An overview of the host spectrum and distribution of *Calodium hepaticum* (syn. *Capillaria hepatica*): part 1—Muroidea

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Abstract *Calodium hepaticum* (syn. *Capillaria hepatica*) is a worldwide-distributed species of zoonotic nematodes with a high affinity to the liver. Several rodent species of the superfamily Muroidea serve as main hosts for this pathogen. *C. hepaticum* has been found in Muroidean hosts in more than 60 countries in Europe; North, Central, and South America; Asia; Africa; and Oceania. *C. hepaticum* was documented in more than 90 Muroidean rodent species (Murinae, Deomyinae, Arvicolinae, Neotominae, Sigmodontinae, Gerbillinae, and Cricetomyinae). Globally, the Norway rat (*Rattus norvegicus*) seems to be the main host species for this nematode. However, locally high prevalences (above 50 %) have also been observed in several other synanthropic (commensal and non-commensal) Muroidea species (e.g., *Rattus tanezumi*, *Ondatra zibethicus*, *Apodemus sylvaticus*). This review gives an overview of the distribution and host spectrum of *C. hepaticum* in Muroidea host species.

Introduction

*Calodium hepaticum* (syn. *Capillaria hepatica*) is a zoonotic nematode parasite distributed worldwide. Adults of this nematode parasitize the liver of mammals and lay their eggs into the liver parenchyma causing hepatic capillariasis. The eggs are only released into the environment with the death of the host. The main hosts of this parasite are rodents of the superfamily Muroidea (Schmidt 2001). Furthermore, this parasite has been documented in numerous other mammalian species including more than 70 human cases (reviewed in Fuehrer et al. 2011; Fuehrer 2013). Hepatic capillariasis is diagnosed through necroscopy or biopsy only, because with hepatic infections eggs are not shed into the environment with the feces.

This review focuses on the Muroidea host spectrum and its geographic distribution in those hosts only. Information about the pathogenesis, ecology, and host spectrum in humans and other mammals is given elsewhere (e.g., Fuehrer et al. 2011; Fuehrer 2013; Schmidt 2001).

For data evaluation, the systematic search was based on electronic databases (Scopus, PubMed, Google Scholar) and previous summaries (e.g., Schmidt 2001). The search terms *Capillaria hepatica*, *Calodium hepaticum*, *Hepaticola hepatica*, *Trichocephalus hepaticus*, and hepatic capillariasis were used. An attempt was made to include only those studies where the scientific names of the host and parasite were given clearly. Furthermore, spurious infections (= pseudoparasitism) were differentiated as far as possible from hepatic capillariasis. A short overview of spurious *C. hepaticum* infections in animals is given in Fuehrer (2013).

Taxonomy

*C. hepaticum* is a nematode out of the family Capillaridae (order Trichocephalida). Moravec (1982) categorized *C. hepaticum* in the genus *Calodium*. However, the name *C. hepaticum* is rarely used, and most researchers use the term *Capillaria hepatica*. Further synonyms are *Trichocephalus hepaticus* (Bancroft, 1893) and *Hepaticola hepatica* (Hall 1916) (Fuehrer et al. 2011).

The taxonomy of the family Capillaridae is disputed and pending. In the past, most species were included in the genus *Capillaria*. Recently, a molecular phylogenetic study revealed that Capillaridae can be clearly separated from Trichuridae (Guardone et al. 2013). However, the former genus *Capillaria* consists of a complex group of parasites including several
parasites of carnivores and rodents of the genera *Calodium*, *Eucoleus*, *Capillaria*, *Paracapillaria*, *Pearsonema*, and *Aonchotheca* (Guardone et al. 2013). Three species are of zoonotic importance, namely *Paracapillaria philippinensis* (syn. *Capillaria philippinensis*), *Eucoleus aerophila* (syn. *Capillaria aerophila*), and *C. hepaticum* (syn. *C. hepatica*).

**Life cycle**

The life cycle of *C. hepaticum* is a direct one with a high affinity to the liver. After the ingestion of embryonated eggs, larvae hatch in the area of the caecum and invade the liver via the portal vein system. Adult worms.parasitize in the liver of its mammalian hosts where the females lay eggs into the liver parenchyma after mating. The life span of adult worms is short (18–60 days post infection in mice) (Juncker-Voss et al. 2000; Schmidt 2001). The eggs develop in the host's liver to the eight-cell stage only. Unembryonated eggs are only released into the environment with the death of the host only (decay of host; excretion in feces of carnivores and omnivores or after cannibalism). Depending on the environmental conditions (e.g., humidity, temperature), eggs embryonate within 5–8 weeks. Laboratory studies revealed that embryonated eggs are viable for 25 months (reviewed in Juncker-Voss et al. 2000). The life cycle is closed when embryonated eggs are ingested from a mammalian host. The ingestion of non-embryonated eggs leads to pseudoparasitosis (= spurious infections) where the non-embryonated eggs are re-released with the feces and lead to mild symptoms only (reviewed in Fuehrer et al. 2011).

