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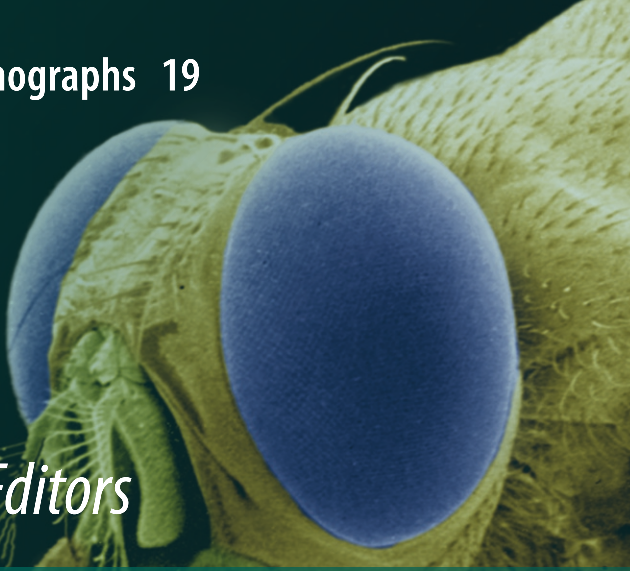

Jian Li
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Echinococcus: Control and Elimination of *Echinococcosis* with a Focus on China and Europe

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Jian Li • Wei Wang • Heinz Mehlhorn
Editors

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Preface

Humans and their animals live since thousands of years close together and thus both groups are endangered by life-threatening diseases being transmitted vice versa. Echinococcosis is based on infections by the so-called tapeworms of the genus *Echinococcus*. The present book offers insider knowledge on the situation in China and Europe, since common standards of diagnosis and treatment have been developed and become constantly ameliorated.

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Brief Recognition History of *Echinococcus* Tapeworm

1

Xu Wang, Shuai Han, and Jianping Cao

Abstract

The cognitive history of *Echinococcus* began with the description of the diseases it caused by doctors more than 2000 years ago, but it was not until the seventeenth century that scholars began to discover the pathogens of the parasite, and in the next 200–300 years, its classification system was continuously debated and revised through morphology and molecular methods. After entering the twenty-first century, through the phylogenetic researches, nine existing valid natural species of *Echinococcus* were ultimately identified and preserved.

Keywords

Echinococcus · Echinococcosis · Cognitive history · Hydatids · Species

The larva of *Echinococcus*, a tapeworm of the phylum Platyphyllum, parasitizes animals and can cause liver, lung, brain, and other organ lesions, called echinococcosis, which can lead to death in severe cases (Eckert and Thompson 2017). It is a zoonotic parasitic disease that has attracted worldwide attention. Among the various

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types of echinococcosis, the most common is the cystic echinococcosis (CE) caused by the *Echinococcus granulosus*. Its appearance is characterized by a number of translucent fluid-filled cysts of varying sizes, which appear as space-occupying swelling in the lesion of humans or other animals. Therefore, echinococcosis is also collectively referred to as hydatids.

1.1 Some Vague and Trivial Records of Cystic Lesions

Early physicians did not have a clear understanding of echinococcosis. So, we can only correlate them from some of the probable pathologic descriptions they left behind. For example, in ancient Greece, Hippocrates (~460–377 BC), the founder of Western medicine, wrote in his classic *Aphorisms* (VII, 55): “In those who water stuffed lives open into the //omentum, the bell is filled with water, and they die” (Eckert and Thompson 2017). Almost at the same time in ancient China, the *Miraculous Pivot* (475–221 BC), the foundation literature for the formation of the Chinese theoretical system of traditional medicine, described several cases of abdominal swelling, such as (IX, 57): “when you press the abdomen of a patient with your hand, the depressed part will rise with your hand, as if pressed on a bag containing water,” and “at the beginning, the abdominal mass is as large as an egg, and with the development of the disease, the mass also gradually increases, and when it is fully formed, the abdominal bulge is like pregnancy, and the course of the disease is long, which can go through several years. When pressed by hand, the lump is hard and can move when pushed” (Jia 2015). Due to the limitations of early observation techniques and methods, the ancient doctors’ cognition of echinococcosis was often limited to the description of appearance characteristics, and did not give an essential definition of this disease, so that we cannot conclude that these diseases are what modern scientists call echinococcosis from the perspective of later generations. This dilemma has undergone some changes with the rise and development of anatomy. During the Roman Empire, Aretaeus (50 AD) from Cappadocia described in his work of *De causis et signa acutorum morborum* as “there were many small fluid filled blisters in the patient’s abdomen, and some fluid flowed out during needle puncture.” In the seventeenth century, scientists began to discover similar pathological features in other animals. For example, Bartholin first observed transparent egg-like lesions in pigs in a slaughterhouse in 1653. Wille recorded in his monograph the presence of grape clusters on the surface of the liver and lungs of livestock in 1675. These descriptions are very similar to those of cystic echinococcosis (CE). However, due to the fact that microscopic observation technology and systematic parasitology have not yet been developed, there have been various opinions on the cause and true nature of echinococcosis. Some ancient scholars even believed that this disease came from the pathological changes of patients’ own tissues, possibly from the accumulation of mucus between layer cells, or from the differentiation of blood vessels and their contents (Eckert and Thompson 2017).

