An overview of the host spectrum and distribution of Calodium hepaticum (syn. Capillaria hepatica): part 2—Mammalia (excluding Muroidea)

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Abstract Calodium hepaticum (syn. Capillaria hepatica) is a globally distributed zoonotic nematode with low host specificity and a high affinity to the liver. Although murid rodents are the main definite hosts, various other mammals can be affected with hepatic capillariasis: non-murid rodents, Insectivora, Chiroptera, Lagomorpha, Artiodactyla, Perissodactyla, Hyracoidea, Marsupialia, Carnivora, and Primates. Overall, more than 180 mammalian species (including humans) are known as suitable hosts of this pathogen. This review gives an overview of the distribution and host spectrum of C. hepaticum in non-Muroidean mammals in wildlife and zoos as well as in domesticated and laboratory animals. Furthermore, the role of spurious infections in animals and the dissemination of C. hepaticum are summarized. Information about the pathogenesis, ecology, and host spectrum in Muroidea 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.

Introduction

Calodium hepaticum is a worldwide-distributed zoonotic parasite with a high affinity to the liver. It is the causative agent of hepatic capillariasis and has low host specificity. This parasite is mainly diagnosed during liver biopsies or through necroscopy because the eggs of this nematode are only released into the environment after the host's death (after predation, cannibalism, or decay). The main hosts are rodents of the subfamilies Murinae and Arvicolinae. Although murids are the most important hosts, this parasite was documented in more than 70 non-murid species. This review focuses on the mammalian (excluding Muroidea) host spectrum and its geographic distribution in those hosts. Furthermore, the role of spurious infections in animals and the dissemination of C. hepaticum are summarized. Information about the pathogenesis, ecology, and host spectrum in Muroidea is given elsewhere (e.g., Fuehrer et al. 2011; Fuehrer 2013; Schmidt 2001).

The taxonomy of the family Capillaridae is pending. All species out of the former genus Capillaria are included in the family Capillaridae. A recent study has shown that the family Capillaridae seems to be monophyletic and can be clearly separated from Trichuridae (Guardone et al. 2013). Although most species parasitize in animals, three are known to also infect humans: Paracapillaria philippinensis (syn. Capillaria philippinensis), Eucoleus aerophila (syn. Capillaria aerophila), and C. hepaticum (syn. C. hepatica).

Adult C. hepaticum are long slender-shaped nematodes with a narrow anterior body part (0.007–0.01 mm). The
posterior body part becomes gradually thicker. Sexual dimorphism is present (females 27–100 mm; males 15–50 mm) (reviewed in Schmidt 2001). The eggs resemble typical trichurid eggs but differ in size (40–67×27–35 μM). The eggs are barrel-shaped, striated, and with polar plugs. Numerous minipores are present on the outer shell. The four larval stages differ in size (reviewed in Schmidt 2001).

_C. hepaticum_ has a high affinity to the liver and is the causative agent of hepatic capillariasis. The life cycle is a direct one. After the ingestion of embryonated eggs, L1 larvae hatch in the area of the caecum and invade the liver via the portal vein system. Adult _C. hepaticum_ nematodes live in the liver parenchyma (life span 18–60 days) where females lay unembryonated eggs into the liver parenchyma. The eggs develop in the liver parenchyma to the eight-cell stage. After the death of the host (cannibalism, predation, decay), the eggs are released into the environment and embryonate (depending on the environmental conditions) to the infective stage. The cycle closes with the ingestion of embryonated eggs by a new host (reviewed in Schmidt 2001). The ingestion of unembryonated eggs leads to spurious infections (= pseudoparasitism) where the non-infective eggs are shed into the environment with the feces.

**Host spectrum**

The main hosts of _C. hepaticum_ are several murid rodent species with the highest prevalences in synanthropic Murinae (e.g., Norway rat). The parasite was documented in more than 90 Muroidean rodent species of the subfamilies Murinae, Deomyinae, Arvicolinae, Neotominae, Cricetinae, Sigmodontinae, Gerbillinae, and Cricetomyinae (Führer et al. 2010; Fuehrer 2013).

