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Invited review

Emergence/re-emergence of *Echinococcus* spp.—a global update

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Abstract

This review provides an update of the biological aspects of the genus *Echinococcus* and focuses on newly recognized endemic areas. Infection with the intermediate cystic stage of all species of *Echinococcus* causes disease and incapacity in animals and humans, and in the most serious cases, death of the host. Transmission of *Echinococcus* to new continents has occurred during European colonisation and the parasite has often taken advantage of *Echinococcus*-naive wildlife populations in these new environments, incorporating them into its transmission pattern. *Echinococcus granulosus* consists of a complex of 10 strains. Host specificities of these strains have important implications for transmission and control. As a result of human behaviour and/or political instability in a number of countries *Echinococcus* is re-emerging as an important public health issue. The importance of wildlife reservoirs in perpetuating transmission and as a source of infection for domestic animals and humans is addressed. The review also refers to the transmission pattern of a recently described new species, *Echinococcus shiquicus*, from China.

Keywords: Echinococcus spp.; Echinococcus granulosus; Echinococcus granulosus strain complex; Australia; Africa; America; Asia; China; Europe

1. Introduction

At least one species of the genus *Echinococcus* occurs on all inhabited continents of the world. Members of the genus are cyclophyllidean cestodes with an indirect, two-host lifecycle. Small tapeworms (2–3 mm long) live in the small intestine of carnivores (definitive hosts, usually wild or domestic canids, less commonly felids), and either unilocular or multilocular fluid-filled, hydatid cysts (metacestodes) develop in the internal organs (mainly liver and/or lungs) of intermediate hosts (usually herbivorous or omnivorous mammals). Hydatidosis in intermediate hosts results from accidental ingestion of tapeworm eggs passed into the environment with faeces from definitive hosts. The next generation of tapeworms develops as protoscoleces within the metacestodes and these must be consumed by a definitive host to complete the life cycle. *Echinococcus* species are of medical and veterinary importance because infection with metacestodes may cause severe illness and death in the intermediate host. Transmission occurs through predator/prey relationships in the wild or through deliberate feeding of infected livestock or wildlife offal to dogs, or through dogs scavenging carcasses of intermediate hosts.

Echinococcus granulosus and *Echinococcus multilocularis* are the most important members of the genus in respect of their public health importance and their geographical distribution. Infection with *E. granulosus* metacestodes results in the development of one or several unilocular hydatid cysts that may grow for the life of the host, in humans hydatid cysts can reach a capacity of several litres (Pawlowski et al., 2001). *Echinococcus multilocularis* metacestodes develop as a series of small, interconnected cysts, growing as a metastasising lesion that eventually completely infiltrates the infected organ. Hydatid cysts of *E. granulosus* in humans develop mainly in the liver (70%)

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but also lungs (20%) and 10% of cysts can occur almost anywhere in the body (e.g. brain, body musculature, wall of the heart, kidneys, orbit of the eye, marrow cavity of bones) whilst hydatid lesions of *E. multilocularis* develop almost exclusively in the liver (98–100%), in the later phase of infection distant metastases in other organs may occur (Pawlowski et al., 2001). Diagnosis of infection in humans is reviewed in detail by Pawlowski et al. (2001), but the safest and most convenient method of diagnosing hydatidosis of *E. granulosus* and *E. multilocularis* in humans is with ultrasonography (Macpherson et al., 2003).

The taxonomy of *Echinococcus* has suffered from many decades of uncertainty regarding the taxonomic status of described species and sub-species (Williams and Sweatman, 1963; Verster, 1965; Rausch, 1967; Kumaratilake and Thompson, 1982; Thompson and Lymbery, 1988). This has resulted in confusion regarding the nomenclature of intraspecific variants and impacted negatively on our understanding of the epidemiology of echinococcosis, particularly the nature of transmission patterns (Thompson, 1995; Thompson et al., 1995; Thompson and McManus, 2002). The recent application of molecular tools has helped to resolve many of these issues and Table 1 summarises the current situation that has been extensively reviewed (Thompson and McManus, 2001; 2002; McManus and Thompson, 2003).

There are six species currently recognized in the genus *Echinococcus* with a seventh, *Echinococcus shiquicus,* recently described (Xiao et al., 2005). The *E. granulosus* complex consists of three species and eight defined strains, based on morphology, host specificity and molecular characteristics (Pearson et al., 2002; McManus and Thompson, 2003). The present recognition of *Echinococcus* species reflects a series of largely host-adapted species that are maintained in distinct cycles of transmission (Thompson, 2001; Thompson and McManus, 2002). These are characterised by the principal intermediate hosts, sheep, horses, cattle, camels and different species of rodents (Table 1). Although these cycles of transmission may overlap in some geographical areas, the parasites involved have been shown to maintain their genetic identity (Thompson et al., 1995; Thompson and McManus, 2001; 2002; McManus and Thompson, 2003; Haag et al., 2004).

Echinococcus granulosus is the most widely distributed species and exists as a series of genetically distinct strains/genotypes, some of which are likely to warrant species status in the future, particularly those in pigs, camels, and cervids (Harandi et al., 2002; Thompson and McManus, 2002; Lavikainen et al., 2003). However, more research is required to determine their host and geographic ranges and whether their genetic characteristics are conserved between different endemic regions. With *E. multiloocularis*, a number of isolates have been described from different geographical areas but whether they represent genetic variants with characteristic phenotypes remains to be determined. Studies to date have demonstrated little genetic variation between isolates of *E. multilocularis* (Haag et al., 1999; Rinder et al., 1997; Kedra et al., 2000a). To date, there is no evidence of significant intraspecific variation in *Echinococcus equinus*, *Echinococcus ortleppi*, *Echinococcus oligarthrus* and *Echinococcus vogeli*.