1.2 An Infectious Disease Caused by Parasites

In 1684, Francesco Redi (1626–1697) discovered the mobile cysticerci in patients in Florence, proposing the hypothesis that this disease may be caused by *Taenia* spp (Grove 1990). tapeworm. Facts have proven that this is a correct direction. The following year (1685), Professor Philip Jacob Hartmann (1648–1707) once again demonstrated in a research at the University of Konigsberg that this cysticerci has the same scolex as a tapeworm, with its tail connected to a spherical bladder, which is believed to be the metacestode of *Taenia hydatigena* and referred to as *Cysticercus tenuicollis*, which is the first report on the morphology of *Echinococcus*. Soon, in 1687, Edward Tyson (1650–1708), a physician at Oxford University, described the characteristics of the motor behavior of *Cysticercus tenuicollis* in his report, called it "lumbrici hydropici," which means that the fluid-filled hydatids in animals are actually worms with independent life forms, providing a new way for continuing to study the origin of echinococcosis (Enigk 1986). In 1760, Peter Simon Pallas (1741–1811) of the University of Leiden described in his medical paper that the hydatids were remarkably similar in sick people and animals, with some small brood capsules attached to the inner walls, redefining the parasites as bladder worms (Enigk 1986). In 1782, Priest John August Ephraim Goeze (1731–1793) of Germany studied the structure of the hydatids through the microscope and discovered a large number of protoscoleces, as well as tapeworm-like scoleces in the inner capsules, confirming their association with the *Taenia* family, and defined it as *Taenia visceral socialis granulosa (*Enigk 1986*)*. In 1786, professor Batsch summarized the previous research results and named the parasite *Hydatigena granulosa*, which causes cystic lesions in internal organs in humans and animals, and usually completes its life cycle with domestic animals and dogs as intermediate and definitive hosts (Romig et al. 2015). In 1800, Zedder described the cysts in sheep and classified them into genus *Polycephalus*. Finally, Dr. Carl Asmund Rudolphi (1771–1832) classified this species as a new genus *Echinococcus* in 1801, formally included in the zoology classification, and has been used up to now (Rudolphi 1801).

1.3 Multiplex Echinococcosis and *Echinococcus*

1.3.1 Dualism of CE and AE

According to previous research, cysts formed by the larvae of *E. granulosus* are generally unilocular hydatid, but in some patients, doctors have discovered some abnormalities. In 1852, Ludwig Buhl (1816–1880), a pathologist in Germany, found a rare tumor in the human liver, initially described it as "alveolarcolloid," and speculated that it might be caused by tissue canceration (Eckert and Thompson 2017). In 1855, Rudolf Ludwig Virchow (1821–1902), a professor of pathology at the University of Würzburg, described in detail the infiltrating and growing multilocular hydatid, which grew like a tumor. Unlike the unilocular hydatid previously seen in humans and livestock, he believes that this lesion is caused by parasite invasion of surrounding tissue, rather than malignant hyperplasia of the patient's tissue itself (Virchow 1856). In 1863, German scientist Rudolf Leuckart proposed to refer to this parasite within multilocular hydatid as *Echinococcus multilocularis* (Leuckart 1862). However, due to the limitations of parasitic morphological techniques at the time, there was a heated debate at that time over whether the previously discovered unilocular hydatid and the later reported multilocular hydatid were caused by the same parasite or by different species. Many scholars, including R. Virchow, initially believed that both hydatids were caused by *E. granulosus*, and that the differences in pathological features were dependent on patient's own specificity. In contrast, professor A. Morin of the University of Bern, Switzerland, is a dualist in his paper, arguing that multilocular hydatid is caused by a new pathogen. His view was supported by Adolf Poselt (1867–1936), a professor at the University of Innsbruck in Austria later, and confirmed by the morphological, pathological, histological, and clinical manifestations of infection in dogs conducted by Posselt in 1901 (Eckert and Thompson 2017). The cause of multilocular hydatid was identified as a new pathogenic species, which was the worm of *E. multilocularis* mentioned earlier. In the 1950s, Robert L. Rausch and E.L. Schiller found a similar hydatid lesion in the lungs of Inuit people in Alaska, and related it to the alveolar metacestodes from local voles and the *Echinococcus* eggs in Arctic fox. The parasite was named *Echinococcus sibiricensis* (Rausch and Schiller 1951; Rausch and Schiller 1954; Rausch and Schiller 1956). However, in 1955, Johannes Vogel (1900–1980), a German helminthologist, found there is no significant difference between *E. sibiriensis* and *E. multilocularis* after conducting morphological analysis of echinococcosis infections in voles, foxes, dogs in Europe and Alaska. Therefore, the combination of the two kinds of *Echinococcus* was defined as the same species, officially named *E. multilocular*is Leuckart, 1863, could cause the alveolar echinococcosis (AE) of human but with a completed life cycle by small rodents (intermediate hosts) and foxes (definitive hosts) in the wild (Vogel 1955; Vogel 1957a). Because the tapeworm has a wide variety of morphological and biological characteristics, some scholars even proposed to separate it into a new genus, *Alveococcus* Abuladze, 1959, but this proposal was not recognized by the academic community (Lukashenko and Zorikhina 1961). So far, this parasite still belongs to *Echinococcus*. Thus, the pathogen discovery and species dispute of the major echinococcoses (AE and CE) and *Echinococcus* (*E. multilocularis* and *E. granulosus*) in Eurasia came to an end.