However, hepatic _C. hepaticum_ infections were also found in Caviidae, Erethizontidae, Castoridae, Myocastoridae, Sciuridae, Geomyidae, Dipodidae, Nesomyidae, and Cuniculidae (Table 1). In wildlife, North American porcupines (USA; 9 % of 53), nutrias (Argentina; 3.6 % of 108), northern pocket gophers (USA; 39 % of 46), Brazilian guinea pigs (Peru; 6.9 % of 143), and lowland pacas (Brazil; 20 % of 5) were evaluated as suitable hosts of this parasite (Dittmar 2002; Hamir and Rupprecht 2000; Martino et al. 2012; Todd et al. 1971).

Furthermore, _C. hepaticum_ was documented in at least 69 species out of 25 families in non-rodent mammalian including Insectivora, Chiroptera, Lagomorpha, Artiodactyla, Perissodactyla, Hyracoidea, Marsupialia, Carnivora, and Primates (Table 2). In wildlife, hepatic capillariasis was documented in several studies: pronghorn antelopes (Canada; 4/41), red foxes (Italy; 1/75), crab-eating foxes (Brazil; 5.56 %), pampas foxes (Brazil; 13.64 %), and mountain gorillas (Rwanda; 10/19) (Barrett and Chalmers 1972; Graczyk et al. 1999; Macchioni et al. 2013; Ruas 2005). The true burden of this parasite in wildlife is not clear. Numerous documented cases of _C. hepaticum_ in non-murid mammals were reported from zoological gardens and laboratories or in domesticated animals.

**Zoos**

Several hepatic cases with _C. hepaticum_ had been observed in zoological gardens. Various studies documented single cases of this parasite. In some reports, more than one animal of a single species were infected: black-tailed prairie dogs (USA; 5/21; UK; 45 % of 20) and Kirk’s dik-diks (USA; 7/18) (Landolfi et al. 2003; Partington and Montali 1986; Redrobe and Patterson-Kane 2005). Most of the cases in primates were found in zoos.

Several studies tried to analyze the relationships of commensal rodents (e.g., Norway rats, house mice) to infections of animals in zoos (e.g., Juncker-Voss et al. 2000). In zoos, high prevalences of free-ranging rats, mice, and shrews were observed: Norway rats (Baltimore Zoo, USA; 75 % of 845; Lisbon Zoo, Portugal 42 % of 50), house mice (Vienna Zoo, Austria, 42.7 % of 166; Lisbon Zoo, Portugal 22 % of 50), and greater white-toothed shrews (France; 10–25 %) (Apéry 2012; Crespo 2012; Farhang-Azad 1977; Juncker-Voss et al. 2000).

**Laboratory animals and pet shops**

_C. hepaticum_ was found in various pet shops and laboratories, for example, in one out of four Korean squirrels imported from China to Spain, 3 out of 155 lab groundhogs imported from the USA to Germany, 13 out of 160 New Zealand White rabbits in France from a commercial distributor, two cases in common chimpanzees which were lab animals originating from West Africa, and 0.6 % of 472 wild-caught laboratory-maintained crab-eating macaques (Abbott and Majeed 1984; Carrasco et al. 2006; Hilken et al. 2003; Mowat et al. 2009; Sadun et al. 1970). It can be hypothesized that animals ingested embryonated eggs while living wild and/or with contaminated food.