**Muroidea host spectrum**

The mammalian superfamily Muroidea consists of rodents with a worldwide distribution (with the exception of Antarctica) including animals like rats, true mice, gerbils, and hamsters. Recent molecular phylogenetic studies classified the superfamily into 6 families, 19 subfamilies, around 280 genera, and over 1,300 species (e.g., Steppan et al. 2004).

The host spectrum of *C. hepaticum* in Muroidea hosts (and in other mammals) indicates very low host specificity. More than 90 species of at least 44 genera of the superfamily Muroidea (Murinae, Arvicolinae, Neotominae, Cricetinae, Sigmodontinae, Gerbillinae, and Cricetomyinae) are known as hosts of this parasite (Table 1). Of these, more than 55 species are rodents of the subfamily Murinae including the Norway rat (*Rattus norvegicus*), Black rat (*Rattus rattus*), and house mouse (*Mus musculus*). Prevalences above 50 % are regularly documented in Norway rats (*R. norvegicus*) and Tanezumi rats (*R. tanezumi*), and rarely in house mice (*M. musculus*), long-tailed field mice (*Apodemus sylvaticus*), muskrats (*Ondatra zibethicus*), and bank voles (*Myodes glareolus*). All of these species are known as (commensal or non-commensal) synanthropic species. Human hepatic capillariasis cases are associated with poor hygienic conditions and the presence of rodents (e.g., rats) (Fuehrer et al. 2011). Davis (1951) reported that *C. hepaticum* is significantly less prevalent in decreasing rat populations than in stationary or increasing populations. A study conducted in Michigan (USA) with deer mice revealed that parasite prevalences are correlated negatively with heterozygosity when the effects of population density were held constant (Meagher 1998). Meagher further hypothesizes that inbred populations are more susceptible to parasite infestations. Differences in the prevalences of *C. hepaticum* in different rodent host species are thought to be associated with different living and nutritional habits (Schmidt et al. 1998). Several authors report that *C. hepaticum* occurs in localized foci of the examined study areas (e.g., Reperant and Deplazes 2005; Stojčević et al. 2002). Furthermore, cannibalism may be an important egg-releasing mechanism and is an important source of infection in burrows. On the other hand, predation seems to be responsible for scattered foci of infection (Farhang-Azad 1977a, b; Stojčević et al. 2002). Decomposition is thought to be a less important egg-releasing mechanism. Environmental conditions (humidity and temperature) are also associated with the distribution of these pathogens (e.g., Resendes et al. 2009). The pathogenicity of *C. hepaticum* in Muroidea hosts is considered low, although experimental infections of rats and mice have been demonstrated to lead to hepatic failure and the death of the host (the host survival rate is reduced by 5–10 %) (Singleton and Chambers 1996). However, individual variations of the host's inflammatory reaction to the parasite have been reported. Furthermore, hypersensitivity is associated with repeated infections (Borucinska and Nielsen 1993).

