ECHINOCOCCUS SPP.: TAPEWORMS THAT POSE A DANGER TO BOTH ANIMALS AND HUMANS – A REVIEW*

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Species of the genus *Echinococcus* (Cestoda; Taeniidae) are minute tapeworms of carnivores. Their larvae are known as hydatids (metacestode), which proliferate asexually in various mammals. Like the majority of cestodes, *Echinococcus* spp. require two different host species to complete their life cycle. Definitive hosts harbouring the adult cestodes in the small intestine are exclusively carnivores of the Canidae and Felidae families. A wide range of mammal species including humans is susceptible to infection by the metacestode of *Echinococcus* spp., which develops in their viscera. The disease, caused by species of the genus *Echinococcus,* is called echinococcosis, and it is one of the most dangerous zoonoses in the world. The traditional species *Echinococcus granulosus* and *Echinococcus multilocularis* are agents of significant diseases due to the high number of cases and the wide geographical species range. The taxonomy of the genus is controversial; in the current state of ongoing complex revisions, the agent of cystic echinococcosis *E. granulosus* sensu lato is divided into five species (*E. granulosus* sensu stricto, *E. felidis, E. equinus, E. ortleppi, E. canadensis*), in addition to the agents of alveolar echinococcosis (*E. multilocularis*, *E. shiquicus*) and polycystic/unicystic echinococcosis (*E. vogeli, E. oligarthrus*). Here we provide an overview of the current situation, which continues to develop.

Echinococcus granulosus s.l., *Echinococcus multilocularis, Echinococcus oligarthrus, Echinococcus shiquicus, Echinococcus vogeli,* echinococcosis

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INTRODUCTION

Echinococcosis is a zoonotic infection caused by adult or larval (metacestode) stages of cestode species belonging to the genus *Echinococcus* (R o m i g , 2003; E c k e r t , D e p l a z e s , 2004). This disease remains a significant problem worldwide (T h o m p s o n , 2008; U m h a n g et al., 2016). Of the three types of echinococcosis, alveolar and cystic echinococcosis are of special importance in humans due to their wide geographical distribution as well as to their medical and economic impact. Polycystic echinococcosis is less frequent and is restricted to areas of Central and South America (E c k e r t , D e p l a z e s , 2004). Species of the genus *Echinococcus* require two different host species to complete their life cycle, the definitive and intermediate host (R o m i g , 2003). Humans are an aberrant intermediate host for the disease, developing life-threatening tissue cysts predominantly in the liver, lungs, and other organs. Infection follows accidental ingestion of eggs released in faeces of infected dogs, foxes, and wild canines. When a human is infected,

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treatment is complicated and carries significant risk (Nasseri-Moghaddam et al., 2011).

The taxonomy of the genus *Echinococcus* has been a controversial issue for decades, and the outcome of recent molecular epidemiological studies reinforces the need to revise the taxonomy of this genus. Several species and subspecies were classified over the last 50 years and subsequently invalidated; however, taxonomic and genetic studies are still ongoing worldwide (Thompson, McManus, 2002; Thompson, 2008; Romig et al., 2015). For instance, Romig (2003) reported four recognized species of the genus *Echinococcus*: *E. granulosus* Batsch, 1786, *E. multilocularis* Leuckart, 1863, *E. oligarthrus* Diesing, 1863, and *E. vogeli* Rausch and Bernstein, 1972 (Fig. 1). Wang et al. (2008) reported seven species in this genus: *E. granulosus*, *E. multilocularis*, *E. oligarthrus*, *E. vogeli*, *E. ortleppi* (Lopez-Neyra and Soler, 1943), *E. equinus* Williams and Sweatman, 1963, and *E. shiquicus* Xiao et al. 2006. Moro, Schantz (2009) reported six recognised species in the genus *Echinococcus*, yet only four of them are of public concern: *E. granulosus*, *E. multilocularis*, *E. oligarthrus,* and *E. vogeli*; the zoonotic transmission potential of the remaining two species – *E. shiquicus* from Tibetian fox and *E. felidis* Ortlepp, 1937 from African lions – is unknown. Romig et al. (2015) provided an overview of the following nine species in the genus *Echinococcus* that is still in place *E. granulosus* sensu stricto: *E. felidis, E. equinus, E. ortleppi, E. canadensis* (these four species cause cystic echinococcois and belong to the species *E. granulosus* sensu lato), *E. multilocularis*, *E. shiquicus* (agents of alveolar echinococcosis), and *E. vogeli* and *E. oligarthrus* (agents of polycystic/multicystic echinococcosis). Genetically, individual species of *E. granulosus* sensu lato (s.l.) include various strains referred to as G1–G10 (Nakao et al., 2007; Huttner et al., 2008; Thompson, 2008; Nakao et al., 2013; Boufana et al., 2015; Romig et al., 2015).