Transmission of *Echinococcus*, particularly within the domestic situation, is influenced by human activities and behaviour, politics and the presence of wildlife reservoirs. It has been demonstrated that concerted action and political will can result in the eradication of *Echinococcus*

Table 1
Echinococcus species, strains and genotypes

Species	Strain/genotype	Known intermediate hosts	Infective to humans	Disease in humans	Known definitive hosts
Echinococcus granulosus	Sheep/G1	Sheep (cattle, pigs, camels, goats, macropods)	Yes	Cystic (Unilocular)	Dog, fox, dingo, jackal and hyena
	Tasmanian sheep/G2	Sheep (cattle?)	Yes	Cystic (Unilocular)	Dog, fox
	Buffalo/G3	Buffalo (cattle?)	?	?	Dog, fox?
	Camel/G6	Camels (sheep)	Yes	Cystic (Unilocular)	Dog
	Pig/G7	Pigs	Yes	Cystic (Unilocular)	Dog
	Cervid/G8 and G10	Cervids	Yes	Cystic (Unilocular)	Wolf, dog
	?/G9		Yes	Cystic (Unilocular)	
	Lion/?	Zebra, wildebeest, warthog, bushpig, buffalo, various Antelope, giraffe? Hippopotamus?	?	?	Lion
Echinococcus equines	Horse/G4	Horses and other equines	No	–	Dog
Echinococcus ortleppi	Cattle/G5	Cattle	Yes	Cystic (Unilocular)	Dog
Echinococcus multilocularis	Some isolate variation (see text)	Rodents, domestic and wild pig, dog, monkey, (hors?)	Yes	Alveolar (multivesicular)	Fox, dog, cat, wolf, racoon-dog, coyote
Echinococcus shiquicus	?	Lagomorphs (pika)	?	?	Tibetan fox
Echinococcus vogeli	None reported	Rodents	Yes	Polycystic	Bush dog
Echinococcus oligarthrus	None reported	Rodents	Yes	Polycystic	Wild felids

Data from Thompson et al., 1995; Thompson and McManus, 2001; McManus and Thompson, 2003; Xiao et al., 2005.

(in the absence of a wildlife reservoir), as with *E. granulosus* from Iceland (Beard, 1973) and more recently also from Tasmania, Australia (Beard et al., 2001) and New Zealand (Pharo, 2002). However, more commonly human activities and/or behaviour, promotes transmission of *Echinococcus*. For example, on a global level, European colonisation was responsible for the translocation of *E. granulosus* with domestic animals from the northern hemisphere to all the continents of the southern hemisphere. Despite efforts to control *Echinococcus* in many parts of the world it remains a public health problem and in a number of countries, particularly following recent political changes, *Echinococcus* is re-emerging as an major public health issue, for example in Central Asia (see Western and Central Asia, below).

This review, while giving an overview of the current epidemiological situation worldwide, highlights newly recognised endemic areas and apart from the brief mention above, recent advances in human screening, diagnosis and treatment are not covered.

2. Echinococcus granulosus complex

It has long been recognised that *E. granulosus* possesses a high degree of genetic divergence. Various strains (designated G1 to G10) also exhibit differences in morphology, development rate, host range, pathogenicity and geographical distribution (Thompson et al., 1995; Thompson and McManus, 2001). While some of these strains are still poorly characterised, the available data for others are sufficient for preliminary epidemiological analyses. For two former strains, the evidence was sufficient to recognize them as species (*E. equinus* and *E. ortleppi*) on the basis of their genetic distinctness, different intermediate host preferences and sympatric occurrence without inter-breeding (Thompson and McManus, 2002).

Two strains of *E. granulosus* appear to be specifically adapted to sheep as intermediate hosts, although they may also affect other animals. One of them, the common sheep strain (G1) occurs on all continents in areas of extensive sheep farming. The presence of this strain coincides with areas of high prevalence of human cystic echinococcosis (CE) (e.g. in Morocco, Tunisia, Kenya, Kazakhstan, western China and Argentina), and preliminary genetic analyses of isolates suggest that it is the principal strain infecting humans (Thompson and McManus, 2001; 2002; Eckert et al., 2001a; Dinkel et al., 2004).

A genetically closely related assemblage of strains, tentatively retained in *E. granulosus*, consists of the camel strain (G6), the pig strain (G7), two cervid strains (G8 and G10) and a genotype which was found in human patients in Poland (G9). They are poorly distinguished from each other, and may be geographic variants of the same taxon (species). Epidemiological data on this group are still limited, but they are clearly distinct from the common sheep strain (Thompson and McManus, 2002). The camel strain is found in the Middle East, Africa, southern Asia and South America, and principally affects camels and goats (Thompson and McManus, 2001). Sporadic cases of human infection are known from Nepal, Iran, Mauritania, Kenya and Argentina (Thompson and McManus, 2002; Dinkel et al., 2004). The pig strain is transmitted by domestic pigs in Europe, Asia and South America, and a closely related genotype (G9) (with an unknown animal reservoir) has been described from Polish patients (Scott et al., 1997). The cervid strains are known from arctic and subarctic regions of Europe, Asia and North America, where they are transmitted between wolf (*Canis lupus*) and wild cervids (e.g. moose (*Alces alces*)). In northern Eurasia, dogs and domestic reindeer can also be involved. Human cases are known, but the resulting disease is described as more benign than CE caused by other forms of *E. granulosus* (Wilson et al., 1968). In total, human pathogenicity of this group of genotypes appears to be low (awaiting further data), and the predominant presence of these taxa may explain the relative scarcity of human CE in some regions where infection is highly endemic in animals, e.g. the Middle East, parts of north-eastern Africa, and parts of eastern Europe.

Echinococcus equinus was formerly known as the horse strain (G4) of *E. granulosus*. It is known from Europe, the Middle East and South Africa, and appears to use equines (horses, donkeys and zebras), exclusively, as intermediate hosts. No human cases are known, and epidemiological evidence suggests that it may be apathogenic to humans (Thompson and McManus, 2001; Thompson, 1995).

Echinococcus ortleppi, the former cattle strain (G5), is adapted to transmission by cattle (a poor host species for other *Echinococcus* taxa) and is on record from Europe, Asia, parts of Africa and South America. Only one isolate from a human patient has been allocated to this species (Bowles et al., 1992) that suggests this species may be less pathogenic to humans than the sheep strain of *E. granulosus*.

Apart from the taxa mentioned above, more strains or species of the *E. granulosus* complex undoubtedly exist. There is a poorly characterised form transmitted by water buffalo in South Asia, and in Africa a wildlife strain ('lion strain') was described from lions (*Panther leo*) and a variety of wild ungulates, including various species of antelope, and warthogs (*Phacochoerus aethiopicus*) (Macpherson and Wachira, 1997). Currently, nothing is known about the susceptibility of humans to these forms.

3. New data from geographical regions

3.1. Australia

Details of the origins of *Echinococcus* in Australia and transmission patterns have been reviewed in Jenkins and Macpherson (2003); Jenkins (2005). The G1, common sheep strain of *E. granulosus* (Pearson, 2002; McManus and Thompson, 2003) is the only member of the genus currently found in Australia, but a strain designated G2 was previously also found in Tasmania. This G2 strain was biologically distinct from the mainland G1 strain, in that the pre-patent period for adult G2 tapeworms was several days shorter than for G1 tapeworms (McManus and Bryant, 1995). The G2 variant is thought to have evolved either as a result of selection pressure during the rigid six weekly anthelmintic dosing of dogs during the Tasmanian hydatid control campaign, or from a rare genotype (that may also be present on the mainland) becoming dominant because of the limited gene pool on an island (McManus and Bryant, 1995). Despite *E. granulosus* being highly prevalent in domestic animals and a major public health problem in Tasmania (Schantz et al., 1995), the absence of dingoes (*Canis lupus dingo*) on the island appears to have been the key factor for hydatid infection never establishing in Tasmanian wildlife. Following 30 years of intense hydatid control, provisional eradication of *E. granulosus* from Tasmania was announced in 1996 (Beard et al., 2001).

