canada, CE has been associated with indigenous people hunting cervids and living with free-roaming dogs (see Himsworth et al., 2010). In Alaska, more than 300 human CE cases were documented from 1940 through 1990, mostly among natives, but only three cases were reported in 1991–1999 (see Castrodale et al., 2002). In a recent study in an indigenous community in northern Canada, 6% (9/155) of canine faecal samples contained *Echinococcus* eggs, which proved to be G10, and 11% (12/106) of humans were found seropositive (Himsworth et al., 2010), which shows that the potential for human infection is present. The emergence of human diagnoses coincides with mass chest radiography campaigns for active case finding of tuberculosis (Golub et al., 2005). In Canada radiographic surveys were initiated in 1941 (Grzybowski and Allen, 1999). Because Canadian (Meltzer et al., 1956) and Alaskan (Wilson et al., 1968) CE was regarded as relatively benign, a policy of non-intervention was recommended instead of surgery (see Castrodale et al., 2002). Without radiography, asymptomatic cases were not even diagnosed.

4.3. Herding dog–reindeer cycle and its association with cystic echinococcosis in humans

Reindeer were domesticated considerably later than other domesticated animals, evidently independently in Russia and Fennoscandia (Røed et al., 2008). In Northern Russia and Mongolia, apparently the oldest report of reindeer domestication is from 499 AD (see Jernsletten and Klokov, 2002), but herding may have developed significantly earlier. In Fennoscandia, the earliest report of reindeer domestication is from the 800s, when the Norse Chieftain Ottar claimed that he possessed both tamed and wild reindeer (see Bjørklund, 2013). Following domestication, the contact between reindeer, humans and dogs became intimate. Reindeer were milked and used as draft animals. Dogs were given viscera after reindeer were slaughtered for hide and meat.

The first reports of reindeer echinococcosis were obviously from Northern Norway, where infection was seen in 1859, with subsequently several cases in Troms County (Harbitz, 1913, cited in Söderhjelm, 1946). In Kåbdalis, Sweden, 3 cysts were seen in 60 reindeer in 1941 and 7 cysts in 70 reindeer in 1944, while no infection was seen in 300 reindeer in 1945 in Gällivare, about 100 km from the former location (Söderhjelm, 1946). The author pointed out that reindeer have an appetite for salt and eat urine-soaked snow around reindeer herder settlements and speculated that female reindeer herding dog urine especially might be contaminated with *Echinococcus* eggs, thus forwarding the parasite life cycle (Söderhjelm, 1946).

In 1940 and 1942, two human abdominal hydatid disease cases were diagnosed in reindeer herding families in Sodankylä, Finnish Lapland (Cederberg, 1946). Absence of sheep contacts led the author to believe that reindeer, and perhaps elk, were involved in the local life cycle. One of the patients had a giant peritoneal cyst containing more than 13 l of fluid. Apparently, only one human pulmonary hydatid case had been reported in Finland, compared with 20 liver infections (Mikkonen, 1935, cited in Cederberg, 1946). However, most of the cases not involving reindeer herding families were probably imported.

Until 1953, 12 human cases had been reported in Norway, 4 of them from the two northernmost counties, Troms and Finnmark (Arnesen, 1953). Mandatory thorax radiographic surveillance for tuberculosis had been established in 1943, and from 1952, it covered the entire country (Folkehelseinstituttet, 2013). Obviously, thorax screening was one of the factors leading to an emergence of reported human cases. Kautokeino in Western Finnmark County proved to be a hotspot of infection; among a population of 1710, 17 cases were diagnosed within a few years, 14 of them pulmonary and 3, hepatic (Rein, 1957). A total of 34 cases were diagnosed in Northern Troms and Finnmark Counties in 1951–1956 (Skjenneberg, 1959). In 1956–1958, 2204 slaughtered reindeer were inspected at the new reindeer slaughterhouse. Of them, 9.6% were found to be infected.