***Echinococcus granulosus* (Batsch, 1786)**

The adult *E. granulosus* (Fig. 2) is a small tapeworm that normally has three segments and a body length of 2–6 mm (Thompson, 1995). The penultimate segment is mature, and the gravid uterus is characterized by well-developed lateral sacculations. The genital pore normally opens posterior to the middle of both the mature and gravid segments (Thompson, McManus, 2001). The metacestode stage (cyst) is a fluid-filled bladder that is usually unilocular, though communicating chambers also occur (Thompson, 1995). This cyst consists of an inner germinal or nucleated layer and an acellular laminated layer of varied thickness. *E. granulosus* typically produces a single-chambered unilocular cyst. In some hosts, especially in humans, large cysts may develop, and daughter cysts may form in the primary mother cyst (Thompson, McManus, 2001). Cystic echinococcosis is caused by the metacestode stage of ten strains or genotypes of *E. granulosus* sensu lato, as is specified below. Two types of hydatid cysts can be observed in various intermediate hosts: (1) fertile cysts, in which brood capsules contain protoscoleces and (2) infertile cysts, which may not produce protoscoleces or are immature and therefore unable to sustain the life cycle of this parasite (Kamenetzky et al., 2000; Lahmar et al., 2004). Hydatid disease infects about 2–3 million humans living in endemic areas of North and South America, Europe, Africa, and Asia (Cummings

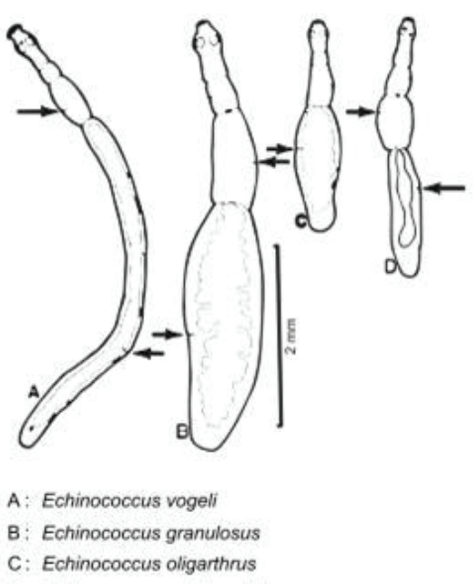

Fig. 1. Four species of the genus *Echinococcus* (Thompson, McManus, 2001)

Fig. 2. Adult *Echinococcus granulosus* (www.phsource.us/PH/PARA/Chapter_8.htm)

et al., 2009). Secondary infection in humans occurs through the expansion of protoscoleces after the accidental rupture of cysts, and the ability of the protoscoleces to develop into new cysts (Thompson, 1995). Typical treatments of this disease include surgery (cyst removal), the PAIR method inside the cyst (puncture, aspiration, injection, re-aspiration), and chemotherapy with benzimidazoles (Kern, 2003). The EG95 vaccine (GenBank 1996, Accession No. Q24797) is effective in protecting grazing animals from infection with *E. granulosus*. With the intention of promoting long-lasting immunity, Umair et al. (2017) tested a chitosan thermo-responsive gel in order to create a depot effect for the EG95 antigen.

Diagnosis of cystic echinococcosis in patients is based on the identification of cyst structures through imaging techniques (ultrasonography, computed tomography, X-ray examinations), and results are confirmed using immunodiagnostic tests to detect specific serum antibodies using immunodiagnostic tests (Kern et al., 2001; Teggi, DiVico, 2002).

The life cycle of *E. granulosus* involves dogs and other canids as definitive hosts of adult intestinal tapeworms, and domestic and wild ungulates as intermediate hosts of the tissue invading metacestode larval stage (Thompson, 1995). *E. granulosus* can be transmitted through the sylvatic cycle, involving wild carnivores and ungulates, or via the domestic cycle, which usually involves dogs and farm livestock. For example, in Australia (Queensland) dingoes serve as definitive hosts and the intermediate hosts include black-striped wallabies *Macropus dorsalis (Gray, 1837*), feral pigs, wallaroos *Macropus robustus Gould, 1841*, and grey kangaroos *Macropus giganteus Shaw, 1790*. A common cause of infection in dogs is the ingestion of sheep offal which contains hydatids.

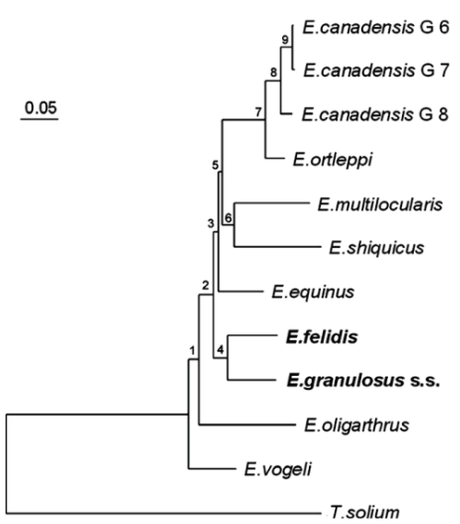

Fig. 3. Phylogram of *Echinococcus* species (Huttner et al., 2008).

This offal often harbours the common G1 genotype, a sheep strain responsible for most cases of human cystic echinococcosis (Yang et al., 2005,2006).