**Hepatic capillariasis—geographic distribution in Muroidea hosts**

*C. hepaticum* has been found in Muroidean hosts in more than 60 countries in Europe; North, Central, and South America; Asia; Africa; and Oceania. *R. norvegicus* is the rodent species with the highest prevalences worldwide. In Europe, North America, South America, and Asia, several studies reported prevalences above 50 % in Norway rats (e.g., Easterbrook et al. 2007). Also other murid host species can present high prevalences in certain regions. In Asia, the nematode was found in prevalences above 50 % in the common species *R. tanezumi* and the white bellied rat (*Niviventer fuloscens*) (e.g., Yuan et al. 2000; Zhou et al. 1998). Furthermore, the muskrat (*O. zibethicus*) seems to be an important host of *C. hepaticum* in North America (Borucinska and Nielsen 1993). In the UK, high prevalences of this parasite were observed in long-tailed...
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
| Muridae        |         |                |                |            |
| Murinae        | Norway rat (Rattus norvegicus) | 82 % (of 86) | USA (Connecticut) | Childs et al. (1988); Shorb (1931); Wantland et al. (1956) |
|                |         | 75 % (of 845) | USA (Maryland—Baltimore area and zoo) | Farhang-Azad (1977a) |
|                |         | 75 % (of 845) | USA (Maryland—Baltimore Zoo) | Farhang-Azad (1977b) |
|                |         | 87.9 % (176/201) | USA (Maryland, Baltimore) | Easterbrook et al. (2007) |
|                |         | 85.6 % | USA (New York) | Herman (1939) |
|                |         | 94.1 % (of 1,460) | USA (North Carolina) | Luttermoser (1936) |
|                |         |                | USA (District of Columbia) | Davis (1951) |
|                |         |                | USA (Pennsylvania and Rhode Island) | Harkema (1936) |
|                |         |                | USA (California) | Hill (1916) |
|                |         | Spurious infection 6 % (of 150) | Canada (Quebec) | Firlotte (1948) |
|                |         |                | Puerto Rico | Leon de (1964) |
|                |         |                | Venezuela | Vogelsang and Espin (1949) |
|                |         | 20.1 % (51/254) | Colombia | Duque et al. (2012) |
|                |         |                | Brazil (Bahia) | Araújo (1967); Galvão (1981); Chieffi et al. (1981); Ferreira and Andrade (1993) |
|                |         | 54.1 % (13/24) | Brazil (Belém) | Moreira et al. (2013) |
|                |         | 30 % | Argentina (Buenos Aires) | Hancke (2011) |
|                |         | 33.3 % (5/15) | Chile | Torres and González (1972); Rojas et al. (1971) |
|                |         | 1 case | England | Simmons and Walkey (1971) |
|                |         | 1 case | England (zoo) | Redrobe and Patterson-Kane (2005) |
|                |         | A: 90.4 % (38/42) | England | Owen (1976) |
|                |         | B + C: none of 38 | England | Webster and MacDonald (1995) |
|                |         | 23 % (n =44) | England | Redrobe and Patterson-Kane (2005) |
|                |         | 60 % (of 29) | Portugal (Azores) | Roque (1989) |
|                |         | 20 % (of 20) | Portugal (Azores) | Cruz (2006) |
|                |         | 62.5 % (of 73) | Portugal | Roque et al. (1984) |
|                |         | 42 % (21/50) | Portugal Lisbon Zoo | Crespo (2012) |
|                |         | 20 % | Spain | }
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
|                |         |                |                | Mascato et al. (1993); Feliu et al. (1985); Castro (1944); Gillego Berenguer (1959) |
|                |         |                |                | Duvoust et al. (1997) |
|                |         |                |                | Perugia (1893) |
|                |         | 80 % (of 28)   | Italy          | Davoust et al. (1997) |
|                |         | 30 % (of 100)  | Italy (Pisa)   | Vanni (1938); Vanni (1947) |
|                |         | 30 % (of 50)   | Italy          | Ghelardoni (1966) |
|                |         | 36 % (17/49)   | Italy (Milano) | Casarosa and Ghelardoni (1965) |
|                |         | 54.55 % (of 143)| Italy (Sicily) | Ceruti et al. (2001) |
|                |         | 74.6 %         | Austria        | Milazzo et al. (2010b) |
|                |         | 1 case         |奥地利          | Rydlo (1966) |
|                |         | 16.4 % (of 864)| Belgium        | Frank (1977) |
|                |         | 100 % (26/26)  | Former CSSR    | Hörning (1966) |
|                |         | 1.95 % (6/307) | Croatia        | Cotteleer et al. (1982) |
|                |         | 10.9 % (of 147)| Serbia (Belgrad)| Mészáros and Kemenes (1973) |
|                |         |                | Turkey         | Stojčević et al. (2002) |
|                |         |                | Kazakhstan     | Kataranovski et al. (2010) |
|                |         |                | Japan          | Merdivenci (1970) |
|                |         |                |                | Pleščev and Kozlov (1978) |
|                |         | 52.7 % (1,272/2,222)| Japan (Osaka)| Shimatani (1961); Sato and Shimatani (1960); Iwaki et al. (1993); Ito et al. (1996); Yagisawa (1978) |
|                |         | 90 %           | Philippines    | Momma (1930) |
|                |         | 60/138 (42 %)  | Thailand       | Tubangui (1931) |
|                |         | 12.5 % (of 16) | Thailand       | Chaiyabutr (1979) |
|                |         |                | Malaysia       | Namue and Wongswad (1997) |