In Finland, mandatory thoracic radiographic surveillance for tuberculosis was initiated in 1950. All persons over 15 years old were to be screened every three years (Pukkila, 2009). However, the number of published cases of pulmonary echinococcosis is lower than in Norway or Sweden (Lavikainen, 2005). The mass radiographic surveillance was finally discontinued in 1990 (Tala-Heikkilä, 2003).

5. Break-up of the herding dog–reindeer cycle

Because the CE situation in humans was regarded as alarming, and the prevalence in reindeer was high (9.6%) in Kautokeino, Norway, a control program was initiated in spring 1957, consisting of information ("*huspropaganda*") about the life cycle of the parasite and control possibilities given to reindeer herders by the active reindeer veterinarian Sven Skjenneberg, together with the local doctor, nurse and the regional Sami Bailiff, visiting reindeer herder dwellings. They delivered arecoline hydrobromide to all dogs at a dose of 0.5 mg/kg. Another roundtrip was done in spring 1958, when information was repeated and arecoline was given to herders for treating dogs. At slaughter, reindeer offal were destroyed or disinfected by boiling. An information leaflet was printed in Sami language and distributed widely in Finnmark. Reindeer slaughterhouses were to be renovated in order to be able to better take care of offal (Skjenneberg, 1959). After that, reindeer meat inspection was developed, and in 1977, when the prevalence in reindeer was about 1.5%, annual praziquantel treatment of dogs was initiated. The reindeer EG prevalence further declined, and was 0.1% after four years (Kummeneje et al., 1981).

In Northern Finland and Sweden, reported prevalence in reindeer, 1.2% and 1.6%, respectively (Pöysti and Pöysti, 1969; Ronéus, 1974) was similar to the Norwegian prevalence at the start of the new phase of eradication in 1977. Obviously, no stringent control effort was made in these countries. Still, comparable decrease in prevalence in reindeer was seen also in Sweden and Finland (Hirvelä-Koski et al., 2003; Lavikainen, 2005; Lavikainen et al., 2003, 2006). The best explanation is in the disappearance of the reindeer herding dog as snowmobiles were introduced (Lavikainen, 2005).

It is worth reminding that already when the importance of CE in the North was only emerging into public knowledge, Rausch (1952) wrote somewhat prophetically "*. . .it may be premature to attempt to control a disease of the relative small importance of echinococcosis until tuberculosis is brought under control.*" Another scientific opinion expressed in the same paper to be considered today was "*. . .the fact that the wolf is involved in the life cycle of this cestode does not constitute any appreciable threat to human health and this information should not be construed as support for those in favour of generalized wolf destruction.*" (Rausch, 1952).

6. Current situation and future of *E. canadensis* transmission in the North

In Alaska and Canada, reported human autochthonous CE diagnosis incidence has much decreased during the last half a century (see Castrodale et al., 2002). The condition is probably underdiagnosed (Somily et al., 2005; Hueffer et al., 2013) as the life cycle goes on involving free-roaming dogs in rural villages (Himsworth et al., 2010), but because of limited clinical importance (Wilson et al., 1968), it probably receives the public health attention it is worthy of. Natural wolf-cervid cycles are still flourishing (Schurer et al., 2013).

In Russia, the identification of both G6, G8 and G10 sympatrically in Yakutian cervids led Konyaev et al., (2013) to assume that these genotypes can mate and produce hybrid offspring. Apart from that, little new information has been published on the epidemiology and transmission of CE in northern Russia since the review by Rausch (2003). During the 1990s, as before, the problem was severest among the indigenous peoples in Siberia, where reindeer herding and subsistence hunting were supposed to have had increasing importance. In Chukotka, where both CE and alveolar echinococcosis are prevalent, CE is more common in the central and northern regions (Lebedev et al., 1996), with both wild and semi-domesticated reindeer (Jernsletten and Klokov, 2002). As indigenous people in Siberia feed dogs with reindeer offal and sleep with the dogs in traditional tents called "chum" (Konyaev et al., 2013), the life cycle is expected to go on as previously.