Historically, hydatidosis has been a serious public health issue in Australia (Gemmell, 1990). However, determining current prevalence in Australian is difficult because routine reporting/monitoring of hydatidosis/echinococcosis is not undertaken for any species. Any recording is ad hoc by interested individuals, making identification of trend changes difficult to determine. Nevertheless, available data highlights wildlife reservoirs as important in the perpetuation of *E. granulosus* on mainland Australia, acting as a constant source for transmission to domestic livestock, domestic dogs and humans (Banks, 1984. Epidemiology of *Echinococcus granulosus* in Tropical Queensland. PhD Thesis, James Cook University of North Queensland; Hope et al., 1992; Jenkins and Morris, 1991; 2003; Thompson et al., 1987; Grainger and Jenkins, 1996; Jenkins and Power, 1996; Jenkins et al., in press).

The areas of most active transmission of *E. granulosus* in wildlife are associated with the Great Dividing Range in the eastern states of Australia and in Western Australia, south of Perth (Jenkins and Macpherson, 2003). In south eastern Australia, infection prevalence in wild dog (dingoes and dingo/domestic dog hybrids) populations may be as high as 100% with worm burdens in excess of 100,000 worms (Grainger and Jenkins, 1996; Jenkins and Morris, 1991; 2003). Prevalence in some species of native wildlife intermediate hosts, locally, can be more than 60% (Jenkins and Morris, 2003). The intermediate hosts most commonly involved in transmission in eastern Australia are eastern grey kangaroos (*Macropus gigantea*), red necked wallabies (*Macropus rufogriseus*) black striped wallabies (*Macropus dorsalis*) and swamp wallabies (*Wallabia bicolour*) (Banks, 1984. Epidemiology of *Echinococcus granulosus* in Tropical Queensland. PhD Thesis, James Cook University of North Queensland; Jenkins and Morris, 2003) and in Western Australia, western grey kangaroos (*Macropus fuliginosus*) (Thompson et al., 1988). Other native and introduced species may also be involved in transmission, these include other species of macropodid marsupials (Jenkins and Macpherson, 2003), wombats (*Vombatus ursinus*) (Grainger and Jenkins, 1996), feral pigs (*Sus scrofa*) (Banks, 1984. Epidemiology of *Echinococcus granulosus* in Tropical Queensland. PhD Thesis, James Cook University of North Queensland; Lidetu, 1992. Epidemiological, serological and histopathological studies on sylvatic hydatid disease in North Queensland. MVSc Thesis, James Cook University of North Queensland; Thompson et al., 1988; Jenkins and Morris, 2003) and foxes (*Vulpes vulpes*) (Jenkins and Craig, 1992; Grainger and Jenkins, 1996; Jenkins and Morris, 2003; Jenkins et al., 2005). A recently described phenomenon in Australia has been the infiltration of urban centers by *E. granulosus*-infected wildlife definitive hosts. This trend was first described in Australia with foxes (Jenkins and Craig, 1992) and in 2003 Brown and Copeman reported infection in wild dogs caught in the outer suburbs of Townsville (Queensland). Most recently, wild dogs trapped in urbanised areas and in bush adjacent to urban development on the Sunshine Coast (Queensland) have also been found to be infected with *E. granulosus* (Jenkins and Allen, unpublished data). This infiltration of urban centers with *E. granulosus*-infected wildlife definitive hosts is of concern because these animals are attracted to public recreation areas, especially those with barbecue and picnic facilities, to scavenge food scraps, places also commonly frequented by urban residents.

A recent *E. granulosus*-coproantigen study of faeces from wild quolls (*Dasyrurus maculatus*), the largest native marsupial carnivore still inhabiting mainland Australia, failed to identify a positive sample (Jenkins et al., 2005). These animals were living in an area where *E. granulosus* infection in dingoes and foxes is common and the faeces from some of the animals tested contained the remains of swamp wallabies, an important intermediate host for *E. granulosus* in the same area. Experimental infection studies with other dasyurid species have failed to induce infection (references cited in Jenkins et al., 2005) and this led the authors to speculate dasyurids may be refractory to infection with *E. granulosus*. This speculation prompted Jenkins (in press) to suggest a reason for the lack of *E. granulosus* infection in wildlife in Tasmania could have been because the thylacine (*Thylacinus cynocephalus*) top order predator, also a dasyurid, was refractory to infection and despite thylacines being common and predating settler's sheep in Tasmania, they never acted as the conduit for transmission of *E. granulosus* from sheep to macropodids as occurred with dingoes on the Australian mainland.

Hydatid infection is still seen regularly in sheep in abattoirs but anecdotal reports suggest that the occurrence of infected sheep seen at slaughter is lower than 20 years ago. Infected sheep usually occur on farms where domestic dog management is poor and/or where there is a problem with wild dogs predating sheep and contaminating the pasture with eggs of *E. granulosus* (Grainger and Jenkins, 1996). Anecdotal evidence also suggests that hydatid infection in cattle sent for slaughter in Queensland is becoming more common. Hydatidosis has been identified as a major economic drain for the state's cattle meat industry causing, conservatively, estimated annual losses of $2.7 million (Taylor, Queensland Department of Primary Industries and Mines, quoted in Thompson, 2003). The prevalence of *E. granulosus* infection in wild dogs in many areas of Queensland is high (Durie and Riek, 1952; Banks, 1984). Epidemiology of Echinococcus granulosus in Tropical Queensland. PhD Thesis, James Cook University of North Queensland; Jenkins, unpublished data), with transmission occurring being between wild dogs and macropodid marsupials, with cattle as accidental intermediate hosts. High levels of hydatid infection in cattle have also been reported in northern Western Australia (Lymbery et al., 1995), but the source of infection has yet to be confirmed.

The number of new cases of human hydatidosis diagnosed annually in Australia appears stable at somewhere between 80 and 100 (Jenkins and Power, 1996; Jenkins, 2004). Human hydatidosis has traditionally been a public health problem of rural people but there is increasing potential for accidental exposure of urban residents to *E. granulosus*-infected wild dog and fox faeces (Jenkins and Craig, 1992; Brown and Copeman, 2003; Jenkins and Allan, unpublished data). The dogs of recreational pig hunters living in urban centers have also been demonstrated to be a potential public health risk (Thompson et al., 1988). Alternatively, urban residents could become accidentally exposed to *E. granulosus* eggs through direct contact with wild dog/fox faeces or via coprophagous flies when visiting parks and forests for recreational purposes or through visiting their own bush retreats, in remote locations.