|                |         |                | China          | Liat et al. (1977); Sinniah et al. (1979) |
|                |         | 30.4 %         | China (Soochow)| Lagrange (1924) |
|                |         | 7.1 %          | China (Canton)| Wu (1930) |
|                |         | 61.9 %         | China (Hubei Province) | Chen (1933) |
|                |         | 66.7 %         | China (Yunnan Province) | Zhou et al. (1991) |
|                |         | 1 case         | China (Yunnan Province) | Zhou et al. (1998) |
|                |         | 77 %           | China (Yunnan Province) | Xiong et al. (1999) |
|                |         | 66.7 %         | China (Fujian Province) | Shen et al. (2003) |
|                |         |                |                | Yuan et al. (2000) |
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
|                |         |                | China (Fujian Province) | Xue et al. (1998) |
|                |         |                | China (Fujian Province) | Zhang et al. (2003) |
|                |         |                | China (Henan Province) | Lin et al. (2007) |
|                |         |                | China (Henan) | Wang et al. (2013) |
|                |         |                | Taiwan | Yang and Lu (2000) |
|                |         |                | Taiwan | Tung et al. (2009) |
|                |         |                | Taiwan | Tung et al. (2013) |
|                |         |                | South Korea (Seoul) | Nakamura and Kobashi (1935) |
|                |         |                | South Korea (Seoul) | Seo et al. (1964) |
|                |         |                | South Korea (Seoul) | Min (1979) |
|                |         |                | South Korea (Seoul) | Yi et al. (2010) |
|                |         |                | South Korea (Chunchon) | Seong et al. (1995) |
|                |         |                | Iran | Pakdel et al. (2013) |
|                |         |                | Australia (Queensland) | Singleton et al. (1991) |
|                |         |                | Egypt | El-Nassery et al. (1991) |
|                |         |                | Tunisia | Mishra and Gonzalez (1975) |
|                |         |                | New Zealand | Roberts (1990) |
|                |         |                | Australia (Queensland) | Singleton et al. (1991) |
|                |         |                | Federated States of Micronesia (Pohnpei) | Størmer (1962) |
|                |         |                | Bangladesh | Bhuian et al. (1995) |
|                |         |                | India | Malsawmthluangi and Tandon (2009) |
|                |         |                | India | Shama et al. (2012) |
|                |         |                | India | Patel et al. (2004) |
|                |         |                | Pakistan | Ahmad et al. (2011) |
|                |         |                | Iran | Pakdel et al. (2013) |
|                |         |                | Thailand | Chaiyabutr (1979) |
|                |         |                | Thailand | Namue and Wongsawad (1997) |
|                |         |                | Taiwan | Tung et al. (2009) |
|                |         |                | Taiwan | Tung et al. (2013) |
|                |         |                | Japan | Sato and Shimatani (1960); Shimatani (1961) |
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
| Turkey         | -       | 3.1 % (2/65)   | Israel         | Merdivenci (1970) |
|                |         |                | Spain          | Wilamowski et al. (2002) |
|                |         |                | Portugal (Azores) | Feliu et al. (1985); Castro (1944); Gallego Berenguer (1959) |
|                |         |                | France         | Casanova et al. (1996); Roque (1989) |
|                |         | 34.2 % (of 37) | Italy (Sicily) | Milazzo et al. (2010a) |
|                |         |                | Switzerland    | Höming (1966) |
|                |         |                | USA            | Layne (1970) |
|                |         |                | Brazil (Bahia) | Chieffi et al. 1981 |
|                |         |                | Brazil (São Paulo) | Almeida-Silva et al. (2011) |
|                |         |                | Brazil (Belém) | Moreira et al. (2013) |
|                |         |                | Egypt          | El-Nassery et al. (1991) |
|                |         |                | Ethiopia       | Farhang-Azad and Schlitter (1978) |
|                |         | 69.8 % (30/43) | Democratic Republic of the Congo | Dubois (1933) |
|                |         | 38.4 % (10/26) | Philippines    | Onyenwe et al. (2009) |
|                |         | 6.2 % (19/308) | Japan (Southern Anami Islands) | Claveira et al. (2005) |
|                | Rattus spp. (R. norvegicus and/or R. rattus) | 100 % (of 12) | Philippines | Kamiya et al. (1968) |
|                | Rattus spp. (Rattus rattus diardii, R. norvegicus, and R. exulans) | 34 % | Japan (Southern Anami Islands) | Davoust et al. (1997) |
|                | Rattus sp. | 21.6 % | Malaysia | Paramasvaran et al. (2009) |
|                |         | 11.9 % | France—Lyon Zoo | Apéry (2012) |
|                |         | 13 % | France—Vincennes Zoo | Apéry (2012) |
|                | Rattus rattus sladerni | 38.8 % | China (Yunnan Province) | Shan et al. (2003) |
|                |         | 33 % (1/3) | China (Yunnan Province) | Xiong et al. (1999) |
|                | Polynesian rat (Rattus exulans) | 37.5 % | New Zealand | Roberts (1990) |
|                |         | | Indonesia | Brown et al. (1975b) |