In the past, molecular studies of predominantly mitochondrial DNA sequences have identified 10 genotypes or strains (G1–G10) in *E. granulosus* s.l. (Scott et al., 1997; Lavikainen et al., 2003; McManus, Thompson, 2003; Ito et al., 2007) and the former lion strain (Huttner et al., 2008). Nakao et al. (2007) and Romig et al. (2015) clarified the phylogenetic relationship within this taxonomic group, and in their study, they support classifying genotypes G1 (sheep strain), G2 (tasmanian sheep strain), and G3 (buffalo strain) as *E. granulosus* sensu stricto; genotype G4 (horse strain, *E. equinus*) and G5 (cattle strain, *E. ortleppi*) were confirmed to be species; genotypes G6 (camel strain), G7 (pig strain), G8 and G10 (two cervid strains) were grouped under the species name *E. canadensis.* The species status of genotypes G6–G10 is still ambiguous. Although they currently belong to *E. canadensis,* there is a debate whether the closely related G6 and G7 should be placed in a separate species; however, additional morphological and biological data are needed to support or reject this view (Romig et al., 2015). *E. felidis* (lion strain) was first described in 1937 from lions *Panthera leo* (Linnaeus, 1758) in south Africa. Its life cycle involves wild carnivores and large herbivores. This species has been confirmed in lions and spotted hyenas *Crocuta crocuta* (Erxleben, 1777) as definitive host (Huttner et al., 2009; Kagendo et al., 2014). Huttner et al. (2008) collected faecal samples from lions in Uganda and reported that *E. felidis* and *E. granulosus* sensu stricto are sister species (Fig. 3).

The geographical expansion of *E. granulosus* s.l. is global, and the endemic foci are present on all of the inhabited continents. The highest prevalence of cystic echinococcosis in humans and animal hosts is found in the countries of the temperate zones, including several parts of Eurasia, Australia, some parts of the Americas, and northern and eastern parts of Africa (Dakkak, 2010; Inangolet et al., 2010).

***Echinococcus multilocularis* (Leuckart, 1863)**

The body length of the adult tapeworm *E. multilocularis* (Fig. 4) varies between 1.2 and 4.5 mm, and usually it has four or five segments. The antepenultimate segment is characteristically mature and the genital pore is anterior to the middle of mature gravid segments; the gravid uterus is sac-like structure (Thompson, 1995; Thompson, McManus, 2001). The larval stage (metacestode) of *E. multilocularis* is a complex structure and develops quite differently in comparison to *E. granulosus*. The structure consists of small vesicles containing protoscoleces, which are produced by a germinal layer. The mass of larval stage usually contains a semisolid matrix rather than fluid. Proliferation

occurs endogenously and exogenously (Deplazes, Eckert, 2001; Thompson, McManus, 2001).

Human alveolar echinococcosis is a zoonosis of public health significance as the parasite in a human host behaves like a malignant tumour, predominantly in the liver. Lethality rates had been nearly 100% in untreated patients before the 1970s, when modern treatment methods were not yet established (Eckert, 1998). This disease was first reported in 1852 by Ludwig Buhl and in 1855 by Rudolf Virchow (Tappe, Frosch, 2007). Alveolar echinococcosis is less common in humans. In comparison to cystic echinococcosis, it is more pathogenic, more difficult to treat, and has a higher rate of mortality (Bristow et al., 2012). In Europe, human infections are rare since the tapeworm develops mainly during sylvatic cycle. However, reports show that the parasite is already spreading in Europe (Sreter et al., 2003). Diagnosing human alveolar echinococcosis is based mainly on identifying the parasite lesions using imaging methods (ultrasound examination, computed tomography etc.) and through the detection of specific serum antibodies. Sasaki, Sako (2017) reported that putative serine protease inhibitors (serpins) can influence the mechanisms underlying infiltration into host tissue, as well as immune evasion by larval stage parasites. Treatment is still difficult and complete recovery is only achieved when alveolar echinococcosis is diagnosed early and the entire parasite lesion can be removed surgically; even in such cases, at least two years of chemotherapy is recommended by the WHO (Craig et al., 1996). Symptoms will only occur after long-term incubation (Eckert et al., 2001).

E. multilocularis typically appears during the sylvatic cycle, which includes foxes (predominantly those of the genus *Vulpes* and *Alopex*) as definitive hosts and small mammals, predominantly rodents, as intermediate hosts. In some endemic areas, other species of wild carnivores, such as coyotes, wolves, and racoon dogs, serve as definitive hosts. A synanthropic cycle is known to exist in various epidemiological situations with domestic dogs and cats as definitive hosts, which become infected from rodents originating from the sylvatic cycle (Thompson, 1995; Eckert, 1998; Machnicka-Rowinska et al., 2002). The survival time of this parasite in definitive hosts is estimated to be about 5 months (Eckert, 1998). The larval stage in intermediate hosts and aberrant hosts (including humans) is characterized by the formation of multivesicular cysts and tumour like proliferation in the liver or other organs. This cestode is known as a causative agent of dangerous alveolar echinococcosis in humans (Miterpakova, Dubinsky, 2011). In addition to foxes, dogs and cats can occasionally serve as definitive hosts of the parasite (Dyachenko et al., 2008). Proglotids and eggs are shed in the faeces of the definitive host and can be ingested by rodents such as the common vole (*Microtus arvalis* Pallas, 1778), the water vole (*Arvicola terrestris* Linnaeus, 1758), and the bank vole (*Clethrionomys glareolus* Schreber, 1780) (Eckert, Deplazes, 2004). In Europe the fox population is increasing alongside the prevalence of *E. multilocularis* infection in foxes. Barring historically endemic areas, more and more regions previously considered to be disease-free are now experiencing a higher prevalence of infection (Torgerson, Budke, 2003). Maas et al. (2016) described a new method based on a magnetic capture based DNA extraction, followed by qPCR developed for the detection of the zoonotic parasite *E. multilocularis* in definitive hosts. This method has the advantage of not requiring hazardous chemicals such as phenol-chloroform. Maksimov et al. (2017) demonstrated that the performance of commercial DNA extraction kits for processing *E. multilocularis* eggs in fox faecal samples can vary widely, but certain combinations of DNA extraction kits and PCR protocols can analyze samples containing even a small number of parasite eggs and yield acceptable diagnostic sensitivity as well as diagnostic specificity.