The prevalence of *E. granulosus* infection in Australian rural domestic dogs has steadily decreased during the last 30 years to levels below 10% (Jenkins, 1996). This has largely been due to the development and use of praziquantel (Andrews et al., 1983) and commercial, inexpensive, nutritionally balanced dry dog food. However, two recent surveys of coproantigens of *E. granulosus* in the faeces of rural domestic dogs in south eastern Australia revealed prevalence levels of 29% in New South Wales and 18% in Victoria (Jenkins et al., in press). These unexpected results strongly suggested a re-emergence of domestic transmission of *E. granulosus* in some areas of rural south eastern Australia. Wildlife was found to be the main source of infection through some farmers reported feeding raw meat and offal to their dogs, commonly from kangaroos and feral pigs. The farms most commonly found with infected dogs were those with more than five dogs, located in the vicinity of national parks or state forest where farmers commonly hunted wildlife. However, the superior sensitivity of the coproantigen assay over arecoline purging and serum antibody detection (Craig et al., 1995) as the survey tool may have been partly responsible for the unexpectedly high prevalence of infection in these rural dogs.

3.2. Western and Central Asia

In Iran, the sympatric existence of G1 and G6 transmission cycles was recently shown by morphological and molecular methods (Harandi et al., 2002). While G1 was most common, affecting sheep, goats, cattle and camels, G6 was found in camels, sheep and cattle. In humans, three of 33 were diagnosed as G6, the rest as G1.Apart from confirming the pathogenicity of G6 for humans, the study underlines the need for discrimination of different *Echinococcus taxa* when assessing the epidemiological situation in western and central Asia.

For a detailed insight into the present Echinococcus infection situation in Central Asia, the reader is directed to a collection of papers contained in the proceedings arising from a meeting held in Cholpan Alta, Kyrgystan in September 2004 (Shaikenov and Torgerson, 2004; Aminjanov and Aminjanov, 2004; Muminov, et al., 2004; Isakov et al., 2004; Kuttubaev et al., 2004).

The collapse of the Soviet Union in 1992 caused major social and political disruption in the newly independent central Asian states (Kazakstan, Uzbekistan, Kyrgystan, Tajikistan and Turkmenistan) with concomitant collapse of veterinary and public health services followed by the re-emergence of hydatid disease. The breakdown of large state farms under veterinary supervision, treatment of rural dogs and large state-run abattoirs with offal disposal are factors in hydatisdosis re-emergence. Since 1992 in Kazakstan, for example, the large state farms have been broken into many small private farms each with a few sheep, cattle, horses and dogs that live in close proximity to the living area of the owners and their family. During the Soviet administration two to three dogs and three to four shepherds were responsible for the husbandry of 600–700 sheep that were rotated around several grazing pastures. Under the present system, flocks of around 10,000 sheep may now be under the supervision of about 35 people accompanied by about 50 dogs. Farmers now kill sheep at home for their own consumption and commonly feed the raw offal to their dogs. Prevalence of infection in sheep ranges from 20 to 25% in 1-year-old sheep to 74–80% in sheep 6 years old and over. The prevalence of infection in rural and village dogs is 23 and 6%, respectively, with the highest worm burdens also in rural dogs (Shaikenov and Torgerson, 2004). While village dogs have a lower prevalence of infection and worm burden, their proximity to human habitation amplifies their role in transmitting disease to humans (Shaikenov and Torgerson, 2004). Human infection in Kazakstan was steady at around 200 surgical cases annually from 1992 until 1995, but after 1995, the number of surgical cases began to increase to the current level of nearly 1000 cases per year (Torgerson et al., 2000; 2002). A similar increase in human cases has been noted in all other Central Asian countries. The contribution of wildlife in the transmission of *E. granulosus* in Central Asia is incompletely understood.

3.3. China

It is difficult to determine if cystic hydatidosis is increasing in China. Increasing numbers of people are treated annually, but this may just reflect improved diagnostic methods and improved outreach programs contacting communities hitherto poorly served with medical facilities. For a detailed description of the Chinese situation, the reader is referred to the review of Craig (2004).

Since the 1950s about 35,000 cases of human cystic echinococcosis have been treated surgically in China but this figure underestimates incidence as many people lack symptoms or access to medical treatment. In Xinjiang alone, 21,560 cases have been identified from 58 hospitals and prevalence rates up to 80 cases/100,000 population have been reported for north central Xinjiang (Chi et al., 1990). Ultrasound surveys indicate a high endemic zone for *E. granulosus* stretching from western Xinjiang to Sichuan with the highest prevalence rates occurring in pastoral communities on the eastern Tibetan Plateau (south western Qinghai and north western Sichuan) and the Tibetan autonomous area of south Gansu (references cited in Craig, 2004). In addition, human hydatidosis is also a major public health problem in large areas of Tibet, especially Nakqu and Lhasa Prefectures, Xinjiang Uygar Automonous Region and south Ningxia Hui Autonomous Region. Hydatid disease also occurs at lower altitudes, particularly on small farms run by Han Chinese who own a few dogs and small numbers of livestock (Craig, 2004).

China has large national herds of livestock, more that 250 million sheep and goats and over 100 million other livestock species (horses, donkeys, camels, yaks and cattle). High prevalence of hydatid infection has been reported in all species (up to 99% in sheep and yaks; 88% in cattle; 70% in pigs), although there is no doubt hydatid disease is highly prevalent in many areas, some of these data should be regarded with caution because in some instances, it has been revealed metacestodes of *Taenia hydatigena* were included in hydatid cyst counts (Craig, 2004). Prevalence of *E. granulosus* in necropsy surveys in domestic dogs has been reported up to 82.3% Transmission of *E. granulosus* in wildlife has not been fully elucidated (Craig, 2004) but cycles between ungulates and wolves are likely.

3.4. Africa

Africa contains great diversity of the *E. granulosus* complex, with five taxa confirmed or suspected. However, most regions are poorly researched, and only limited information is available (Macpherson and Wachira, 1997; Ibrahem and Gusbi, 1997; Kachani et al., 1997). The highest human incidence rates are reported from sheep raising areas of North and East Africa, where the common sheep strain (G1) appears to be the dominant taxon. On the other hand, the exclusive presence of the camel strain (G6), although it may be frequent in livestock and dogs, was found to be associated with few human cases e.g. in Mauretania (Bardonnet et al., 2001). An extensive genetic survey of *Echinococcus* isolates from human surgical patients was undertaken in the border area of northwestern Kenya and south-eastern Sudan. Of 179 isolates from humans, only one to the camel strain (G6) and the remaining 178 were the common sheep strain (G1) despite both G1 and G6 being highly prevalent in local livestock (Dinkel et al., 2004). In contrast, recent surveys in central Sudan found G6 and *E. ortleppi*, but failed to detect any isolate of G1, which, despite the presence of large numbers of sheep, may be absent from that region (Elmahdi et al., 2004). Animals, especially camels, are frequently infected (44.6% of 242 camels), but human echinococcosis cases from that area (Elmahdi et al., 2004) were all diagnosed as G6 (Omer et al., 2004). These new results call for a re-assessment of the reasons for the curiously focal distribution of human cystic echinococcosis in Africa (Macpherson and Wachira, 1997). In addition to behavioural practises, high prevalence may also reflect different levels of infectivity of the locally occurring strains and species of *Echinococcus*.