|                |         | | Malaysia | Liat et al. (1977); Sinniah et al. (1979) |
|                | Sikkim rat (Rattus andamanensis) | 8.3 % (1/12) | Bangladesh | Fuehrer et al. (2012) |
|                | Rice-field rat (Rattus argentiventer) | 5.4 % | Taiwan | Yang and Lu (2000) |
|                | Lesser rice-field rat (Rattus kosea) | 38.9 % | China (Fujian Province) | Yuan et al. (2000) |
| Classification                  | Species                          | Prevalence (%) | Country/region       | References                                    |
|---------------------------------|----------------------------------|----------------|----------------------|-----------------------------------------------|
| Hoffmann’s rat (Rattus hoffmanni) | Indonesia                        |                |                      | Brown et al. (1975b)                          |
| Opossum rat (Rattus marmosaurus) | Indonesia                        |                |                      | Brown et al. (1975b)                          |
| Tanezumi rat (Rattus tanezumi)   | Indonesia                        |                |                      | Brown et al. (1975b); Wiroreno (1978)         |
|                                 | Malaysia                         |                |                      | Liat et al. (1977); Sinniah et al. (1979)     |
| *Rattus fuscipes* (syn. for Rattus tanezumi) | 12.9 % (20/155) | China (Henan) |                      | Wang et al. (2013)                            |
|                                 | China (Henan Province)           | 12.9 %         |                      | Lin et al. (2007)                             |
|                                 | China (Hubei Province)           | 61.9 %         |                      | Zhou et al. (1991)                            |
|                                 | China (Yunnan Province)          | 65.1 %         |                      | Zhou et al. (1998)                            |
|                                 | China (Yunnan Province)          | 49.4 % (of 881)|                      | Xiong et al. (1999)                           |
|                                 | China (Yunnan Province)          | 77.5 %         |                      | Shen et al. (2003)                            |
|                                 | China (Fujian Province)          | 44.3 %         |                      | Yuan et al. (2000)                            |
|                                 | China (Fujian Province)          | 13.1 %         |                      | Xue et al. (1998)                             |
|                                 | China (Fujian Province)          | 66.7 %         |                      | Zhang et al. (2003)                           |
| Malayan field rat (Rattus tiomanicus) | Malaysia                        |                |                      | Mulkit and Cheong (1971); Liat et al. (1977); Sinniah et al. (1979) |
| Annandale’s rat (Rattus annandalei) | Malaysia                        | 44.4 %         |                      | Syad-Amez and Mohd Zain (2006)                |
| Himalayan field rat (Rattus nitidus) | India                          | 40.1 %         |                      | Liat et al. (1977); Sinniah et al. (1979)     |
| Bush rat (Rattus fuscipes)       | Australia                        |                |                      | Malasawmthluangi and Tandon (2009)            |
| Müller’s giant Sunda rat (Sundamys muelleri) | Malaysia                        | 33.3 %         |                      | Liat et al. (1977)                            |
| Greater bandicoot rat (Bandicota indica) | Malaysia                        | 11.5 %         |                      | Syad-Amez and Mohd Zain (2006)                |
|                                 | Taiwan                           |                |                      | Liat et al. (1977)                            |
|                                 | Sri Lanka                        |                |                      | Yang and Lu (2000)                            |
|                                 | Bangladesh                       |                |                      | Dissanaike and Panamanthan (1961)             |
| Lesser bandicoot rat (Bandicota bengalensis) | Bangladesh                       | 33.3 % (6/18)|                      | Bhuian et al. (1995)                          |
|                                 | India                            |                |                      | Pasricha et al. (1941)                        |
|                                 | India                            |                |                      | Singhla et al. (2013)                         |
| Bower’s white-toothed rat (Berylmys bowersi) | Malaysia                        | 16.6 %         |                      | Liat et al. (1977)                            |
| Kenneth’s white-toothed rat (Berylmys mackenziei) | India                          | 31.8 %         |                      | Malasawmthluangi and Tandon (2009)            |
| Gray tree rat (Lenothrix canus)   | Malaysia                         |                |                      | Malasawmthluangi and Tandon (2009)            |
| White-bellied rat (Niviventer niviventer) | Indonesia                       |                |                      | Liat et al. (1977)                            |
| Chestnut white-bellied rat (Niviventer fulvescens) | Malaysia                        | 40 %           |                      | Malasawmthluangi and Tandon (2009)            |