1.3.2 Echinococcus in the New World (America)

At the same time, in the New World, i.e., the American continent, the process of understanding *Echinococcus* is also taking place simultaneously. With the exception of *E. granulosus* and *E. multilocularis*, which are found in North America and common to Eurasia, the earliest records of endemic species can be traced back to 1836 (Eckert and Thompson 2017). Austrian scientist Johann Naterer (1781–1843) collected some parasites in a cougar (*Puma concolor*) in Brazil (Tappe et al. 2008); In 1863, Karl Moritz Diesing (1800–1867) classified these parasites as a new species, *Taenia oligarthra*, preserved in the Hofmuseum in Vienna (Luhe 1910). In 1909, Dr. Maximilian F.L. Luhe (1870–1916) of the University of Konigsberg carefully reviewed previous materials and believed that this parasite was closely related to the genus *Echinococcus*. In 1914, Brumpt (1877–1951) and Joyeux (1881–1966), French parasitologists, discovered some multilocular metacesteodes from agoutis in Brazil, temporarily named it as *Echinococcus cruzi* and speculated to be related to the previous *T. oligarthra* (Brumpt and Joyeux 1924). In 1926, professor Thomas W.M. Cameron (1894–1980) formally classified this parasite as *Echinococcus* based on the autopsy of a jaguarundi (*Felis yagouaroundi*) in London Zoo, namely *E. oligarthrus* (Cameron 1926). Eventually, it was confirmed that the species was transmitted and propagated with cats (cougar, jaguar, jaguarundi, etc.) and rodents (opossum agoutis, pacas, opossums, etc.) from South America as the definitive host and intermediate host. At present, sporadic cases of human infection have been reported, and the characteristics of the single cyst caused by *E. oligarthrus* are also known as unicystic echinococcosis (UE) (Eckert et al. 2001).

1.3.3 Echinococcus in Africa

On the other hand, in the African continent, the earliest record of *Echinococcus* is from Gough's note in 1908, which described *E. granulosus* obtained from silver-backed jackal (*Canis mesomelas*) in South Africa and successfully infecting sheep (Hüttner and Romig 2009). The native species of Africa was discovered in 1926 by Thomas W. M. Cameron in the African wild dog (*Lycaon pictus*) in South Africa and named it as *Echinococcus logimanubrius* because of its unique small hook with long-handle morphology (in the same publication, Cameron also mentioned an *Echinococcus minimus* found in *Canis lupus* in Macedonia) (Cameron 1926). In 1934, Ortlepp also discovered another species with a different large hook shape, *Echinocccus lycaontis*, from *L. pictus* (in that article, Ortlepp renamed a tapeworm collected from foxes in the United Kingdom as a new species of *Echinococcus cameroni*) (Ortlepp 1934). Today, however, the population of African wild dog populations are in rapid decline and threatened with extinction, making further research difficult (Hüttner and Romig 2009). A major discovery was in 1937 when Ortlepp continued to discover a new species of *Echinococcus* tapeworm in the intestines of South African lions (*Panthera leo*), and recognized as a separate species based on the morphology of obvious rough folds on the rostellar hooks and characteristics of the feline as the nature definitive host, it was confirmed as an independent species, named *Echinococcus felidis* (Ortlepp 1937). Subsequently, scientists successively found signs of infection of *E. felidis* in wild animals such as zebras (*Equus quagga*, *Equus zebra*), warthogs (*Phacochorus* sp.), and bushpig (*Potamochoerus larvatus*, *Potamochoerus porcus*) (Hüttner and Romig 2009). It has been identified as an *Echinococcus* species with independent transmission ecological chain among wildlife in African. Interestingly, in 1943, Lopez Neyra and Soler Planas first described the presence of *E. felidis* and *E. lycaontis* in domestic dogs in southern Spain, as well as other two new species, *E. ortleppi* and *E. intermedius* (Lopez-Neyra and Soler Planas 1943).