In Fennoscandia, the herding dog–reindeer life cycle was broken by the disappearance of the herding dog during the 1960–70s, and the loss of the final host was seen in reindeer meat inspection (Lavikainen et al., 2003, 2006). In Finland, a re-emergence was seen in reindeer near the Russian border starting in the early 1990s (Hirvelä-Koski et al., 2003; Lavikainen et al., 2003, 2006), and the causative agent was identified as the previously unknown genotype G10 (Lavikainen et al., 2003, 2006). Now, the life cycle goes between wolf and wild and semi-domesticated cervids in the eastern part of the country where the wolf population is strongest. Human infections have not been seen since the 1960s (Lavikainen, 2005). However, in March 2015, a clinical case of obviously autochthonous human G10 infection was diagnosed in North Karelia, eastern Finland (Miika Arvonen, Kuopio University Hospital, pers. comm., 2015).

Even though the wolf's distribution has spread during the 2000s, it appears that the parasite has not expanded its range along with that of the definitive host, but has remained stable in the core areas of wolf pack territories in eastern Finland (south from the reindeer husbandry area). Of 252 wolves examined in Finland 2000–2010, 25 (10%) were positive. In the core area in eastern Finland with high density of wolves, 46% were found infected (Marja Isomursu, Evira, pers. comm. 2011). Only G10 has been identified in wolves or cervids in Finland. If the wolf population in Fennoscandia substantially increases, the parasite may also expand its range. In Estonia and Latvia, *E. canadensis* has been found in wolves, with a prevalence of 4% (Moks et al., 2006) and 2.6% (Bagrade et al., 2009), respectively. Both G8 and G10 have been identified in Estonia (Moks et al., 2008).

7. Conclusion

After the disappearance of the herding dog–reindeer cycle of *E. canadensis*, the situation is back in the origin, with wolf–cervid cycles sustaining the parasite in Fennoscandia. The trendy preference to give hunting and sled dogs raw meat or offal may sporadically infect them if proper precautions are not taken. These include the total ban of giving raw unfrozen or uncooked cervid lungs and other offal, in addition to regular deworming with a cestocidic drug before and after the hunting season, as advised e.g., by the Finnish Food Safety Authority Evira (www.evira.fi). The perhaps increasing number of pet dogs will probably not play a significant role in *E. canadensis* epidemiology and transmission.

In Alaska, Canada and Russia, where subsistence hunting is practiced, semi-synanthropic life cycles still exist. Human infections are underdiagnosed, but not really neglected, because they are relatively benign and preferably not treated even if diagnosed.

Was CE an emerging disease during the 1950s in the North?—We believe not. Without much direct new evidence, we once more wish to refer to Rausch (1952): "*The scarcity of records from some countries (such as Finland), would seem to indicate lack of knowledge or inadequate medical facilities rather than any rarity of the parasite.*" Probably the life cycles were present whenever the presence of definitive and intermediate hosts allowed, and humans got infected from hunting, sled, and reindeer herding dogs, but the comparatively benign nature of infection left them subclinical and undiagnosed. Modern health technology, in the form of mobile radiography equipment to detect tuberculosis, also permitted the diagnosis of subclinical CE.

Acknowledgements

We thank Terje Josefsen, The Norwegian Veterinary Institute (NVI), Tromsø, Norway, for finding older Norwegian literature, and especially for showing us the possibility to online access the digitalized yearly reviews on veterinary services and meat inspection.

References

Alvarez Rojas, C.A., Romig, T., Lightowlers, M.W., 2014. *Echinococcus granulosus* sensu lato genotypes infecting humans—review of current knowledge. Int. J. Parasitol. 44, 9–18.

Anon., 1905. Beretning om Veterinærvæsenet og Kjødkontrollen i Norge for året 1903. [Review on veterinary services and meat inspection in Norway in the year 1903.] NOS IV 116. http://www.ssb.no/a/histstat/nos/#xi (In Norwegian).