|                                 | India                            |                |                      | Liu et al. (1977)                             |
|                                 | Malasawmthluangi and Tandon (2009) | 55.6 %         |                      | Yuan et al. (2000)                            |
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
| Dark-tailed tree rat *Niviventer cremoriventer* | Malaysia | Mulkit and Cheong (1971) |
| Chinese white-bellied rat *Niviventer confucianus* | 30 % | China (Fujian Province) | Yuan et al. (2000) |
| *Rattus niviventer* (sug. syn. for *Niviventer* sp.) | 6.12 % (3/49) | China (Henan) | Wang et al. (2013) |
| Edwards's long-tailed giant rat *Leopoldamys edwardsi* | Malaysia | Brown et al. (1975b) |
| Long-tailed giant rat *Leopoldamys sabanus* | Indonesia | Mulkit and Cheong (1971); Liat et al. (1977) |
| Bartels's spiny rat *Maxomys bartelsii* | Indonesia | Brown et al. (1975b); Wiroreno (1978) |
| Hellwald's spiny rat *Maxomys hellwaldii* | Indonesia | Brown et al. (1975b) |
| Rajah spiny rat *Maxomys rajah* | Malaysia | Mulkit and Cheong (1971); Liat et al. (1977) |
| Musschenbroek's spiny rat *Maxomys musschenbroekii* | Indonesia | Brown et al. (1975b) |
| Whitehead's spiny rat *Maxomys whiteheadi* | Malaysia | Mulkit and Cheong (1971); Liat et al. (1977) |
| Red spiny rat *Maxomys surifer* | Malaysia | 25 % | Syed-Arne and Mohd Zain 2006 |
| Fawn-footed mosaic-tailed rat *Melomys cervinipes* | Malaysia | 30.6 % | Syed-Arne and Mohd Zain 2006 |
| Giant white-tailed rat *Uromys caudimaculatus* | Australia | 24 % | Singleton et al. (1991) |
| Kaiser's rock rat *Aethomys kaiser* | Rwanda | Fain (1955) |
| Hinde's rock rat *Aethomys hindei* | Democratic Republic of the Congo | Fain (1953) |
| Peters's striped mouse *Hybomys univittatus* | Democratic Republic of the Congo | Schwetz (1956) |
| African grass rat *Arvicanthis niloticus* | Democratic Republic of the Congo | Fain (1953) |
| African marsh rat *Dasymys incomtus* | Democratic Republic of the Congo | Fain (1953); Schwetz (1956) |
| House mouse *Mus musculus* | Spain | Mascato et al. (1993); Feliu et al. (1985); Castro (1944); Gallego Berenguer (1959) |
| | Israel | Wilamowski et al. (2002) |
| | Russia | Romašov (1983) |
| | Russia | Romašov (1996) |
| | Kazakhstan | Plesčev and Kozlov (1978) |
| | Turkey | Mertvene (1970) |
| | Austria | Juncker et al. (1998) |
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
| Long-tailed field mouse (*Apodemus sylvaticus*) | 42.7 % (of 166) | Austria (Vienna—zoo) | Juncker-Voss et al. (2000) |
| | | Switzerland | Höming (1966) |
| | 80 % (of 5) | Italy | Vanni (1947) |
| | 5.5 % (of 37) | Italy (Sicily) | Milazzo et al. (2010a) |
| | 21.2 % (of 52) | Portugal (Azores) | Casanova et al. (1996) |
| | 19.6 % (10/51) | Portugal (Azores) | Resendes et al. (2009) |
| | 40.2 % (of 92) | Portugal (Azores) | Perera (2009) |
| | 22 % (11/50) | Portugal Lisbon Zoo | Crespo (2012) |
| | | USA | Childs et al. (1988) |
| | | USA (Maryland) | Luttermoser (1938) |
| | | USA (Pennsylvania) | Doran (1955) |
| | 0.9 % (of 110) | Iran | Pakdel et al. (2013) |
| | 4.6 % (of 410) | Pakistan | Ahmad et al. (2011) |
| | 2.1 % (1/47) | Bangladesh | Fuehrer et al. (2012) |
| | 19.1 % | China (Hubei Province) | Zhou et al. (1991) |
| | 21.1 % | China (Yunnan Province) | Zhou et al. (1998) |
| | 4.6 % | China (Fujian Province) | Xue et al. (1998) |
| | 10 % | China (Henan Province) | Lin et al. (2007) |
| | 10 % (13/130) | Australia (Queensland) | Singleton et al. (1991) |
| | | Australia release study | Singleton and Chambers (1996) |
| | 7 % (of 99) | Switzerland (Geneva Canton) | Reperant and Deplazes (2005) |
| | | Belgium | Bernard (1961) |
| | | Former UDSSR | Pavlov (1955) |
| | | Spain | Feliu et al. (1984, 1985, 1987); Mas-Coma and Feliu (1977); Prokopič and Tenora (1975) |
| | 75 % (of 58) | England | Baylis (1931) |
| | 100 % | St. Kilda, UK | Canning et al. (1973) |
| | 18 % (2/11) | UK Shetland Islands | Berry and Tricker (1969) |
| | | Wales | Wilson et al. (1998) |
| | | Slovakia | Lewis (1968) |
| | | | Mituch (1966/1970) |
| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
| Yellow-necked mouse (*Apodemus flavicol lis*) | 5.93 % (of 135) | Russia | | Romašov (1978, 1996) |
| | 2 cases | Bulgaria | | Genov (1984); Prokopič and Genov (1974) |
| | 8.5 % (24/284) | Germany (Saxony-Anhalt) | | Schmidt (2001) |
| | 6 cases | Denmark | | Tenora et al. (1991) |
| | 1.5 % (of 96) | France (forested area near Dijon) | | Scandola et al. (2013) |
| | | Iran | | Mbedi and Arfa (1971) |
| | 3.37 % (of 297) | Russia | | Romašov (1978) |
| | 0.2 % | Russia (Southern West Siberia) | | Chechulin et al. (2011) |
| | 4.27 % (5/117) | Russia (Novosibirsk Region) | | Kovačević and Bonina (1981) |
| | | China (Henan) | | Wang et al. (2013) |
| Small Japanese field mouse (*Apodemus argentineus*) | | Japan | | Chabaud et al. (1963); Ishimoto (1974); Iwaki et al. (1993) |
| Korean field mouse (*Apodemus peninsulae*) | | Japan | | Iwaki et al. (1993) |
| Large Japanese field mouse (*Apodemus speciosus*) | | Japan | | Iwaki et al. (1993) |
| Typical striped grass mouse (*Lemniscomys striatus*) | | Democratic Republic of the Congo | | Fain (1953) |
| Southern multimammate mouse (*Mastomys coucha*) | | Democratic Republic of the Congo | | Fain (1953); Schwetz (1956) |
| Natal multimammate mouse (*Mastomys natalensis*) | | Ghana | | Papeka et al. (1970) |
| Jackson's soft-furred mouse (*Praomys jacksoni*) | | South Africa | | Cochrane et al. (1957) |
| Tropical Vlei rat (*Otomys tropicalis*) | | Democratic Republic of the Congo | | Fain (1953) |
Table 1 (continued)