1.4 A Large and Complex Genus Group

1.4.1 Morphological Method

With the recognition of the "taxonomic status" of the genus *Echinococcus* Rudoiphi, 1801, and the common characteristic of the dual host life-cycle, scientists around the world have successively reported various newly discovered species, but most of them are identified based on the description of morphological structure (Rausch 1953). However, some scholars have proposed that these morphological differences (such as the size or length of the rostellar hooks) may be within the range of normal individual differences, and it is necessary to reevaluate these features as a basis for species differentiation (Hüttner and Romig 2009). In 1953, Robert Rausch conducted morphological analysis based on stored sample materials and believed that the hook size of adults with mature eggs in the uterus was the only reference for species classification. In addition, the shape of the hook, the number of testes, and the species specificity of the host were also important reference criteria. Therefore, seven species of *Echinococcu*s (*E. granulosus* Batsch, 1786; *E. oligarthrus* Dieing, 1863; *E. longimanubrius* Cameron, 1926; *E. minimus* Cameron, 1926; *E. cameroni* Ortlepp, 1934; *E. lycaontis* Ortlepp, 1934; *E. felidis* Ortlepp, 1937) were reclassified for biological classification, and proposed *E. longimanubrius* and *E. minimus* are the species inquirendae to be studied, and it is believed that they may be *E. granulosus*; *E. cameroni* is also considered to be conspecific with *E. granulosus*; but there was no response to *E. intermedius* and *E. ortleppi* for evaluation. Combining with previously identified *E. multilocularis*, a total of six species are considered valid (Rausch 1953). In 1963, Rausch and Nelson reviewed their previous classification studies and concluded that there were some omissions in their early conclusions, and collected *E. granulosus* isolates from all over the world (Britain, Germany, and Yugoslavia in Europe, Alaska in North America, Siberia in Asia, Australia in Oceania, and Kenya in Africa), as well as some *Echinococcus* previously reported, such as *E. cameroni*, *E lycaontis*, *E. intermedius*, and *E. ortleppi* (Rausch and Nelson 1963). According to the systemic morphological characteristics, it was concluded that *E. cameroni*, *E. intermedius*, *E. longimanubrius*, *E. lycaontis*, *E. minimus*, and *E. ortleppi* were of the same species as *E. granulosus*, replacing them as independent valid species. And ultimately, only five nature species were left, including three species that can be clearly distinguished by morphology (*E. granulosus*, *E. multilocularis*, and *E. oligarthrus*), and two species to be confirmed: one is *E. felidis* because of the uniqueness of felines as terminal hosts rather than morphological differences (Rausch and Nelson 1963); another one is *Echinococcus patagonicus*, which was reported by Szidat in 1960 and found in the intestine of the foxes in Argentine (Szldat 1960). Due to the lack of sufficient information, *E.*

patagonicus needs to be further identified, but is presumed to be closely related to *E. granulosus* (Rausch and Nelson 1963).

1.4.2 Naming of Subspecies

In 1960, according to the high incidence of echinococcosis among Indians in northwestern Canada, Cameron successfully identified a species of *Echinococcus* that only found cysts in the lungs of various deer (wolves are the natural host for the adults, but dogs are also susceptible to infection), and the anatomical structures of both the adults and the larvae were different from those previously found. The *Echinococcus* was found mainly in the high latitudes of North America and Eurasia, but is still considered to be a variant of *E. granulosus*, so Cameron named it as *Echinococcus granulosus* var. *canadensis* (or *Echinococcus granulosus canadensis*) (Cameron 1960). Thus, Rausch and Nelson realized that some morphological characteristics of the adult stage may be due to collection and preservation methods, while differences in the larval stage may be influenced by different hosts, and that these so-called species may actually be only subspecies or synonymous species of valid natural species (Rausch 1967). In this period, some scholars have classified the isolates of *E. granulosus* found from native wolves, moose, and other deer in North America as *E. granulosus orealis* Sweatman, 1963 (Sweatman and Williams 1963); isolates obtained from silverback jackals infected by the larvae inside sheep in African were described as *E. granulosus africanus* Verster, 1965 (Verstr 1965); isolates collected from livestock in New Zealand was defined as *E. granulosus newzealandensis* Verster, 1965 (Verstr 1965); isolates found in horses in the United Kingdom was identified as *E. granulosus equinus* Williams and Sweatman, 1963 (Williams and Sweatman 1963); the *E. sibiricensis* Rausch and Schiller, 1954, previously discovered in North America, redefined as *E. multilocularis sibiricensis* Vogel, 1957 (Vogel 1957b); and isolates of *E. multilocularis* found in sheep in Kazakhstan was identified as *E. multilocularis Kazakhensis* Shul'ts, 1961 (may actually be *E. granulosus*) (Shul'ts 1962). In addition, Lothar Szidat (1892–1973) described two new species of *Echinococcus* in South America, *Echinococcus cepanzoi* and *Echinococcus pampeanus* (Szidat 1971). However, according to Verster's revised classification standard of *Echinococcus* in 1965, number of adult segments, arrangement of mature segments, number and distribution of testis, and host preference were also used as the basis for division. Finally, only *E. granulosus* and *E. multiloculus* retained their independent classification status as natural species. *E. oligarthra* is considered to be the species inquirendae, and all other species are considered to be congeners or subspecies of these three species (Verstr 1965). According to this approach, *E. patagonicus* and *E. cepanzoi* were identified as *E. granulosus*, while *E. pampeanus* was same with *E. oligarthrus* (Eckert and Thompson 2017).