Arnesen, K., 1953. *Echinokokkcyste* i lunge. [*Echinococcus* cyst in lung.] Tidsskrift for Den norske legeforening 73, 132–134. (In Norwegian).

Bagrade, G., Kirjušina, M., Vismanis, K., Ozoliņš, J., 2009. Helminth parasites of the wolf *Canis lupus* from Latvia. J. Helminthol. 83, 63–68.

Bessonov, A.S., 2002. Echinococcoses of animals and humans in the Russian Federation. In: Craig, P., Pawlowski, Z. (Eds.), Proceedings of the NATO Advanced Research Workshop on Cestode Zoonoses: Echinococcosis and Cysticercosis: an Emergent and Global Problem. Poznan, Poland, 10–13 September 2000, pp. 91–98.

Bjørklund, I., 2013. Domestication, reindeer husbandry and the development of sami pastoralism. Acta Boreal. 30, 174–189.

Cardona, G.A., Carmena, D., 2013. A review of the global prevalence, molecular epidemiology and economics of cystic echinococcosis in production animals. Vet. Parasitol. 192, 10–32.

Castrodale, L.J., Beller, M., Wilson, J.F., Schantz, P.M., McManus, D.P., Zhang, L.H., Fallico, F.G., Sacco, F.D., 2002. Two atypical cases of cystic echinococcosis (*Echinococcus granulosus*) in Alaska, 1999. Am. J. Trop. Med. Hyg. 66, 325–327.

Cederberg, O.-E., 1946. Beiträge zur Kenntnis über das Vorkommen von Echinokokkus-Fällen in Finnland. [Contributions to the knowledge on the existence of echinococcal cases in Finland.]. Acta Chir. Scand., 111–131 (in German).

Eckert, J., Thompson, R.C.A., 1997. Intraspecific variation of *Echinococcus granulosus* and related species with emphasis on their infectivity to humans. Acta Trop. 64, 19–34.