The nature of *Echinococcus* in African wildlife is poorly understood. On the basis of morphology, isolates from South African zebra (*Equus burchelli*) have been allocated to *E. equinus* (as the 'horse strain') (Kumaratilake et al., 1986) and cysts of zebra origin were shown to be infective to lions (*P. leo*) (Young, 1975). However, also in South Africa, from lions a distinct 'lion strain' was described (Verster, 1965). In central Africa, *Echinococcus* of lions was shown to be transmitted via warthogs, and cysts from warthogs there were experimentally non-infective to dogs (refs. in Macpherson and Wachira, 1997). This apparent confusion can in future only be resolved with molecular methods. The same applies to the questions, of whether these taxa interact with domestic animals (cattle, sheep, dogs) and/or if they infect humans.

3.5. Europe

Within Europe, cystic echinococcosis of animals is rare in northern and central Europe (with the exception of Poland and regions further east). Human cases only occur sporadically, the most affected region being the Mediterranean (e.g. parts of Spain, southern Italy and Sardinia), where annual incidence rates for human CE of four to eight per 100,000 have been reported, and the sheep raising areas of Great Britain (Eckert et al., 2001a). These foci appear to coincide with the distribution of the sheep strain (G1), which supports the hypothesis of this strain as the principal cause of human cystic echinococcosis.

Members of the strain cluster G6-G10 occurring in Eastern Europe are referred to as the 'pig strains'. Confirmed records of domestic pig infection exist from

Poland, Slovakia and Ukraine, but human infection is rare. Wild boar (*S. scrofa*) may also be involved in transmission in some areas (e.g. Ukraine) (Kedra et al., 2000b; Snabel et al., 2000). Cervid-transmitted echinococcosis has been reported to occur in northern Fennoscandia (Finland). Recently, isolates from cervids in Finland were found to differ genetically from the previously described North American cervid strain G8, and were allocated to a new strain, G10 (Lavikainen et al., 2003). Transmission seems to occur between wolves (*C. lupus*) and semi-domesticated reindeer (*Rangifer tarandus fennicus*) in Finland (Hirvelä-Koski et al., 2003) but other prey of wolves such as wild forest reindeer and elk (*A. alces*) populations may be involved. This report is the first for *E. granulosus* in wolves. Between 1979 and 1991 there was a single case from abattoir-slaughtered reindeer and while numbers have been steadily increasing, the prevalence remains extremely low. Finland has a small, but slowly increasing, wolf population (Kojola 2000, 2001) but there are no resident wolf packs in the reindeer herding areas and lone wolves straying into these areas are quickly killed. This situation should continue to be regularly monitored, including sampling domestic dogs in the areas from which any infected reindeer arise.

There are no recent epidemiological data on other members of the *E. granulosus* complex in Europe. *Echinococcus equinus* appears to use equines, exclusively, as intermediate hosts and it appears not to be infective to humans (Thompson, 1995). *Echinococcus ortleppi* is adapted to transmission by cattle. The previous cattle-based transmission cycles in Germany and Switzerland (Eckert et al., 2001a) are attributed to this species. Frequent records from slaughtered animals occurred until as late as the 1980s (Eckert and Thompson, 1988), but the taxon is by now considered to be extinct in many regions or reduced to sporadic occurrence. A single isolate from a human patient in the Netherlands has been the only case allocated to this species (Bowles et al., 1992).

Echinococcus granulosus is endemic in parts of central Wales and the borderlands with England. A recent re-emergence of *E. granulosus* in Wales has been reported (Buishi et al., 2005) following the cessation of six weekly dosing of farm dogs with praziquantel in 1989, in favour of hydatid education of children in schools. Between 1989 and 2002 prevalence in rural dogs rose from 3.4 to 8.1%.

3.6. North America

For the most recent detailed review of the situation in North America the reader is referred to Schantz et al. (1995). Two strains of *E. granulosus* occur in North America, the cervid strain occurring in wildlife mainly in Canada, Alaska and Minnesota (Peterson, 1977). Cysts reported in mule deer (*Odocoileus hemionus*) in California (Romano et al., 1974) may also be the cervid strain. The sheep strain occurs in sheep and domestic dogs and coyotes (*Canis latrans*) in sheep rearing areas in the western States (Arizona, California, New Mexico and Utah), but human cases are rare, restricted to high-risk groups, sheep farmers and some tribes of native Americans farming sheep (Schantz et al., 1995).

Echinococcus granulosus is thought to have been introduced into the USA with infected livestock and the parasite initially became established in a domestic dog/domestic pig transmission pattern in Mississippi, Louisiana, Tennessee and Arkansas also with transmission to humans (Schantz et al., 1995). Hydatid disease has been a problem in the sheep rearing areas of the western United States including Arizona, California, New Mexico and Utah from the 1960s. The source of these *E. granulosus* was Australian sheep dogs imported into Utah in 1938 (Crellin et al., 1982) and the parasite spread to sheep rearing areas of adjoining states through trading live sheep from Utah (Crellin et al., 1982). A focus of sheep and human infection in California in the mid-1960s was traced back to an area where transhunant grazing was practiced by people of Basque origin who fed their dogs on sheep carcasses and offal (Schantz et al., 1995). In Arizona and New Mexico, infection occurs in some tribes of native Americans that raise sheep, home slaughter and keep many dogs (Schantz, 1977). Transmission in Utah has been greatly reduced through a control program (Andersen 1997).

Echinococcus granulosus was first reported in Canada by Osler (1883, cited in Webster and Cameron, 1967), human infection was considered to be rare until the 1950s following the instigation of routine chest X-rays for tuberculosis. These X-rays identified many native Americans (Indians and Eskimo) with pulmonary hydatidosis, in the north west territories, more than 40% of members of some tribes were found infected (Webster and Cameron, 1967). A wildlife reservoir was reported between the larger cervids and wolves, coyotes and domestic dogs and it was considered that the *E. granulosus* strain in wildlife did not infect domestic livestock (Webster and Cameron, 1967).