It is worth mentioning that in 1970, another new species of *Echinococcus* with distinct morphological characteristics from native America was isolated by Rausch and Bernstein from bush dog (*Speothos venaticus*) captured from Ecuador and kept at the Los Angeles Zoo. It is named after Professor Johannes Vogel as *Echinococcus vogeli* in honor of his remarkable contribution to the study of *Echinococcus* (Rausch and Bernstein 1972). Researches have shown that *E. vogeli* completes its life cycle primarily through food chain relationships between bush dogs (terminal hosts) and paca (intermediate hosts), which can cause a predominance of polycystic echinococcosis (PE) in humans (Rodrigues-Silva et al. 2002).

1.4.3 Concept of Strains (Genotypes)

The proposal of subspecies was of great help to the classification of *Echinococcus* with certain scientific significance, but it also causes some problems. Due to the deviation of sampling, preservation and measurement methods of observers, scholars proposed a lot of subspecies. According to statistics, there were more than 85 species or subspecies of *Echinococcus* with binomial or trinomial Latin names at that time, which caused some confusion in the taxonomy of *Echinococcus* (Romig et al. 2015). In 1967, according to the definition of subspecies (part of the population of a species inhabits a local geographic area within its distribution range is affected by the living environment in the area leading to specific changes in morphological structure or physiological function, which is called a subspecies) given by Ernst Walter Mayr, a famous evolutionary biologist (Mayr 1963), Rauch equated different host combinations of *Echinococcus* with different geographical habitat divisions of free living animals. He believed that different tapeworms will form a certain isolation in the stable relationship of food chains between hosts, and then evolve into different subspecies. In this view, he refuted the previous concept of various subspecies of *Echinococcus*, because many of the so-called subspecies coexist within the same biological link of a clear predator (final host) – prey (intermediate host), and do not form significant reproductive isolation (Rausch 1967). However, due to the limitations of research technology at the time, it could not provide more proposals to revise taxonomy of *Echinococcus*. Therefore, some scholars have proposed to temporarily classify all these taxa in the form of strains within the *E. granulosus* complex, called *E. granulosus* sensu lato (Bowles et al. 1992). In the 1990s, Bowles used the emerging DNA sequencing technology to test the sequence of some mitochondrial gene fragments (*cox*1 and *nad*1) of *Echinococcus* from different host sources and summarized the genotypes of eight strains of *E. granulosus*: the G1–G8 genotypes represent the common sheep strain, Tasmania sheep strain, India buffalo strain (buffalo strain), UK horse strain (horse strain), Holland bovine strain (cattle strain), African camel strain (camel strain), Poland pig strain (pig strain), and USA cervid strain, respectively; there are also two strains (genotypes) of *E. multilocularis*: the North American strain of the M1 genotype and the European strain of the M2 genotype (Bowles et al. 1992; Bowles and McManus 1993; Bowles et al. 1995). In 1997, Scott identified a new genotype in human echinococcosis cyst by molecular method and named it G9 genotype or Poland human strain (human strain) (Scott et al. 1997), but this strain was not accepted and was later considered as a microvariant of G7, so it was also called pig variant strain (or human–pig strain) (Kedra et al. 1999). Until the end of the twentieth century, it was recognized that there were four valid species of *Echinococcus*, namely *E. granulosus* with nine genotypes/strains (including the lion strain, also known as *E. felidis*), *E. multilocularis* with two genotypes/strains, *E. oligarthrus*, and *E. vogeli (*Eckert et al. 2001*)*.

1.5 Increasingly Defined Population Relationships

1.5.1 New Genotypes, New Species

In 2003, Lavikainen collected five isolates of *E. granulosus* from four reindeer and a moose in northeastern Finland. Through DNA sequencing, it was found that the genotype of the isolates was closely related to the G5 and G7 genotypes, but also had some similarities with G8. This isolate is considered to be a unique and previously undocumented new genotype, named G10 or Fennoscandian cervid strain (Lavikainen et al. 2003). So far, a total of 11 genotypes/strains have been reported in the *E. granulosus* system (Romig et al. 2015):

G1/common sheep strain;
G2/Tasmanian sheep strain;
G3/buffalo strain;
G4/horse strain;
G5/cattle strain;
G6/camel strain;
G7/pig strain;
G8/American cervid strain;
G9/variant pig strain;
G10/Fennoscandian cervid strain;
lion strain/*E. felidis*.