Finstad, G.L., Kielland, K.K., Schneider, W.S., 2006. Reindeer herding in transition: historical and modern day challenges for Alaskan reindeer herders. Nomadic Peoples 10, 31–49.
Folkehelseinstituttet, 2013. Landsomfattende skjermbildeundersøkelser for tuberkulose 1943–1999. [Country-wide X-ray screening for tuberculosis 1943–1999] http://www.fhi.no/artikler/?id=98700 (in Norwegian).
Galibert, F., Quignon, P., Hitte, C., André, C., 2011. Toward understanding dog evolutionary and domestication history. C. R. Biol. 334, 190–196.
Golub, J.E., Mohan, C.I., Comstock, G.W., Chaisson, R.E., 2005. Active case finding of tuberculosis: historical perspective and future prospects. Int. J. Tuberc. Lung Dis. 9, 1183–1203.
Grzybowski, S., Allen, E.A., 1999. Tuberculosis: 2. History of the disease in Canada. Can. Med. Assoc. J. 160, 1025–1028.
Guarnera, E.A., Parra, A., Kamenetzky, L., Garcia, G., Gutierrez, A., 2004. Cystic echinococcosis in Argentina: evolution of metacestode and clinical expression in various *Echinococcus granulosus* strains. Acta Trop. 92, 153–159.
Hellesnes, P., 1935. Rensnyltere. [Reindeer parasites]. Norsk. Vet. Tidskr. 47, 117–137, 194–204. (in Norwegian, with English summary).
Himsworth, C.G., Jenkins, E., Hill, J.E., Nsungu, M., Ndao, M., Thompson, R.C.A., Covacin, C., Ash, A., Wagner, B.A., McConnell, A., Leighton, F.A., Skinner, S., 2010. Emergence of sylvatic *Echinococcus granulosus* as a parasitic zoonosis of public health concern in an indigenous community in Canada. Am. J. Trop. Med. Hyg. 82, 643–645.
Hirvelä-Koski, V., Haukisalmi, V., Kilpelä, S.-S., Nylund, M., Koski, P., 2003. *Echinococcus granulosus* in Finland. Vet. Parasitol. 111, 175–192.
Hueffer, K., Parkinson, A.J., Gerlach, R., Berner, J., 2013. Zoonotic infections in Alaska: disease prevalence, potential impact of climate change and recommended actions for earlier disease detection, research, prevention and control. Int. J. Circumpolar Health 72, http://dx.doi.org/10.3402/ijch.v72i0.19562
Jabbar, A., Narankhajid, M., Nolan, M.J., Jex, A.R., Campbell, B.E., Gasser, R.B., 2011. A first insight into the genotypes of *Echinococcus granulosus* from humans in Mongolia. Mol. Cell. Probes 25, 49–54.
Jernsletten, J.L., Klokov, K., 2002. Sustainable reindeer husbandry. In: Arctic Council, Centre for Saami Studies. University of Tromsø, 57 pp.
Joly, D.O., Messier, F., 2004. The distribution of *Echinococcus granulosus* in moose: evidence for parasite-induced vulnerability to predation by wolves. Oecologia 140, 586–590.
Konyaev, S.V., Yanagida, T., Ingovatova, G.M., Shoikhet, Y.N., Nakao, M., Sako, Y., Bondarev, A.Y., Ito, A., 2012. Molecular identification of human echinococcosis in the Altai region of Russia. Parasitol. Int. 61, 711–714.
Konyaev, S.V., Yanagida, T., Nakao, M., Ingovatova, G.M., Shoykhet,Y, N., Bondarev, A.Y., Odnokurtsev, V.A., Loskutoba, K.S., Lukmanova,G, I., Dokuchaev, N.E., Spiridonov, S., Alshinecky, M.V., Tatyana, S.N., Andreyanov, O.N., Abramov, S.A., Krivopalov, A.V., Karpenko, S.V., Lopatina, N.V., Dupal, T.A., Sako, Y., Ito, A., 2013. Genetic diversity of *Echinococcus* spp. in Russia. Parasitology 140, 1637–1647.
Kummeneje, K., Rognerud, B., Korbi, K., 1981. Echinococcosis in slaughtered reindeer (*Rangifer tarandus*) in northern Norway. Preliminary results of a combat/eradication program. Acta Vet. Scand. 22, 592–593.
Lavikainen, A., 2005. Ihmisen ekinokokkitauti Suomen, Ruotsin ja Norjan Lapissa [Human echinococcosis in Lapland]. Suom. Eläinlääkärilehti 110, 7–13 (in Finnish).