More recently (2002/2003) hydatid infection was found unexpectedly in farmed elk (*A. alces*) in Alberta (Olson and Ralston, unpublished data). The prevalence rate in 400 slaughtered mature elk was 4% with no infection found in any of the reindeer (*Rangifer tarandus*) so far examined. The source of infection for these farmed elk is unclear, but it is suspected to be domestic farm dogs and/or coyotes. Molecular studies are currently underway to determine the strain and transmission pattern of these parasites.

3.7. South America

As in Australia, all species of the *E. granulosus* complex have been accidentally introduced from Europe or other regions together with domestic animals. It is therefore not surprising, that a variety of species and genotypes exist in this subcontinent. The most ubiquitous taxon is the *E. granulosus* G1, which is well documented in the major sheep raising regions, e.g. of Argentina and Chile

(Eckert et al., 2001a). The economic and public health impact of sheep-transmitted echinococcosis can be considerable, and a re-emergence of transmission has been documented in Peru after the collapse of previous control activities. There, in the central Andes, 77% of 212 sheep were found to be infected (Dueger and Gilman, 2001). The presence of other strains or species in South America is complex, and only partially resolved. In Argentina, four strains (G1, G2, G6, G7 and some variants) of *E. granulosus* and *E. ortleppi* were found in different host animals (Kamenetzky et al., 2002; Haag et al., 2004), while in neighbouring southern Brazil (Rio Grande do Sul) *E. granulosus* G1 and *E. ortleppi* were recorded (Haag et al., 1999; De la Rue et al., 2004). In the absence of camels, goats seem to be the principal hosts for G6—their suitablility as hosts corresponds to findings from East Africa (Wachira et al., 1993; Dinkel et al., 2004). Isolates from human patients in Argentina could be allocated to G1, G2, G6 and *E. ortleppi*. The number of genetically characterized isolates is too small to allow conclusions on economic and public health impact of different taxa, but a recent survey in Argentina demonstrated that the geographical distribution of genetic variants is likely to reflect time and origin of livestock introduction (Haag et al., 2004).

4. Echinococcus multilocularis

In contrast to the *Echinococcus* species causing cystic echinococcosis (*E. granulosus* complex), this species exploits predator–prey relationships between members of the dog family (e.g. dogs, foxes, coyotes, wolves) and rodents or other small mammals. In obvious adaptation to the small size of the intermediate hosts the parasite forms solid metacestodes consisting of small vesicles filled with protoscolices (alveolar echinococcosis). Thus, a large number of protoscolices can be produced within the limited space available in a small mammal. *Echinococcus multilocularis* is restricted to temperate and cold regions of the northern hemisphere, where it appears to be the most serious parasitic zoonosis (Eckert et al., 2001b). Information on the exact distribution has to be interpreted with care since the data quality differs considerably among regions, and little information is available from many areas outside the confirmed range. Since epidemiology, host ranges and the levels of general knowledge about the parasite differ in various parts of the world, the current situation is discussed separately for Europe, Asia and North America.

4.1. Europe

The typical transmission cycle in Europe involves red foxes (*V. vulpes*) as final hosts and rodents (especially *Microtus arvalis* and *Arvicola terrestris*) as intermediate hosts. For endemic areas of west-central Europe, most of the parasite's biomass is estimated to be present in this wildlife cycle. While domestic dogs and cats are also sporadically infected, they appear to be of secondary importance for the lifecycle (Eckert, 1996). They may, however, play a key role in transmission to humans due to close contact. Dogs are highly suitable hosts with an even longer patency period than foxes (Deplazes et al., 2004a), the low infection rates in domestic dogs in Europe are likely due to low exposure to the parasite. The suitability of cats as final hosts is less clear. Published prevalences are generally low and, although some cats show high infection intensities, mean worm burdens of experimentally infected cats are much lower than those of canids, rendering their contribution to the transmission cycle doubtful (Deplazes et al., 1999; Jenkins and Romig, 2000; Deplazes et al., 2004a).

In Poland and eastern Germany, the raccoon dog (*Nyctereutes procyonoides*), a neozootic species introduced from eastern Asia, appears to have drastically increased its population density in recent years. Since this species is highly susceptible to infection, and does not seem to compete directly with fox populations, an additional pool of definitive hosts may be developing in central Europe (Thiess et al., 2001; Machnicka-Rowinska et al., 2002). Other wildlife species with confirmed susceptibility such as wolf (*C. lupus*), lynx (*Lynx* spp.), wild cat (*Felis silvestris*) and jackal (*Canis aureus*) are of limited or no importance in Europe (Martinek et al., 2001a). Numerous records of *E. multilocularis* exist from the arctic fox (*Alopex lagopus*) in Siberia and Alaska (Rausch, 1995), but the first record in Europe came only recently from the Norwegian arctic island of Svalbard where the parasite had been introduced together with a neozootic vole species, *Microtus rossiaemeridionalis* (Henttonen et al., 2001). Apart from rodents, metacestodes of *E. multilocularis* are recorded from a number of 'dead end' hosts which do not play any role in the transmission. Infections in wild boars (*S. scrofa*) and domestic pigs appear to be self-limiting without development of protoscolices (Sydler et al., 1998), while various species of non-human primates kept in zoos have been reported to succumb rapidly to the disease (Deplazes and Eckert, 2001). Coypu (*Myocastor coypus*), a neozootic rodent originating from South America which has established feral populations in Europe, was shown to be less susceptible to *E. multilocularis* infection than microtine rodents, and plays only a marginal role for transmission. In a recent survey in western Germany only one of 119 feral coypu harboured fertile metacestodes, compared with 13 of 92 muskrats (*Ondatra zibethicus*) from the same habitat (Hartel et al., 2004).

Data on *E. multiolocularis* from human cases are difficult to evaluate, because of low human prevalence levels (Eckert et al., 2001a) and the long asymptomatic period of AE (Pawlowski et al., 2001) makes identification of time and place of infection uncertain. Prevalence estimates for human AE in high endemicity areas of central Europe have been previously estimated to range between 2 and 40 cases per 100,000 (Eckert et al., 2001a; Romig et al., 1999b). The highest published value was reported from eastern France with 152/100,000 but this study included cases of inactive AE and concentrated on farmers, a recognised higher infection-risk group (Bresson-Hadni et al., 1994). In a review of 210 AE cases from central Europe, 61.4% of patients were engaged in professional or part-time farming, gardening or other outdoor activities, while 70.5% owned dogs or cats (Kern et al., 2000). A recent case–control study in Germany with 40 AE cases and 120 matched controls showed the strongest AE disease risk associations were with the ownership of free roaming dogs, farming, and living on or near farms (Kern et al., 2004).