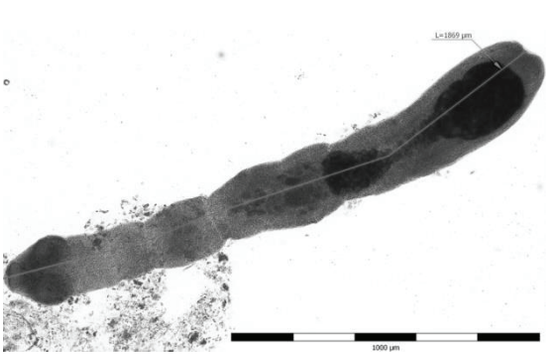

Fig. 4. Adult *Echinococcus multilocularis* (Photo: Adéla Brožová)

The geographical expansion of *E. multilocularis* is confined to palearctic regions of the northern hemisphere, extending from central Europe throughout northern and central Eurasia to the Far East, including Japan, and to North America (Alaska, Canada, northern and central USA). Prior to the end of the 1980s, *E. multilocularis* endemic areas in Europe were limited to eastern France, Switzerland, southern Germany, and western Austria (Schantz et al., 1995; Eckert et al., 2000, 2001). The occurrence of *E. multilocularis* in Western and Central Europe includes regions in Austria, Switzerland, France, Germany, Liechtenstein, Luxemburg, Belgium, the Netherlands, Poland, the Czech Republic, the Slovak Republic, Denmark, and the Norwegian Islands of Svalbard (Schantz et al., 1995; Pavlasek et al., 1997; Dubinsky et al., 1999; Kolarova, 1999; Romig et al., 1999; van der Giessen et al., 1999; Eckert et al., 2000; Vervaeke et al., 2003). The presence of this tapeworm in their definitive or intermediate hosts

has not been evidenced in five European countries: Finland, mainland Norway, Great Britain, Ireland, and Malta (Miterpakova, Dubinsky, 2011; Learmount et al., 2012; Murphy et al., 2012). Using a program of anthelmintic bait distribution, Budgey et al. (2017) developed a model to predict the probability of successful eliminating a focal outbreak of *E. multilocularis.*

Echinococcus shiquicus **(Xiao et al., 2006)**

The cestode *E. shiquicus* was found exclusively in Tibetan foxes *Vulpes ferrilata* Hodgson, 1842 in China (Qinghai – Tibet plateau region) in 2005. This species has two types of adult tapeworms (Fig. 5) containing gravid segments. The first type consists of premature and gravid segments. The second type consists of immature, mature, and gravid segments. Total body length ranges between 1.3 and 1.7 mm. The larval stage (metacestode) has only been found in plateau pikas *Ochotona curzoniae* (Hodgson, 1858). DNA sequencing revealed that five (5%) of 101 pikas have hydatid cysts in their livers. A pulmonary hydatid cyst was also found in one pika. Most of the larval forms were unilocular cysts approximately 10 mm in diameter, and one appeared an oligovesicular form. *E. shiquicus* infections have not been detected in humans (Xiao et al., 2005, 2006). Ma et al. (2012) collected 70 *Echinococcus* samples (larval and adult) from sheep, yak, pikas, voles, dogs, and humans in the Qinghai-Tibet Plateau. The majority of *Echinococcus* samples were identified as *E. multilocularis* and *E. granulosus* s.l. while *E. shiquicus* was determined only in pikas; it is suggested that *E. shiquicus* had restricted intermediate host specificity.

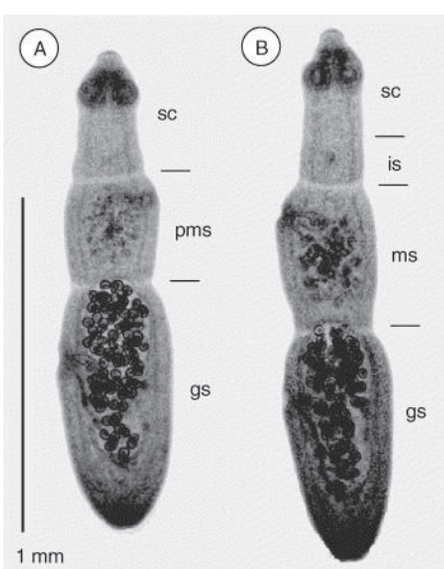

Fig. 5. Two types of adult *Echinococcus shiquicus* (Xiao et al., 2005)

Echinococcus vogeli **Rausch and Bernstein, 1972**

E. vogeli (Fig. 6) has the longest strobila of any member of the genus *Echinococcus*, indicating a maximum length of 12 mm in experimentally infected dogs (D'Alessandro, Rausch, 2008). The adult tapeworm length ranges between 3.9 and 5.6 mm, and usually has three segments. The penultimate segment is mature and the genital pore is situated posterior to the middle of both the mature and gravid segment. The gravid uterus has no lateral branches or sacculations, and is relatively long and tubular in form (Thompson, McManus, 2001).