**Domesticated animals**

_C. hepaticum_ was documented in domesticated mammal species like laboratory Norway rats, rabbits, cattle, pigs, horses, dogs, cats, domesticated guinea pigs, and squirrels. In Japan, hepatic capillariasis was observed in 2.25 % of 400 cattle, but the author did not classify the nematode as _C. hepaticum_ because the pathogen was not reported in cattle before (Nakamura 2005). Furthermore, Ilha and Barros (2000) found...
| Classification | Species | Country/countries | References |
|----------------|---------|-------------------|------------|
| Caviidae       | Domestic guinea pig (*Cavia porcellus*) | Pets: Hungary, Peru | Meszaros and Varga (1976) |
|                |         | Argentina, Peru    | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Dittmar (2002) |
|                | Brazilian guinea pig (*Cavia aperea*) | Argentina, Peru    | Morini and Boero (1958); Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                |         | Brazil             | Dittmar (2002) |
|                |         | Brazil             | Olortegui (1961); Gonzalez (1970) |
|                |         | Brazil             | Costa and Catto (1994) |
|                | Cavia sp. | Brazil             | Mentioned in Dittmar (2002) |
|                | Capybara (*Hydrochoerus hydrochaeris*) | Brazil (Nhecolândia) | Costa and Catto (1994) |
| Erethizontidae | North American porcupine (*Erethizon dorsatum*) | USA | Hamir and Rupprecht (2000) |
| Castoridae     | North American beaver (*Castor canadensis*) | USA (National Zoological Park) | Chitwood BG (Chitwood 1934) |
|                | Eurasian beaver (*Castor fiber*) | Hungary (Zoo) | Mészáros and Kemenes (1973) |
|                |         | Former UDSSR | Pavlov (1955) |
|                |         | Former UDSSR (several cases in a zoological park) | Mentioned in Mészáros and Kemenes (1973) |
|                |         | Russia | Romanov (1996) |
| Myocastoridae  | Nutria (*Myocastor coypus*) | Japan | Matsudate et al. (2003) |
|                |         | Germany (Saxony) | Seidel (1954) |
|                |         | Argentina | Vogelsang and Espin (1949) |
|                |         | Argentina | Martino et al. (2012) |
| Sciuridae      | Brazilian squirrel (*Sciurus aestivalis*) | Brazil | Freitas and Lent (1936) |
|                | Caucasian squirrel (*Sciurus anomalus*) | Former UDSSR | Pavlov (1955) |
|                | Fox squirrel (*Sciurus niger*) | USA (Louisiana) | McQuown (1954) |
|                | Eurasian red squirrel (*Sciurus vulgaris*) | UK (north Wales) | Stidworthy et al. (2009) |
|                | American red squirrel (*Tamiasciurus Hudsonicus*) | Canada (lab infection experiment) | Freeman and Wright (1960) |
|                | Korean squirrel (*Tanias sibericus*) | Spain (wild import) | Carrasco et al. (2006) |
|                | Sciurus sp. | Turkey | Merdivenci (1970) |
|                | Cape ground squirrel (*Xerus inauris*) | South Africa (Eastern Free State) | Erlwanger et al. (2009) |
|                | Richardson's ground squirrel (*Urocitellus richardsonii*) | USA (Montana) | Luttermoser (1938) |
|                | Domesticated squirrels | China | Brown and Roy (1943) |
|                | Black-tailed prairie dog (*Cynomys ludovicianus*) | USA | Mentioned in Wang et al. (2013) |
|                | USA (zoo) | USA | Weidman (1925) |
|                | USA (Pennsylvania) | USA | Landolfi et al. (2003) |
|                | England (zoo) | USA | Doran (1955) |
|                | England (zoo) | USA | Redrobe and Patterson-Kane (2005) |
|                | England (zoo) | USA | Brown and Roy (1943) |
|                | England (zoo) | USA | Mentioned in Wang et al. (2013) |
|                | Alpine marmot (*Marmota marmota*) | Spain | Gortazar et al. (1994) |
|                | Groundhog (*Marmota monax*) | USA | Reynolds and Gavutis Jr. (1975) |
|                | USA (Pennsylvania) | USA | Doran (1955) |
|                | Germany (Lab marmots imported from the USA) | USA | Hilken et al. (2003) |
|                | Red-checked flying squirrel (*Hylopetes abieticus*) | France | Gevrey et al. (1996) |
|                | Geomyidae | Malaysia | Liat et al. (1977) |
|                | Plains pocket gopher (*Geomys bursarius*) | USA | Ubelaker and Downhower (1965) |
|                | Northern pocket gopher (*Thomomys talpoides*) | Canada (Alberta) | Lubinsky (1956; 1957) |
|                | USA (Wyoming) | USA | Law and Kennedy (1932) |
|                | USA (Wyoming) | USA | Todd et al. (1971) |
|                | USA | USA | Rausch (1961) |
|                | Dipodidae | Woodland jumping mouse (*Napaeozapus insignis*) | USA | Freeman and Wright (1960) |
|                | Nesomyidae | Malagasy giant rat (*Hypogeomys antypus*) | England (zoo) | Redrobe and Patterson-Kane (2005) |
|                | Cuniculidae | Lowland paca (*Cuniculus paca*) | Brazil (Acre) | Almeida et al. (2012) |
|                |         | Costa Rica | Matamoros et al. (1991) |
Table 2  *Calodium hepaticum* in other mammals other than rodents