The question of whether or not the geographical range of *E. multilocularis* has been expanding in Europe since the 1980s was addressed in several recent reviews (Eckert et al., 2000; Romig, 2002). Before that time, the range was thought to be restricted to south-central Europe, an assumption largely based on the historical occurrence of human cases. Today the parasite (in foxes) is recorded from an apparently contiguous area in central Europe, extending in the north to Denmark, the Netherlands and Belgium, in the east to Lithuania, Poland and Slovakia, in the south to north eastern Italy and Hungary, and in the west to central France (Romig, 2002; Manfredi et al., 2002; Sreter et al., 2003; Marcinkute et al., 2005). Although, fox prevalence data from within this region differ greatly in number and quality, transmission seems to be most intense in the northern pre-alpine regions, the high Tatra mountains between Poland and Slovakia, the French, Swiss and German Jura mountains, and the mountainous areas stretching from southern Belgium to central Germany; there, prevalence rates in foxes often exceed 50% and approach 100% locally (Vervaeke et al., 2003; Martinek et al., 2001b; Dubinsky et al., 2001; König et al., in press) In contrast, prevalence rates are usually $<5\%$ in the area north of this region. No records of *E. multilocularis* exist from the Iberian Peninsula, Fennoscandia, and the British Isles: no positive animals were detected in surveys of 587 red foxes in Great Britain (Smith et al., 2003), and of 854 red foxes and 335 raccoon dogs in Finland (Oksanen and Lavikainen, 2004). No reliable data are available from a large part of France, regions east of Poland and Slovakia, and south-eastern Europe, although the presence of the parasite in all these areas is strongly suspected (Eckert et al., 2000; Romig, 2002). The reasons for the unequal prevalence distribution are not yet clear, but appear to be linked to agricultural land use and landscape patterns. The presence of permanent grassland (meadows, pastures) favours populations of the parasite's most important intermediate hosts (common and water voles) and is likely to be of primary importance for effective transmission (Giraudoux et al., 2002).

Whether the range of *E. multilocularis*, as recognized today, is the result of an expansion, or more intensive investigations is not known because of the lack of historical data. However, there is mounting evidence of an increase of the parasite density (increase of prevalence and/or increase of host populations) in many areas, e.g. several regions of Germany, the High Tatra mountains in Poland and Slovakia, and the Netherlands (Romig et al., 1999a; Malczewski, 2004; Miterpakova et al., 2004; Van der Giessen et al., 2005). In central Europe, there is a correlation between the increase in the fox population, (as a result of the successful immunization of foxes against rabies since the early 1990s) and the increasing prevalence of *E. multilocularis* in wildlife (Romig et al., 1999a; Chautan et al., 2000). In this context the parasite density (biomass) in south-western Germany is estimated to be 10 times higher than before 1990. This is reflected in data from sympatric intermediate hosts, where the infection rates of muskrats (*O. zibethicus*) with *E. multilocularis* metacestodes increased from 2% in the period 1980–1989 to 26% in the period 1995–2000 (Romig et al., 1999a).

The adaptation of foxes to urban environments appears to have coincided with rural population increase (Chautan et al., 2000) and foxes are now common in many towns and cities of south-central Europe (Gloor et al., 2001). In these locations fox population densities can exceed those in rural habitats due to abundant availability of anthropogenic food (Contesse et al., 2004). Infection rates with *E. multilocularis* can be high (e.g. 44% in Zurich, 43% in Geneva, 17% in Stuttgart) (Deplazes et al., 2004b), but are generally lower than in surrounding rural areas, probably due to the limited presence of habitats suitable for voles. However, due to the high population density the absolute number of infected foxes may still be higher than in agricultural landscapes, and the close proximity between foxes and man poses a considerable infection risk. Transmission to man may not only occur directly from infected foxes, but also from pet dogs and cats which get infected by catching rodents in city parks and gardens (9% of water voles were found infected in the urban to peri-urban areas of Zurich) (Stieger et al., 2002). As is known from other high endemicity areas outside Europe (parts of Alaska and China), the prevalence of human AE can be extremely high where people are in close contact with transmitting animals (domestic dogs). Therefore, the increasingly close association between fox and man in urban areas is cause for concern.

4.2. Asia

Alveolar echinococcosis is widespread across the arctic, subarctic and temperate climate zones of Asia, from Turkey to Japan (Eckert et al., 2001a). From most regions where the parasite is known to be present (e.g. the Russian Federation and the newly independent states of central Asia), few recent data on distribution and frequency are available. In Turkey, cases of human AE are most frequent in central and eastern Anatolia, but there is no information on the local transmission patterns (Altintas, 1998). In the newly independent states of Central Asia, *E. multilocularis* is present, but data on its prevalence in humans and domestic animals is largely unknown. Some human cases are thought to have occurred in patients in Kazakstan (Shaikenov and

Torgerson, 2004) but identification of lesions is uncertain. *Echinococcus multilocularis* infection has been identified in domestic dogs in a mountainous region of Kazakstan (Almaty Oblast) (Stefanic et al., 2004), but the prevalence in humans in that area has yet to be determined. The role of wildlife in the transmission of *E. multilocularis* in Central Asia is unknown.

In China, eight provinces covering the entire western and northern part of the country are known to be endemic for *E. multilocularis* (Vuitton et al., 2003). AE is a serious public health problem mainly in the more sparsely populated regions (including the Tibetan plateau and Inner Mongolia) and is often associated with pastoral minority communities. Domestic dog, wolf (*C. lupus*) and foxes (*Vulpes corsac, Vulpes ferrilata, V. vulpes*) were confirmed as definitve hosts, and a large number of rodent and lagomorph species serve as intermediate hosts (Vuitton et al., 2003). Far more human cases than from any other country are reported from China, with prevalences exceeding 5% locally in Gansu Province, western Sichuan Province and Ninxia Hui Autonomous Region (reviewed in Vuitton et al., 2003). Such foci of human AE seem always to be associated with 'domestic' lifecycles involving dogs as definitive hosts. The particular risk seems to be the keeping of dogs, which feed on grassland-associated rodents or lagomorphs. In several foci of human AE the epidemiological situation appears to have drastically changed some time ago due to eradication of dogs and wild canids by secondary poisoning with rodenticides (Vuitton et al., 2003). In other regions, large-scale deforestation producing vast areas of grass- or scrubland (e.g. on the slopes of the Tibetan plateau) seems to have exacerbated the problem by creating habitats for the rodent intermediate hosts (Giraudoux et al., 2003). Overgrazing of pastures by livestock (e.g. yak) was found to favour populations of intermediate hosts (*Ochotona* spp.), and was associated with a higher risk for human AE (Wang et al., 2004). Overall, the knowledge on the epidemiological situation in China is still very limited. In a recent survey in Inner Mongolia (China), two 'forms' of *E. multilocularis* were reported to be occurring sympatrically, utilising the same host species (*V. corsac* and *Microtus brandti*) (Tang et al., 2004). Based on minor morphological differences, they were tentativley allocated by the authors to *Echinococcus multilocularis multilocularis* and *Echinococcus multilocularis sibiricensis*. However, without any molecular data to support this assertion, no conclusions can be drawn, and the sympatric occurrence of two subspecies is a contradiction in itself.