Lavikainen, A., Lehtinen, M.J., Meri, T., Hirvelä-Koski, V., Meri, S., 2003. Molecular genetic characterization of the Fennoscandian cervid strain, a new genotypic group (G10) of *Echinococcus granulosus*. Parasitology 127, 207–215.
Lavikainen, A., Lehtinen, M.J., Laaksonen, S., Ågren, E., Oksanen, A., Meri, S., 2006. Molecular characterization of *Echinococcus* isolates of cervid origin from Finland and Sweden. Parasitology 133, 565–570.
Lebedev, G.B., Romanenko, N.A., Efanov, A.K., Chernyshenko, A.I., Razvaliaeva, L.I., Novosil'tsev, G.I., Efremov, S.B., Artamoshin, A.S., 1996. [The spread of the principal socially important parasitic disease on the territory of the Chukot Autonomous Okrug (ChAO)]. Med Parazitol. (Mosk), 52–54.
Lymbery, A.J., Jenkins, E.J., Schurer, J.M., Thompson, R.C., 2014. *Echinococcus canadensis*, *E. borealis*, and *E. intermedius*. What's in a name? Trends Parasitol., http://dx.doi.org/10.1016/j.pt.2014.11.003, November 28, pii: S1471-4922(14)00186-X [Epub ahead of print].
McManus, D.P., Zhang, L., Castrodale, L.J., Le, T.H., Pearson, M., Blair, D., 2002. Short report: molecular genetic characterization of an unusually severe case of hydatid disease in Alaska caused by the cervid strain of *Echinococcus granulosus*. Am. J. Trop. Med. Hyg. 67, 296–298.
Meltzer, H., Kovacs, L., Orford, T., Matas, M., 1956. Echinococcosis in North American Indians and Eskimos. Can. Med. Assoc. J. 75, 121–127.
Messier, F., Rau, M.E., McNeill, M., 1989. *Echinococcus granulosus* (Cestoda: Taeniidae) infections and moose–wolf population dynamics in southwestern Quebec. Can. J. Zool. 67, 216–219.
Mogoye, B.K., Menezes, C.N., Wong, M.L., Stacey, S., von Delft, D., Wahlers, K., Wassermann, M., Romig, T., Kern, P., Grobusch, M.P., Frean, J., 2013. First insights into species and genotypes of *Echinococcus* in South Africa. Vet. Parasitol. 196, 427–432.
Moks, E., Jõgisalu, I., Saarma, U., Talvik, H., Järvis, T., Valdmann, H., 2006. Helminthologic survey of the wolf (*Canis lupus*) in Estonia, with an emphasis on *Echinococcus granulosus*. J. Wildl. Dis. 42, 359–365.
Moks, E., Jõgisalu, I., Valdmann, H., Saarma, U., 2008. First report of *Echinococcus granulosus* G8 in Eurasia and a reappraisal of the phylogenetic relationships of 'genotypes' G5–G10. Parasitology 135, 647–654.
Nakao, M., McManus, D.P., Schantz, P.M., Craig, P.S., Ito, A., 2007. A molecular phylogeny of the genus *Echinococcus* inferred from complete mitochondrial genomes. Parasitology 134, 713–722.
Nakao, M., Lavikainen, A., Yanagida, T., Ito, A., 2013a. Phylogenetic systematics of the genus *Echinococcus* (Cestoda: Taeniidae). Int. J. Parasitol. 43, 1017–1029.
Nakao, M., Yanagida, T., Konyaev, S., Lavikainen, A., Odnokurtsev, V.A., Zaikov, V.A., Ito, A., 2013b. Mitochondrial phylogeny of the genus *Echinococcus* (Cestoda: Taeniidae) with emphasis on relationships among *Echinococcus canadensis* genotypes. Parasitology 140, 1625–1636.
Pöysti, H., Pöysti, E., 1969. Havaintoja ekinokokkoosista (*E. granulosus*) poroissa [Observations on echinococcosis (*E. granulosus*) in reindeer]. Suom. Eläinlääkärilehti 75, 135–137 (in Finnish).
Pukkila, O., 2009. Röntgensäteilyn käyttö tuberkuloosin vastustamisessa. [The use of X-rays against tuberculosis]. Duodecim 125, 59–65 (in Finnish).
Rau, M.E., Caron, F.R., 1979. Parasite-induced susceptibility of moose to hunting. Can. J. Zool. 57, 2466–2468.
Rausch, R., 1952. Hydatid disease in boreal regions. Arctic 5, 157–174.