In 2005, Xiao discovered and named a native species in the Qinghai-Tibet Plateau of China in East Asia. By combining more abundant morphological, molecular, ecology, geographical distribution, and other methods, he found that it has interspecific differences, and named it *Echinococcus shiquicus* after Shiqu County where it was first found. *E. shiquicus* is phylogenetically closely related to *E. multilocularis* and has overlapping ecological niches with the latter, so it has been previously mistaken for *E. multilocularis* or one of its subspecies (Xiao et al. 2006). *E. shiquicus* mainly circulates between its terminal host, the Tibetan fox (*Vulpes ferrilata*), and its intermediate host, the pika (*Ochotona curzoniae*), but it is not clear whether it can cause disease in humans (Xiao et al. 2006). Subsequently, in 2007, Tang discovered a kind of new tapeworm from *Vulpes corsac* in the Hulunbuer Grassland in northeast China. She believed that its morphology, especially the shape of uterus, was different from *E. multilocularis*, and named it *Echinococcus russicensis* (Tang et al. 2007). However, this discovery still lacks sufficient evidence to establish the status of independent species. In 2009, Nakao analyzed the mitochondrial genes and found that there was a significant separation of isolates of *E. multilocularis* from different regions, and divided the existing of *E. multilocularis* into four genotypes, namely Asian type, European type, North American type, and Mongolian type. It replaces a variety of previously described species or subspecies related to *E. multilocularis*, including *E. sibiricensis* Rausch and Schiller 1954 and *E. russicensis* Tang 2007 (Nakao et al. 2009).

1.5.2 Phylogenetic Species

After more than 20 years of research and accumulation on the epidemiology, biology, and geographical distribution of *E. granulosus*, with more nuclear and mitochondrial gene loci have been sequenced and analyzed, the previous method of describing *Echinococcus* using genotypes or strains has great limitations and some contradictions (Romig et al. 2015). On the one hand, the genetic distance and relationship between genotypes are not balanced, and some genotypes (e.g., G1 and G3) are so similar that they can only be distinguished at the information level of the mitochondrial genome, but should only be treated as single genotype in taxonomy, and also shown more distant relationships with other genotypes (e.g., G4 or G5), while genotype such as G2 have been considered invalid (Kinkar et al. 2017). On the other hand, naming strains (genotypes) after animals can often cause some confusion. For example, the common sheep strain is actually the most mainstream strain found in the world, spread almost all over the world, and can infect a wide range of herbivores or livestock such as cattle, sheep, pigs, camels, and kangaroos as its intermediate host, while the horse strain parasitizes almost exclusively in horses (Rahman et al. 2014). In 2013, Nakao introduced the concept of phylogenetic species, combined with the phylogenetic analysis of nuclear and mitochondrial genes, and revised all the recognized species and genotypes (strains) of *Echinococcus* into nine naturally valid species, namely *E. granulosus* (combining G1 and G3 of the previous *E. granulosus*), *E. equinus* (the previous G4), *E. ortleppi* (the previous G5), and *E. canadensis* (combined with the previous G6, G7, G8, and G10), *E. felidis* (the previous lion strain), *E. multilocularis*, *E. shiquicus*, *E. oligarthrus*, and *E. vogeli* (Nakao et al. 2013). This classification version was accepted by most of the later scholars and is still in use today. However, in 2014, Lymbery applied the concept of evolutionary species (a single group of organisms with a shared evolutionary trajectory) and proposed reinstating the use of *E. intermedius*, *E. canadensis*, and *E. borealis* to refer to the G6/G7, G10, and G8 as separate species, respectively (Lymbery et al. 2015). This classification is consistent with mitochondrial data analysis and may become an acceptable nomenclature in the future, given the relationship and transmission chain in hosts of the three. In order to accomplish this work, it is first necessary to prove that the genetic characteristics can be stable among the three without being affected by interspecific hybridization. Perhaps obtaining more nuclear loci data from the isolates can help solve this issue (Romig et al. 2015).

1.6 Summary

According to a 2015 estimate by the WHO Foodborne Disease Burden Epidemiology Reference Group (FERG), echinococcosis leads to 19,300 deaths and approximately 871,000 disability-adjusted life years (DALYs) globally each year. The annual global burden of AE and CE are approximately 666,000 DALYs with 18,200 cases and 184,000 DALYs with 188,000 new cases, respectively. Moreover, echinococcosis caused up to US$ 2 billion in economic losses to the global livestock industry every year (Fu et al. 2021; Cardona and Carmena 2013). Echinococcosis has been a highly harmful but neglected infectious disease, and now we may need concerted efforts and increased cooperation on a global scale to control. With the passage of time, the scientific and physicians community's understanding of *Echinococcus* and echinococcosis is gradually deepening, but there are still many questions that need to be further explored. The taxonomic study is only a small part of *Echinococcus* researches, but it carries a high degree of summary and induction of the biological law of *Echinococcus*, and lays a foundation for more far-reaching ecology, epidemiology, diagnosis and treatment, prevention, and control. It took more than 2000 years to go from discovering the *Echinococcus* and artificially expanding it into a large and cumbersome complex to radically simplifying its taxon, finally to using molecular methods to separate the independent species with a never-ending explore. Finally, we would like to state that through the process of literature search, we have found that there are very few relevant materials in China. So, this article will also be rewritten into a review in China and published in Chinese journals for easy access by native Chinese readers.