In Japan, AE is restricted to the northern island of Hokkaido where it was probably introduced accidentally with infected foxes from the Kurile Islands early in the 20th century. Since the early 1980s, the parasite has rapidly spread from the easternmost part of Hokkaido through the entire island, and has recently entered a phase of rapid prevalence increase in animal hosts (Ito et al., 2003). In contrast to Europe and continental Asia, no rodent species is specifically adapted to grassland in northern Japan. There, grey-sided voles (*Clethrionomys rufocanus*) which form large populations in dense undergrowth of forests and scrubland are the most important intermediate hosts, and it appears that the parasite in Japan is exploiting a predator–prey situation which is rather different from other regions. The number of human AE cases is moderate with 373 records between 1937 and 1997, with approximately 10 new cases diagnosed annually (Eckert et al., 2001b). As in Europe, *E. multilocularis* has taken advantage of the increasingly urban lifestyle of foxes, and a transmission cycle has been established in urban areas, e.g. in the outskirts of Sapporo (Ito et al., 2003). A recent case–control study with 134 human AE patients identified cattle and pig farming and the use of well water as risk factors for human infection (Yamamoto et al., 2001).

4.3. North America

The distribution of *E. multilocularis* in North America appears to be fragmented. In the northern tundra region, it is present between western Alaska and the Hudson Bay, including some of the subarctic and arctic islands. While its principal final host, the arctic fox (*A. lagopus*), is widespread, the local occurrence of *E. multilocularis* appears to be limited by the presence of suitable intermediate hosts, mainly *Microtus oeconomus* (Rausch, 1995). In this northern range, human AE cases are rare, not a single patient is known from the entire tundra region of Canada. However, human AE can be extremely frequent where domestic dogs are substantially involved in the lifecycle. This is the case in some villages on St Lawrence Island (Alaska) from where an annual incidence of 98/100,000 has been reported (Schantz et al., 1995; Eckert et al., 2001a).

A second endemicity area exists in the temperate zone of southern Canada to the central USA. There, red foxes (*V. vulpes*) and coyotes (*C. latrans*) are the most important final hosts, main intermediate hosts being the meadow vole, *Microtus pennsylvanicus* and the deer mouse, *Peromyscus maniculatus* (>Eckert et al., 2001a). No records of *E. multilocularis* exist from the interspersed Canadian taiga zone, which is either a non-endemic area, or prevalence levels are still too low to allow infection to be detected (Schantz et al., 1995). The endemicity region in central North America may be of rather recent origin, after becoming suitable for *E. multilocularis* transmission due to anthropogenic deforestation. In this central region, both the geographical range and the prevalence levels in animal hosts are increasing. While a survey of red foxes in South Dakota during the late 1960s resulted in one infected fox out of 222, prevalence in the period 1987–1991 had increased to 74.5% of 137 red foxes, in addition, four of nine coyotes were also found infected (Schantz et al., 1995; Hildreth et al., 2000; Storandt et al., 2002). It is believed that the parasite will spread further, since suitable hosts for *E. multilocularis* are widespread, especially coyotes, which migrate over much larger distances than foxes and are thought to be important in facilitating the spread of this parasite (Storandt et al., 2002). Curiously, only two human AE cases are known to have originated from central North America since 1939. This is in stark contrast with the situation in Europe and Asia, and no conclusive explanation for this almost complete absence of human infection has been given. Factors under discussion include the genotype of the parasite, behavioural differences of the human population, and misdiagnosis of the disease (Hildreth et al., 2000).

5. Echinococcus shiquicus

Most recently, *E. shiquicus* was described as a new species from the Tibetan plateau of western Sichuan, China (Xiao et al., 2005). Tibetan fox (*Vulpes ferrilata*) and a agomorph, the pika *Ochotona curzoniae*, were identified as definitive and intermediate hosts, respectively. The morphology of adult worms is similar to the sympatrically occurring *E. multilocularis*, differing mainly in smaller hook size, a maximum number of three proglottides, and a more anterior position of the genital pore. In the pika, fertile unilocular cysts of approximately 1 cm diameter or oligovesicular metacestodes were ascribed to this species by genetic analysis. From the latter, the authors conclude that the new species is not closely related to any other *Echinococcus* taxon. *E. shiquicus* may be an endemic of the Tibetan plateau, but from the few isolates known so far, no conclusion can be drawn on host range (including pathogenticity to humans) and geographical distribution.

6. *Echinococcus oligarthrus* and *E. vogeli*

Both species, causing polycystic echinococcosis (PE) in humans, are restricted to South and Central America, and human patients are known from Nicaragua to Argentina and Chile. Both species are transmitted in wildlife-based cycles (Eckert et al., 2001b; D'Alessandro, 1997). *Echinococcus vogeli* uses the bush dog (*Speothos venaticus*), an indigenous South American species, as final host and indigenous large-sized rodent species (e.g. the paca, *Cuniculus paca*) as intermediate hosts. Domestic dogs can also acquire this parasite. In contrast, *E. oligarthrus* is exclusively adapted to members of the cat family, and the range of definitive hosts includes jaguar (*Panthera onca*), cougar (*Felis concolor*) and a number of smaller species of wild cats, while the intermediate host range is similar to that of *E. vogeli*. In obvious adaptation to the rather large-bodied rodent hosts (compared to hosts of *E. multilocularis*), the metacestode consists of multiple large vesicles, a morphology somewhat intermediate between the *E. granulosus* complex and *E. multilocularis* (Thompson and McManus, 2001). Most of the approximately 100 published human PE cases were not identified to species level, but the rest were overwhelmingly caused by *E. vogeli*—only three confirmed PE cases by *E. oligarthrus* are known from Brazil, Surinam and Venezuela (Eckert et al., 2001b). This is certainly due to the susceptibilty of domestic dogs to infection with *E. vogeli*, becoming infected in rural areas by feeding on the viscera of pacas and other large rodents that are hunted for food by local people. *E. oligarthrus*, in contrast, is transmitted by wild cat species, a fact that limits the infection risk for humans to exceptional situations. No details on prevalence rates in the various hosts in any of the different regions are available for either species. Two recently reported cases of *E. oligarthrus,* from patients in India, were shown to have been misdiagnosed (D'Alessandro and Rausch, 2004).

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