| Classification | Species                                | Country/countries            | References                  |
|----------------|-----------------------------------------|------------------------------|-----------------------------|
| Insectivora    | **Erinaceidae**                         |                              |                             |
|                | European hedgehog (*Erinaceus europaeus*)| Switzerland                  | Brander et al. (1990, 1991) |
|                | **Soricidae**                           |                              |                             |
|                | Smoky shrew (*Sorex fumeus*)            | USA                          | Solomon and Handley (1971)  |
|                | Northern short-tailed shrew (*Blorina brevicauda*) | USA                   | Solomon and Handley (1971)  |
|                | Laxmann’s shrew (*Sorex caecutiens*)    | ??                           | Mentioned in Tinnin et al. (2011) |
|                | Long-tailed shrew (*Sorex dispar*)      | USA                          | Solomon and Handley (1971)  |
|                | Cinereus shrew (*Sorex cinereus*)       | USA                          | Solomon and Handley (1971)  |
|                | Common shrew (*Sorex araneus*)          | Austria                      | Frank (1977)                |
|                | Shinto shrew (*Sorex shinto*)           | Japan                        | Iwaki et al. (1993)         |
|                | Long-clawed shrew (*Sorex unguiculatus*)| Japan                        | Chabaud et al. (1963)       |
|                | Asian house shrew (*Suncus murinus*)    | Indonesia                    | Brown et al. (1975a)        |
|                | Eurasian water shrew (*Neomys fodiens*)| England                      | Stidworthy et al. (2009)    |
|                | Greater white-toothed shrew (*Crocidura russula*) | France—Mulhouse Zoo | Apéry (2012)                |
|                |                                          | France—Lyon Zoo              | Apéry (2012)                |
| Chiroptera     | **Pteropodidae**                        |                              |                             |
|                | Lesser short-nosed fruit bat (*Cynopterus brachyotis*) | Indonesia                  | Brown et al. (1974)         |
| Lagomorpha     | **Leporidae**                           |                              |                             |
|                | European hare (*Lepus europaeanus*)     | ??                           | Hall (1916)                 |
|                | Mountain hare (*Lepus timidus*)         | Austria (zoo)                | Eder 2008                   |
|                | European rabbit (*Oryctolagus cuniculus*) | Switzerland              | Brander et al. (1991); Höning (1974) |
|                | Domestic rabbit (*Oryctolagus cuniculus forma domestica*) | Switzerland     | Morgan (1931)               |
|                | New Zealand white rabbits               | UK (rabbits from commercial distributor) | Mowat et al. (2009)         |
|                | Eastern cottontail (*Sylvilagus floridanus*) | USA                  | Layne (1970); Layne and Winegarner (1971) |
| Ochotonidae    | Plateau pika (*Ochotona curzoniae*)     | China (Gansu)                | In Wang et al. (2013)       |
| Artiodactyla   | **Antilocapridae**                      |                              |                             |
|                | Pronghorn antelope (*Antilocapra americana*) | Canada (Alberta)         | Barrett and Chalmers (1972) |
|                | Collared peccary (*Pecari tajacu*)      | Brazil                       | Mandorino and Rebouças (1991) |
|                | White-lipped peccary (*Tayassu pecari*) | Panama                      | Foster and Johnson (1939)   |
|                | *T. pecari* or *P. tajacu*              | Brazil                       | Soares et al. (2011)        |
|                | **Bovidae**                             |                              |                             |
|                | Kirk’s dik-dik (*Madoqua kirkii*)       | USA (zoo)                    | Partington and Montali (1986) |
|                | Cattle (*Bos primigenius*)              | Japan (Hokkaido)             | Nakamura (2005)             |
| Suidae         | Domestic pig (*Sus scrofa domesticus*)  | China                        | Zhang (1990)                |
| Perissodactyla | **Equidae**                             |                              |                             |
|                | Horse (*Equus ferus caballus*)          | Canada                       | Nation and Dies (1978)      |
|                |                                        | England                      | Munroe (1984)               |
|                | **Tapiridae**                           |                              |                             |
|                | Brazilian tapir (*Tapirus terrestris*)  | Brazil (Parana)              | Mangini et al. (2002)       |
|                | **Hyracoidea**                          |                              |                             |
|                | Southern tree hyrax (*Dendrohyrax arborens*) | Democratic Republic of the Congo | Fain (1953)                |