| Classification | Species | Prevalence (%) | Country/region | References |
|----------------|---------|----------------|----------------|------------|
| Creek groov-toothed swamp rat (*Pelomys fallax*) | Democratic Republic of the Congo | Schwetz (1956) |
| Bell groov-toothed swamp rat (*Pelomys campanae*) | Guinea | Joyeux et al. (1928) |
| Target rat (*Stochomys longicaudatus*) | Democratic Republic of the Congo | Schwetz (1956) |
| Ethiopian white-footed mouse (*Stenocephalemys albipes*) | Ethiopia | Farhang-Azad and Schlitter (1978) |
| **Deomyinae** | | | | |
| Yellow-spo tted brush-furred rat (*Lophuromys flavopunctatus*) | Democratic Republic of the Congo | Schwetz (1956) |
| Southern African spiny mouse (*Acomys spinosissimus*) | Zimbabwe | Sandground (1933) |
| **Cricetidae** | Bank vole (*Myodes glareolus*) | Russia | Romašov (1978, 1996) |
| | | Russia | Romašov (1983) |
| | | Russia (Southern West Siberia) | Chechulin et al. (2011) |
| | | Former UDSSR | Pavlov (1955) |
| | | England | Canning et al. (1973) |
| | | France (forested area near Dijon) | Scandola et al. (2013) |
| | | Germany (Saxony-Anhalt) | Schmidt et al. (1998); Schmidt (2001) |
| | | Switzerland (Geneva Canton) | Reperant and Deplazes (2005) |
| | | Slovakia | Mituch (1960) |
| | | Czech Republic | Rupeš (1964) |
| | | Former UDSSR | Pavlov (1955) |
| | | Russia (Southern West Siberia) | Chechulin et al. (2011) |
| | | USA | Fisher (1963) |
| | | USA | Solomon and Handle (1971) |
| | | Canada (Alonquin Park) | Freeman and Wright (1960) |
| | | Japan | Chabaud et al. (1963); Ishimoto (1974); Iwaki et al. (1993) |
| | | Northern mole vole (*Ellobius talpinus*) | Former UDSSR | Pavlov (1955) |
| | | Zaisan mole vole (*Ellobius tancrei*) | USA | Mentioned in Tinnin et al. (2011) |
| | | Siberian brown lemming (*Lemmus sibiricus*) | Former UDSSR | Morozow (1956) |
| | | USA | Rausch (1961) |
| | | Southern bog lemming (*Synaptomys cooperi*) | Canada (Alonquin Park) | Freeman and Wright (1960) |
| | | | Canada (Alonquin Park) | Freeman and Wright (1960) |
| | | | Canada (Ontario) | Price (1931) |
| | | USA | Borucinska et al. (1997) |
| | | Laboratory infection studies | USA (Pennsylvania and Connecticut) | Borucinska et al. (1993) |
| Classification          | Species                              | Prevalence (%) | Country/region                  | References                  |
|-------------------------|--------------------------------------|----------------|---------------------------------|-----------------------------|
|                         |                                      |                | USA (Louisiana)                 | Penn (1952)                 |
|                         |                                      | 17 % (of 104)  | USA (Maine)                     | Meyers and Reilly (1950)    |
|                         |                                      |                | USA (Michigan)                  | Ameel (1942)                |
|                         |                                      |                | Russia                          | Ramašov (1995, 1996)        |
|                         |                                      |                | Former CSSR                     | Tenora and Zavadil (1967)   |
|                         |                                      | 4.21 % (of 1,140) | Belgium                      | Cotteleer et al. (1982)    |
|                         |                                      | 1 case (of 440) | Great Britain                  | Warwick (1937)              |
| Field vole (*M. agrestis*) |                                      | 3 cases (of 5)  | Austria                         | Frank (1977)                |
|                         |                                      | 16.67 % (of 6) | Russia                          | Ramašov (1983)              |
|                         |                                      | 4.5 %           | Russia                          | Ramašov (1978, 1996)        |
|                         |                                      | 0.9 % (3/318)  | Russia                          | Chechulin et al. (2011)     |
| Common vole (*M. arvalis*) |                                      | 4 cases (of 4)  | Austria                         | Fuehrer et al. (2010)       |
|                         |                                      | 20.69 % (of 29) | Russia                          | Ramašov (1983)              |
| Rock vole (*M. chrotorrhinus*) |                                      |                | USA                             | Fisher (1963)               |
|                         |                                      |                | Canada                          | Freeman and Wright (1960); Lubinsky et al. (1971) |
| Meadow vole (*M. pennsylvanicus*) |                                      | 9.4 % (of 769) | Canada                          | Lubinsky et al. (1971)      |
| Tundra vole (*M. oeconomus*) |                                      | 3.4 %           | Russia                          | Chechulin et al. (2011)     |