Rausch, R.L., 1986. Life-cycle patterns and geographic distribution of *Echinococcus* species. In: Thompson, R.C.A. (Ed.), The Biology of *Echinococcus* and Hydatid Disease. Allen & Unwin, London, pp. 45–80.
Rausch, R.L., 2003. Cystic echinococcosis in the Arctic and sub-Arctic. Parasitology 127, S73–S85.
Rausch, R., Williamson, F.S.L., 1959. Studies on the helminth fauna of Alaska. XXXIV. The parasites of wolves, *Canis lupus* L. J. Parasitol. 45, 395–403.
Rein, K., 1957. Echinokokksykdommen i Nord-Norge. Forekomst og bekjempelse [Echinococcosis in Northern Norway. Distribution and control]. Nord. Med. 58, 1853–1857 (in Norwegian).
Ronéus, O., 1974. Prevalence of echinococcosis in reindeer (*Rangifer tarandus*) in Sweden. Acta Vet. Scand. 15, 170–178.
Røed, K.H., Flagstad, O., Nieminen, M., Holand, O., Dwyer, M.J., Røv, N., Vilà, C., 2008. Genetic analyses reveal independent domestication origins of Eurasian reindeer. Proc. R. Soc. B 275, 1849–1855.
Saarma, U., Jõgisalu, I., Moks, E., Varcasia, A., Lavikainen, A., Oksanen, A., Simsek, S., Andresiuk, V., Denegri, G., Gondzález, L.M., Ferrer, E., Gárante, T., Rinaldi, L., Maravilla, P., 2009. A novel phylogeny for the genus *Echinococcus*, based on nuclear data, challenges relationships based on mitochondrial evidence. Parasitology 136, 317–328.
Schneider, R., Gollackner, B., Schindl, M., Tucek, G., Auer, H., 2010. *Echinococcus canadensis* G7 (pig strain): an underestimated cause of cystic echinococcosis in Austria. Am. J. Trop. Med. Hyg. 82, 871–874.
Schurer, J., Shury, T., Leighton, F., Jenkins, E., 2013. Surveillance for *Echinococcus canadensis* genotypes in *Canadian ungulates*. Int. J. Parasitol. Parasites Wildl. 5, 97–101.
Skjenneberg, S., 1959. Ekinokokkose hos rein i Kautokeino. Faren for overforing til menneske. Bekjempelse. [Echinococcosis in reindeer in Kautokeino. Risk of transmission to humans. Control.]. Nord. Vet. Med. 11, 110–123 (in Norwegian).
Söderhjelm, L., 1946. Echinococcus hydatidosus hos ren (*Rangifer tarandus*). [*Echinococcus hydatidosus* in reindeer (*Rangifer tarandus*).]. Skand. Vet. Tidsskr. 36, 378–381 (in Swedish).
Somily, A., Robinson, J.L., Miedzinski, L.J., Bhargava, R., Marrie, T.J., 2005. Echinococcal disease in Alberta, Canada: more than a calcified opacity. B. M. C. Infect. Dis. 17, 34.
Sweatman, G.K., Williams, J.F., 1963. Comparative studies on the biology and morphology of *Echinococcus granulosus* from domestic livestock, moose and reindeer. Parasitology 53, 493–514.
Tala-Heikkilä, M., 2003. Tuberkuloosi Suomessa. [Tuberculosis in Finland.]. Duodecim 119, 1621–1628 (in Finnish).
Taylor, M.A., Coop, R.L., Wall, R.L., 2007. Veterinary Parasitology, 3rd ed. Blackwell Publishing, Oxford, UK, 874 pp.
Thompson, R.C.A., Boxell, A.C., Ralston, B.J., Constantine, C.C., Hobbs, R.P., Shury, T., Olson, M.E., 2006. Molecular and morphological characterization of *Echinococcus* in cervids from North America. Parasitology 132, 439–447.
Thompson, R.C.A., Lymbery, A.J., 1990. *Echinococcus*: biology and strain variation. Int. J. Parasitol. 20, 457–470.
Titus, K., Haynes, T.L., Paragi, T.F., 2009. The importance of moose, caribou, deer and small game in the diet of Alaskans. In: Watson, R.T., Fuller, M., Pokras, M., Hunt, W.G. (Eds.), Ingestion of Lead from Spent Ammunition: Implications for Wildlife and Humans. The Peregrine Fund, Boise, Idaho, USA http://209.161.5.216/subsites/conference-lead/PDF/0312%20Titus.pdf
Wilson, J.F., Diddams, A.C., Rausch, R.L., 1968. Cystic hydatid disease in Alaska. A review of 101 autochthonous cases of *Echinococcus granulosus* infection. Am. Rev. Respir Dis. 98, 1–15.