The life cycle of the South American species *E. vogeli* involves the bush dog (*Speothos venaticus* Lund, 1842) as the natural definitive host, and pacas (*Cuniculus paca* Linnaeus, 1766) and agoutis (*Dasyprocta* spp.) as intermediate hosts. Intestinal stages of *E. vogeli* evidently do not develop in cats or in other species of felids (D'Alessandro et al., 1981; D'Alessandro, Rausch, 2008). *E. vogeli* is a causative agent of polycystic echinococcosis and this disease has been reported in humans in four countries: Colombia, Ecuador, Panama, and Venezuela (D'Alessandro et al., 1979; D'Alessandro, Rausch, 2008).

Fig. 6. Adult *Echinococcus vogeli* (D´Alessandro, Rausch, 2008)

Echinococcus oligarthrus **Diesing, 1863**

It was noted that the frequently used species name *E. oligathrus* is nomenclatorically incorrect (see Huttner, Romig, 2009; Nakao et al., 2013) as *E. oligarthra* is the correct term. However, we have chosen to keep the most commonly used form.

The strobila is 2–3 mm long with three proglottids (Fig. 7). The rostellar hooks are similar to those of *E. vogeli* in length but differ in shape (Rausch, Bernstein, 1972). The genital pore is anterior to the middle in mature segments and approximately at the middle in gravid segments. The gravid uterus is sac-like (Thompson, McManus, 2001).

Neotropical felids serve as definitive hosts of *E. oligarthrus*. Out of ten species indigenous to Central and South America, the following six species have been identified as definitive hosts of this parasite: the pampas cat (*Felis colocolo* Molina, 1782), Geoffroy's cat (*Felis geoffroyi* d'Orbigny and Gervais, 1844), the ocelot (*Felis pardalis* Linnaeus, 1758), the jaguarundi (*Felis yagouaroundi* Geoffroy Saint-Hilaire, 1803), the jaguar (*Panthera onca* Linnaeus, 1758), and the puma (*Puma concolor* Linnaeus, 1771). Moreover, *E. oligarthrus* was found in northern Mexico in one bobcat (*Lynx rufus* Schreiber, 1777), and therefore on agoutis (*Dasyprocta* spp. Illiger, 1811), spiny rats (*Proechimys* spp. Allen, 1899), and pacas (*Cuniculus paca* Linnaeus, 1766) are the documented intermediate hosts. Diseases caused by *E. oligarthrus* are known as unicystic or cystic echinococcosis (D'Alessandro, Rausch, 2008). Basset et al. (1998) observed this disease in a six-year- old boy. The child had a retroocular cystic tumor in the left eye, which caused exophthalmia, chemosis, palpebral ptosis, and blindness.

Fig. 7. Adult *Echinococcus oligarthrus* (D´Alessandro, Rausch, 2008)

CONCLUSION

The taxonomy of *Echinococcus* is not yet to be completely clarified. Diseases caused by agents of this genus remain among the most dangerous zoonoses in the world.

REFERENCES

Basset D, Girou C, Nozais IP, D'Hermies F, Hoang C, Gordon R, D'Alessandro A (1998): Neotropical echinococcosis in Suriname: *Echinococcus oligarthrus* in the orbit and *Echinococcus vogeli* in the abdomen. American Journal of Tropical Medicine and Hygiene, 59, 787–790. doi: 10.4269/ajtmh.1998.59.787.

Boufana B, Lett WS, Lahmar S, Buishi I, Bodell AJ, Varcasia A, Casulli A, Beeching NJ, Campbell F, Terlizzo M, McManus DP, Craig PS (2015): *Echinococcus equinus* and *Echinococcus granulosus* sensu stricto from the United Kingdom: genetic diversity and haplotypic variation. International Journal for Parasitology, 45, 161–166. doi: 10.1016/j.ijpara.2014.10.005.

Bristow BN, Lee S, Shafir S, Sorvillo F (2012): Human echinococcosis mortality in the United States, 1990–2007. PLOS Neglected Tropical Diseases, 6, e1524. doi: 10.1371/journal.pntd.0001524.

Budgey R, Learmount J, Smith GC (2017): Simulating control of a focal wildlife outbreak of *Echinococcus multilocularis*. Veterinary Parasitology, 237, 47–56. doi: 10.1016/j.vetpar.2017.02.022.

Craig PS, Rogan MT, Allan JC (1996): Detection, screening and community epidemiology of taeniid cestode zoonoses: cystic echinococcosis, alveolar echinococcosis and neurocysticercosis. Advances in Parasitology, 38, 169–250. doi: 10.1016/S0065-308X(08)60035-4.

Cummings H, Rodrigues-Sosa M, Satoskar AR (2009): Hydatid disease. In: Satoskar AR, Simon GL, Hotez PJ, Tsuji M (eds): Medical parasitology. Landes Bioscience, Austin, 146–152.

D'Alessandro A, Rausch RL (2008): New aspects of neotropical polycystic (*Echinococcus vogeli*) and unicystic (*Echinococcus oligarthrus*) echinococcosis. Clinical Microbiology Reviews, 21, 380–401. doi: 10.1128/CMR.00050-07.

D'Alessandro A, Rausch RL, Cuello C, Aristizabal N (1979): *Echinococcus vogeli* in man, with a review of polycystic hydatid disease in Colombia and neighboring countries. The American Journal of Tropical Medicine and Hygiene, 28, 303–317. doi: 10.4269/ajtmh.1979.28.303.