| Narrow-headed vole (*M. gregalis*) |                                      | 1 case          | England (zoo)                   | Redrobe and Patterson-Kane (2005) |
| Günther's vole (*M. guentheri*) |                                      | 1.1 % (1/98)    | Austria                         | Fuehrer et al. (2010)       |
| Water vole (*A. terrestris*) |                                      | 10.4 %          | Russia                          | Chechulin et al. (1989); Ramašov (1978, 1996) |
| European snow vole (*C. nivalis*) |                                      | 28.57 % (of 42) | Russia                          | Ramašov (1983)              |
|                         |                                      | 0.2 % (of 466)  | Switzerland                     | Reperant and Deplazes (2005) |
|                         |                                      | 2 cases         | England (zoo)                   | Redrobe and Patterson-Kane (2005) |
| Brandt's vole (*L. brandti*) |                                      |                | China (Inner Mongolia)          | Wan et al. (2007a)          |
| Neotominae              | Eastern wood rat (*N. floridana*)     | 47.1 % (16/34)  | USA                             | Solomon and Handley (1971)  |
| Classification | Species                             | Prevalence (%) | Country/region | References |
|----------------|-------------------------------------|----------------|----------------|------------|
|                 | Bushy-tailed woodrat (*Neotoma cinerea*) |                | USA            | Rausch (1961) |
|                 | Cotton mouse (*Peromyscus gossypinus*) |                | USA            | Layne (1968, 1970); Layne and Winegamer (1971) |
|                 | White-footed mouse (*Peromyscus leucopus*) | 2.9 % (7/239) | USA            | Solomon and Handley (1971) |
|                 | Deer mouse (*Peromyscus maniculatus*) | 10.2 % (73/713) | USA (lab experiments) | Meagher (1998) |
|                 | Florida mouse (*Podomys floridanus*) | 12.7 % (21/723) | USA (Florida) | Layne and Griff Jr (1961) |
|                 | Reithrodontomyss sp. |                | USA            | King and Stanton (1974) |
| Cricetinae      | Gray dwarf hamster (*Cricetulus migratorius*) |                | Former UDSSR | Pavlov (1955) |
|                 | European hamster (*Cricetus cricetus*) |                | Austria        | Frank (1977) |
|                 | Greater long-tailed hamster (*Tscherskia triton*) |                | China (Henan) | Wang et al. (2013) |
|                 | Campbell's dwarf hamster (*Phodopus campbelli*) |                | China (Inner Mongolia) | Wan et al. (2007a, b) |
| Sigmodontinae   | Northern grass mouse (*Necromys urichi*) |                | Venezuela      | Vogelsang and Espin (1949) |
|                 | Hispid cotton rat (*Sigmodon hispidus*) | Freshwater marshes: 30 % (43/142); salt water marshes 12 % (4/34); upland habitats 5 % (1/22) | USA (Texas) | Read (1949); Kinsella (1974) |
| Gerbillinae     | Savanna gerbil (*Gerbilliscus validus*) |                | Democratic Republic of the Congo | Fain (1953) |
|                 | Emir's pouched rat (*Cricetomys emini*) | 17.7 % | Democratic Republic of the Congo | Malekani (1990), 1994 |
|                 | Persian jird (*Meriones persicus*) | 6.9 % (11/160) | Armenia | Kirakosjan et al. (1963) |
| Cricetomyinae   | Emin's pouched rat (*Cricetomys emini*) | 17.7 % | Democratic Republic of the Congo | Malekani (1990), 1994 |
|                 | Gambian pouched rat (*Cricetomys gambianus*) | 30.8 % | Democratic Republic of the Congo | Chine ne and Ibrahim (1984) |
field mice (*A. sylvaticus*) and the bank vole (*M. glareolus*) (Canning et al. 1973).

**Conclusions**

*C. hepaticum* is a worldwide-distributed parasite with rodents of the superfamily Muroidea as main hosts. *C. hepaticum* has been described in more than 90 rodent species. Murinae and Arvicolinae are the hosts with the highest prevalences of this parasite. The Norway rat seems to be the most important host species with reported prevalences above 50% on several continents. However, a high percentage of the studies dealt with Norway rats only, and not with less common murid rodents. Especially synanthropic (commensal and non-commensal) Murinae and Arvicolinae seem to be the most affected hosts.

However, the diagnosis of this pathogen is limited to liver biopsies and necropsy and so the true prevalence in Muroidea and other mammals remains unclear. At spurious infections, care should be taken to exclude mix-ups with other Trichuridae and Capillaridae shedding eggs of almost similar morphology (e.g., Bork-Mimm and Rinder 2011; Di Cesare et al. 2011; Stuart et al. 2013; Traversa et al. 2011). Novel (molecular) diagnostic tools for proper (molecular) species classification are of urgent need.

**Acknowledgments**  I wish to thank all authors who provided personal copies of their manuscripts.

**Conflict of interest** The author declares that he has no conflict of interest.

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