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2 Global Epidemiology of Echinococcosis: Current Status and Future Prospects

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Abstract

Echinococcosis is a zoonotic parasitic infection caused by tapeworms of the genus *Echinococcus*. The disease affects both humans and a wide range of animal hosts, with significant pattern in its epidemiology across different global regions. This chapter aims to explore the global epidemiology of echinococcosis, including its transmission pattern, disease burden, risk factors, control measures, and distribution, and propose the potential challenges toward control of echinococcosis.

Keywords

Echinococcosis · Distribution · Epidemiology · Molecular epidemiology · Control and prevention

Echinococcosis is a worldly distributed zoonotic parasitic disease caused by the larvae of *Echinococcus* spp. It is a serious threat to human and animal health and causes significant economic losses, resulting a serious public health issue (Wen

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et al. 2019). The World Health Organization (WHO) has listed it as one of the 17 neglected tropical diseases, and the Food and Agriculture Organization (FAO) of the United Nations has listed it as the second most serious foodborne parasitic disease in the world (WHO 2015; WHO and FAQ 2012). The causative agent of echinococcosis is the larval stages of *Echinococcus* spp. In taxonomy, the genus *Echinococcus* belongs to the kingdom Animalia, phylum Platyhelminthes, class Cestoda, order Cyclophyllidea, family Taeniidae. It includes *Echinococcus granulosus*, which causes cystic echinococcosis (CE), *Echinococcus multilocularis*, which causes alveolar echinococcosis (AE), *Echinococcus vogeli* and *Echinococcus oligarthra*, which cause polycystic echinococcosis, and *Echinococcus shiquicus*, which is newly discovered in the Qinghai-Tibet Plateau but not found to infect people (Xiao et al. 2005). Each species has a specific geographic distribution, life cycle, host preference, and clinical manifestations. Understanding the taxonomy and characteristics of different *Echinococcus* species is crucial for better understanding and managing echinococcosis. In this chapter, we describe the epidemiology, geographic distribution of echinococcosis, and the potential challenges toward control of echinococcosis.

2.1 Epidemiology

The life cycle of *Echinococcus* involves two hosts, a definitive host (usually a canid), and an intermediate host (typically a herbivore or omnivore). The adult tapeworm resides in the small intestine of the definitive host, which is usually a domestic dog or other canids. The mature tapeworm can produce thousands of microscopic eggs, which are released in the feces of the definitive host. The eggs are shed into the environment through the feces of the definitive host. This ensures the survival of the eggs outside the host's body. If the eggs are accidentally ingested by an intermediate host, such as a sheep, goat, or other grazing animals, the eggs hatch in the small intestine. Once hatched, the larvae penetrate the intestinal wall of the intermediate host to enter the bloodstream. They are then carried to various organs, most commonly the liver and lungs, where they develop into fluid-filled cysts. The hydatid cysts grow slowly over time, and within the cysts, the protoscoleces are formed, which can later develop into adult tapeworms. If a definitive host, such as a dog, consumes the infected intermediate host, the protoscoleces are released from the cysts in the digestive system and develop into adult worms in small intestine of the definitive host, and star reproducing. The cycle then continues when the definitive host sheds the eggs in its feces. Humans can also become intermediate hosts if they accidentally ingest *Echinococcus* eggs through contact with contaminated environments or through close contact with infected definitive hosts; however, humans are generally not involved in the transmission of echinococcosis (McManus et al. 2012; Wen et al. 2019; Craig et al. 2019).

2.1.1 Source of Infection

There are different definitive hosts such as wolves, foxes, and jackals responsible for infection but dog acts a main source of infection. It is worth noting that infected wildlife, including definitive hosts and intermediate hosts, can also cause the transmission of echinococcosis, especially alveolar echinococcosis (Craig et al. 2019).