D'Alessandro A, Rausch RL, Morales GA, Collet S, Angel D (1981): *Echinococcus* infections in Colombian animals. The American Journal of Tropical Medicine and Hygiene, 30, 1263–1276. doi: 10.4269/ajtmh.1981.30.1263.

Dakkak A (2010): Echinococcosis/hydatidosis: a severe threat in Mediterranean countries. Veterinary Parasitology, 174, 2–11. doi: 10.1016/j.vetpar.2010.08.009.

Deplazes P, Eckert J (2001): Veterinary aspects of alveolar echinococcosis – a zoonosis of public health significance. Veterinary Parasitology, 98, 65–87. doi: 10.1016/S0304-4017(01)00424-1.

Dubinsky P, Svobodova V, Turcekova L, Literak I, Martinek K, Reiterova K, Kolarova L, Klimes J, Mrlik V (1999): *Echinococcus multilocularis* in Slovak Republic: the first record in red foxes (*Vulpes vulpes*). Helminthologia, 36, 105–110.

Dyachenko V, Pantchev N, Gawlowska S, Vrhovec MG, Bauer C (2008): *Echinococcus multilocularis* infections in domestic dogs and cats from Germany and other European countries. Veterinary Parasitology, 157, 244–253. doi: 10.1016/j.vetpar.2008.07.030.

Eckert J (1998): Alveolar echinococcosis (*Echinococcus multilocularis*) and other forms of echinococcosis (*E. vogeli* and

E. oligarthrus). In: Palmer SR, Soulsby EJL, Simpson DIH (eds): Zoonoses. Oxford University Press, Oxford, 689–716.

Eckert J, Deplazes P (2004): Biological, epidemiological, and clinical aspects of echinococcosis, a zoonosis of increasing concern. Clinical Microbiology Reviews, 17, 107–135. doi: 10.1128/CMR.17.1.107-135.2004.

Eckert J, Conraths FJ, Tackmann K (2000): Echinococcosis: an emerging or re-emerging zoonosis? International Journal for Parasitology, 30, 1283–1294. doi: 10.1016/S0020-7519(00)00130-2.

Eckert J, Deplazes P, Craig PS, Gemmell MA, Gottstein B, Heath D, Jenkins DJ, Kamiya M, Lightowlers M (2001): Echinococcosis in animals: clinical aspects, diagnosis and treatment. In: Eckert J, Gemmell MA, Meslin FX, Pawlowski ZS (eds): WHO/OIE manual on echinococcosis in humans and animals: a public health problem of global concern. World Organisation for Animal Health, Paris, 72–100.

Huttner M, Romig T (2009): *Echinococcus* species in African wildlife. Parasitology, 136, 1089–1095. doi: 10.1017/S0031182009990461.

Huttner M, Nakao M, Wassermann T, Siefert L, Boomker JDF, Dinkel A, Sako Y, Mackenstedt U, Romig T, Ito A (2008): Genetic characterization and phylogenetic position of *Echinococcus felidis* (Cestoda: Taeniidae) from the African lion. International Journal for Parasitology, 38, 861–868. doi: 10.1016/j.ijpara.2007.10.013.

Huttner M, Siefert L, Mackenstedt U, Romig T (2009): A survey of *Echinococcus* species in wild carnivores and livestock in East Africa. International Journal for Parasitology, 39, 1269–1276. doi: 10.1016/j.ijpara.2009.02.015.

Inangolet FO, Biffa D, Opuda-Asibo J, Oloya J, Skjerve E (2010): Distribution and intensity of *Echinococcus granulosus* infections in dogs in Moroto District, Uganda. Tropical Animal Health and Production, 42, 1451–1457. doi: 10.1007/s11250-010-9574-6.

Ito A, Nakao M, Sako Y (2007): Echinococcosis: serological detection of patients and molecular identification of parasites. Future Microbiology, 2, 439–449. doi: 10.2217/17460913.2.4.439.

Kagendo D, Magambo J, Agola EL, Njenga SM, Zeyhle E, Mulinge E, Gitonga P, Mbae C, Muchiri E, Wassermann M, Kern P, Romig T (2014): A survey for *Echinococcus* spp. of carnivores in six wildlife conservation areas in Kenya. Parasitology International, 63, 604–611. doi: 10.1016/j.parint.2014.04.001.

Kamenetzky L, Canova SG, Guarnera EA, Rosenzvit MC (2000): *Echinococcus granulosus*: DNA extraction from germinal layers allows strain determination in fertile and nonfertile hydatid cysts. Experimental Parasitology, 95, 122–127. doi: 10.1006/expr.2000.4518.

Kern P (2003): *Echinococcus granulosus* infection: clinical presentation, medical treatment and outcome. Langenbeck's Archives of Surgery, 388, 413–420. doi: 10.1007/s00423-003-0418-y.

Kern P, Reuter S, Buttenschoen K, Kratzer W (2001): Diagnosis of Cystic Echinococcosis (Diagnostik der zystischen Echinokokkose). Deutsche Medizinische Wochenschrift, 126, 20–23. doi: 10.1055/s-2001-9880. (in German)

Kolarova L. (1999): *Echinococcus multilocularis*: new epidemiological insights in Central and Eastern Europe. Helminthologia, 36, 193–200.

Lahmar S, Debbek H, Zhang LH, McManus DP, Souissi A, Chelly S, Torgerson PR (2004): Transmission dynamics of the *Echinococcus granulosus* sheep-dog strain (G1 genotype) in camels in Tunisia. Veterinary Parasitology, 121, 151–156. doi: 10.1016/j.vetpar.2004.02.016.

Lavikainen A, Lehtinen MJ, Meri T, Hirvela-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. doi: 10.1017/S0031182003003780.

Learmount J, Zimmer IA, Conyers C, Boughtflower VD, Morgan CP, Smith GC (2012): A diagnostic study of *Echinococcus multilocularis* in red foxes (*Vulpes vulpes*) from Great Britain. Veterinary Parasitology, 190, 447–453. doi: 10.1016/j.vetpar.2012.07.003.

Ma J, Wang H, Lin G, Craig PS, Ito A, Cai Z, Zhang T, Han X, Ma X, Zhang J, Liu Y, Zhao Y, Wang Y (2012): Molecular identification of *Echinococcus* species from eastern and southern Qinghai, China, based on the mitochondrial cox1 gene. Parasitology Research, 111, 179–184. doi: 10.1007/s00436-012-2815-z.

Maas M, van Roon A, Dam-Deisz C, Opseegh M, Massolo A, Deksne G, Teunis P, van der Giessen J (2016): Evaluation by latent class analysis of a magnetic capture based DNA extraction followed by real-time qPCR as a new diagnostic method for detection of *Echinococcus multilocularis* in definitive hosts. Veterinary Parasitology, 230, 20–24. doi: 10.1016/j.vetpar.2016.10.016.

Machnicka-Rowinska B, Rocki B, Dziemian E, Kolodziej-Sobocinska M (2002): Raccoon dog (*Nyctereutes procyonoides*) – the new host of *Echinococcus multilocularis* in Poland. Wiadomosci Parazytologiczne, 48, 65–68.

Maksimov P, Schares G, Press S, Frohlich A, Basso W, Herzig M, Conraths FJ (2017): Comparison of different commercial DNA extraction kits and PCR protocols for the detection of *Echinococcus multilocularis* eggs in faecal samples from foxes. Veterinary Parasitology, 237, 83–93. doi: 10.1016/j.vetpar.2017.02.015.

McManus DP, Thompson RC (2003): Molecular epidemiology of cystic echinococcosis. Parasitology, 127, S37–S51. doi: 10.1017/S0031182003003524.

Miterpakova M, Dubinsky P (2011): Fox tapeworm (*Echinococcus multilocularis*) in Slovakia – summarizing the long-term monitoring. Helminthologia, 48, 155–161. doi: 10.2478/s11687-011-0023-5.

Moro P, Schantz PM (2009): Echinococcosis: a review. International Journal of Infectious Diseases, 13, 125–133. doi: 10.1016/j.ijid.2008.03.037.

Murphy TM, Wahlstrom H, Dold C, Keegan JD, McCann A, Melville J, Murphy D, McAteer W (2012): Freedom from *Echinococcus multilocularis*: an Irish perspective. Veterinary Parasitology, 190, 196–203. doi: 10.1016/j.vetpar.2012.05.009.

Nakao M, McManus DP, Schantz PM, Craig PS, Ito A (2007): A molecular phylogeny of the genus *Echinococcus* inferred from complete mitochondrial genomes. Parasitology, 134, 713–722. doi: 10.1017/S0031182006001934.

Nakao M, Lavikainen A, Yanagida T, Ito A (2013): Phylogenetic systematics of the genus *Echinococcus* (Cestoda: Taeniidae). International Journal for Parasitology, 43, 1017–1029. doi: 10.1016/j.ijpara.2013.06.002.

Nasseri-Moghaddam S, Abrishami A, Taefi A, Malekzadeh R (2011): Percutaneous needle aspiration, injection, and re-aspiration with or without benzimidazole coverage for uncomplicated hepatic hydatid cysts. Cochrane Database of Systematic Reviews, 1: CD003623. doi: 10.1002/14651858.CD003623.pub3.

Pavlasek I, Chalupsky J, Kolarova L, Horyna B, Ritter J (1997): Occurrence of *Echinococcus multilocularis* Leuckart, 1863, in foxes (*Vulpes vulpes*) in the Czech Republic. Epidemiologie, Mikrobiologie, Imunologie, 46, 158–162. (in Czech)

Rausch RL, Bernstein JJ (1972): *Echinococcus vogeli* sp. n. (Cestoda: Taeniidae) from the bush dog, *Speothos venaticus* (Lund). Zeitschrift für Tropenmedizin und Parasitologie, 23, 25–34.

Romig T (2003): Epidemiology of echinococcosis. Langenbeck's Archives of Surgerye, 388, 209–217. doi: 10.1007/s00423-003-0413-3.

Romig T, Bilger B, Dinkel A, Merli M, Mackenstedt U (1999): *Echinococcus multilocularis* in animal hosts: new data from Western Europe. Helminthologia, 36, 185–191.

Romig T, Ebi D, Wassermann M (2015): Taxonomy and molecular epidemiology of *Echinococcus granulosus* sensu lato. Veterinary Parasitology, 30, 76–84. doi: 10.1016/j.vetpar.2015.07.035.