There are many kinds of wildlife as the definitive hosts in the life cycle of *Echinococcus*, including canines and felines, and wildlife as intermediate hosts include rodents and ungulates. Among them, the hosts of canids mainly include *Vulpes vulpes*, *Vulpes ferrilata*, and *Canis lupus*, which are the main wild definitive hosts of *Echinococcus granulosus*, *Echinococcus multilocularis*, and *Echinococcus shiquicus* (Craig et al. 2019; Xiao et al. 2005). Bush dogs are the main definitive host of *Echinococcus vogeli* (Matsuo et al. 2000). Felines mainly include *Prionailurus bengalensis*, *Felis lynx*, *Puma concolor*, and *Panthera onca*, which are the main wild definitive hosts of *Echinococcus oligarthra*. Rodents as intermediate hosts include *Lagomorpha* and *Rodentia*: *Lagomorpha* include *Ochotona curzoniae* and *Lepus oiostolu*; *Rodentia* include *Microtus ilaeus*, *Arvicola terrestris*, *Ondatra zibethicus*, *Microtus brandti*, *Meriones unguiculatus*, *Citellus dauricus*, and *Clethrionomys glareolus*. These are the main wild intermediate hosts of *Echinococcus granulosus* and *Echinococcus multilocularis*. The *Ochotona curzoniae* is the wild intermediate host of *Echinococcus shiquicus*. In addition, *Dasyprocta leporina* and *Cavia porcellus* are the main wild intermediate hosts of *Echinococcus oligarthra* and *Echinococcus vogeli*, respectively. Ungulates such as *Pseudois nayaur* and *Pantholops hodgsoni* and marsupials such as *Macropus eugenii* and *Vombatus ursinus* are mainly wild intermediate hosts of *Echinococcus granulosus* (Deplazes et al. 2017; Craig et al. 2017).

Geographically, the wildlife hosts of *Echinococcus granulosus* and *Echinococcus multilocularis* are the most widely distributed in Europe, Asia, Africa, and other parts of the world while the hosts of *Echinococcus shiquicus* are mainly distributed in the Qinghai-Tibet Plateau region of China, so this species has not been found in other areas so far. The definitive hosts and intermediate hosts of *Echinococcus vogeli* and *Echinococcus oligarthra* are mainly distributed in the Americas, so these two species are currently only found in the Americas (Deplazes et al. 2017; Craig et al. 2017, 2019; Alvi and Alsayeqh 2022).

2.1.2 Transmission Patterns

The transmission patterns of different echinococcosis are basically similar, mainly through fecal–oral transmission. *Echinococcus* eggs are highly resistant to low temperature and dryness in the environment, and can maintain long-term infectivity in a natural state. Humans and animals are infected by eating or drinking food and water contaminated by the eggs. In dry and windy areas, the eggs are scattered with the wind, and there is also the possibility of respiratory tract infection through inhalation of dust and droplets containing eggs. People, especially children, are susceptible to infection during contact with and playing with domestic dogs, as well as when adults engage in livestock fur processing, shearing, and other processes. In addition, animal fur trading, transportation, pet dog transportation, and so on also increase the risk of indirect infection.

The definitive host canines are mainly infected by ingesting animal organs containing *Echinococcus* cysts (Craig et al. 2017; Wen et al. 2019).

2.1.3 Susceptibility

The species and biological characteristics of *Echinococcus*, egg status, environment, host species, and immune status can affect the susceptibility of the host. Humans are generally susceptible to echinococcosis, depending on the intensity of exposure to *Echinococcus* eggs. The susceptible population are mainly in pastoral and semipastoral areas, especially children, women who often take housework, and people engaged in animal husbandry and hunting. For example, in the Qinghai-Tibet Plateau area of China, where echinococcosis is most prevalent, women often undertake more housework than men, feeding cattle and sheep and other livestock and domestic dogs, drying cow dung as fuel, and burying domestic dog feces. Contact with infected dogs or infected livestock, and the level of exposure to *Echinococcus* eggs is higher than men, so women are more likely to be infected (Wu et al. 2018). Children often play closely with domestic dogs, and their range of activities overlaps with that of domestic dogs. In addition, in pastoral areas, there is a lack of good hygiene conditions and health awareness, resulting in a low frequency of hand washing, making them highly susceptible to infection. Due to the slow growth of *Echinococcus* cysts, most children are asymptomatic after infection and may not be diagnosed until adulthood.

For animal intermediate hosts, the host preference of different species is different. *Echinococcus granulosus* has the widest range of hosts, among livestock, sheep are the most susceptible, and are suitable hosts for *Echinococcus granulosus*, followed by cattle; however, cattle are not suitable hosts for *Echinococcus granulosus*, and the cysts formed after infection are mainly infertile cysts. Other animals such as pigs, horses, camels, and deer can also be infected. *Echinococcus multilocularis* primarily infects rodents and is rarely found in livestock. *Echinococcus shiquicus* mainly infects plateau pikas (Craig et al. 2019; Xiao et al. 2006).

Dogs, the definitive host, are susceptible to many kinds of *Echinococcus*. In the Qinghai-Tibet Plateau, *Vulpes vulpes* can be infected with *Echinococcus granulosus* and *Echinococcus multilocularis* and *Vulpes ferrilata* are mostly infected with *Echinococcus shiquicus*, while *Vulpes corsac*, which are the closest relatives to *Vulpes ferrilata*, are not susceptible to these tapeworms (Craig et al. 2019).