Sasaki M, Sako Y (2017): The putative serine protease inhibitor (serpin) genes encoded on *Echinococcus multilocularis* genome and their expressions in metacestodal stage. Veterinary Parasitology, 233, 20–24. doi: 10.1016/j.vetpar.2016.11.019.

Schantz PM, Chai J, Craig PS, Eckert J, Jenkins DJ, Macpherson CNL, Thakur A (1995): Epidemiology and control of hydatid disease. In: Thompson RCA, Lymbery AJ (eds): *Echinococcus* and hydatid disease. CAB International, Wallingford, 233–331.

Scott JC, Stefaniak J, Pawlowski ZS, McManus DP (1997): Molecular genetic analysis of human cystic hydatid cases from Poland: identification of a new genotypic group (G9) of *Echinococcus granulosus*. Parasitology, 114, 37–43. doi: 10.1017/S0031182096008062.

Sreter T, Szell Z, Egyed Z, Varga I (2003): *Echinococcus multilocularis*: an emerging pathogen in Hungary and Central Eastern Europe? Emerging Infectious Diseases, 9, 384–386. doi: 10.3201/eid0903.020320.

Tappe D, Frosch M (2007): Rudolf Virchow and the recognition of alveolar echinococcosis, 1850s. Emerging Infectious Diseases, 13, 732–735. doi: 10.3201/eid1305.070216.

Teggi A, DiVico B (2002): The natural history of human cystic echinococcosis (CE) by imaging methods. In: Craig P, Pawlowski Z (eds): Cestode zoonoses: echinococcosis and cysticercosis: an emergent and global problem. IOS Press, Amsterdam, 125–134.

Thompson RCA (1995): Biology and systematics of *Echinococcus*. In: Thompson RCA, Lymbery AJ (eds): *Echinococcus* and hydatid disease. CAB International, Wallingford, 1–50.

Thompson RCA (2008): The taxonomy, phylogeny and transmission of *Echinococcus.* Experimental Parasitology, 119, 439–446. doi: 10.1016/j.exppara.2008.04.016.

Thompson RCA, McManus DP (2001): Aetiology: parasites and life-cycles. In: Eckert J, Gemmell MA, Meslin FX, Pawlowski ZS (eds): WHO/OIE manual on echinococcosis in humans and animals: a public health problem of global concern. World Organisation for Animal Health, Paris, 1–19.

Thompson RCA, McManus DP (2002): Towards a taxonomic revision of the genus *Echinococcus*. Trends in Parasitology, 18, 452–457. doi: 10.1016/S1471-4922(02)02358-9.

Torgerson PR, Budke CM (2003): Echinococcosis – an international public health challenge. Research in Veterinary Science, 74, 191–202. doi: 10.1016/S0034-5288(03)00006-7.

Umair S, Pernthaner A, Deng Q, Gibson B, Hook S, Heath D (2017): Preliminary evaluation of a thermosensitive chitosan hydrogel for *Echinococcus granulosus* vaccine delivery. Veterinary Parasitology, 236, 117–120. doi: 10.1016/j.vetpar.2017.02.007.

Umhang G, Lahoreau J, Hormaz V, Boucher JM, Guenon A, Montange D, Grenouillet F, Boue F (2016): Surveillance and management of *Echinococcus multilocularis* in a wildlife park. Parasitology International, 65, 245–250. doi: 10.1016/j.parint.2016.01.008.

van der Giessen JWB, Rombout YB, Franchimont JH, Limper LP, Homan WL (1999): Detection of *Echinococcus multilocularis* in foxes in the Netherlands. Veterinary Parasitology, 82, 49–57. doi: 10.1016/S0304-4017(98)00263-5.

Vervaeke M, Dorny P, Vercammen F, Geerts S, Brandt J, Van Den Berge K, Verhagen R. (2003): *Echinococcus multilocularis* (Cestoda, Taeniidae) in Red foxes (*Vulpes vulpes*) in northern Belgium. Veterinary Parasitology, 115, 257–263. doi: 10.1016/S0304-4017(03)00212-7.

Wang Z, Wang X, Liu X (2008): Echinococcosis in China, a review of the epidemiology of *Echinococcus* spp. EcoHealth, 5, 115–126. doi: 10.1007/s10393-008-0174-0.

Xiao N, Qiu J, Nakao M, Li T, Yang W, Chen X, Schantz PM, Craig PS, Ito A (2005): *Echinococcus shiquicus* n. sp., a taeniid cestode from Tibetan fox and plateau pika in China. International Journal for Parasitology, 35, 693–701. doi: 10.1016/j.ijpara.2005.01.003.

Xiao N, Qiu J, Nakao M, Li T, Yang W, Chen X, Schantz PM, Craig PS, Ito A (2006): *Echinococcus shiquicus*,

a new species from the Qinghai-Tibet plateau region of China: discovery and epidemiological implications. Parasitology International, 55, S233–S236. doi: 10.1016/j.parint.2005.11.035.

Yang YR, Rosenzvit MC, Zhang LH, Zhang JZ, McManus DP (2005): Molecular study of *Echinococcus* in west-central China. Parasitology, 131, 547–555. doi: 10.1017/S0031182005007973.

Yang YR, Sun T, Zhang JZ, McManus DP (2006): Molecular confirmation of a case of multiorgan cystic echinococcosis. Journal of Parasitology, 92, 206–208. doi: 10.1645/GE-606.R.1

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