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Table 2 (continued)

| Classification | Species | Country/countries | References |
|----------------|---------|-------------------|------------|
| Marsupialia    |         |                   |            |
| Didelphidae    | Big-eared opossum (*Didelphis aurita*) | Paraguay | Canese (1973) |
|                | Common opossum (*Didelphis marsupialis*) | Columbia | CIAT (1973) |
| Macropodidae   | Agile wallaby (*Macropus agilis*) | Australia | Canfield and Hartley (1992) |
|                | Parma wallaby (*Macropus parma*) | Australia | Canfield and Hartley (1992) |
|                | Red kangaroo (*Macropus rufus*) | Australia | Canfield and Hartley (1992) |
| Potoroidae     | Rufous rat-kangaroo (*Aepyprymnus rufescens*) | Australia | Canfield and Hartley (1992) |
|                | Woylie (*Bettongia penicillata*) | Australia | Canfield and Hartley (1992) |
|                | Potoroideae spp. | Germany | Schmidt (1975) |
| Carnivora      |         |                   |            |
| Mephitidae     | Eastern spotted skunk (*Spilogale putorius*) | USA | Layne and Winegarner (1971) |
| Canidae        | Domestic dog (*Canis lupus familiaris*) | New Zealand | Anon. (1982) |
|                | West highland white terrier cross | Great Britain | Lloyd et al. (2002) |
|                | | Italy | Carta (1939) |
|                | | Switzerland | Brandre et al. (1990, 1991) |
|                | | USA (Washington) | Wright (1930) |
|                | | India | Rao et al. (1975) |
|                | | Brazil | Saliba et al. (1965); Santos and Barros (1973); Silveira et al. (1975) |
|                | | Brazil | Ilha and Barros (Ilha MR da S, Barros CSL de 2000) |
|                | | Brazil | Palma et al. (2009) |
|                | | South Africa | Smit (1960) |
|                | | Nigeria | Ajayi et al. (2011) |
|                | | Australia | Stokes (1973) |
|                | Gray wolf (*Canis lupus*) | Russia | Ronašov (1996) |
|                | Coyote (*Canis latrans*) | Canada | Wobeser and Rock (1973) |
|                | | USA | Crowell et al. (1978); Custer and Pence (1981) |
|                | Red fox (*Vulpes vulpes*) | Italy | Macchioni et al. (2013) |
|                | Crab-eating fox (*Cerdocyon thous*) | Brazil | Ruas (2005) |
|                | Pampas fox (*Lycalopex gymnocercus*) | Brazil | Ruas (2005) |
|                | Maned wolf (*Chrysocyon brachyurus*) | Brazil | Curiel (1954) |
| Felidae        | Domestic cat (*Felis catus*) | Brazil | Santos and Barros (1973) |
|                | | Brazil | Ilha and Barros (2000) |
|                | | Slovakia | Mituch (1968) |
|                | | Nigeria | Okaeme (1985, 1986) |
|                | | Brazil | Quadros et al. (2009) |
| Primates       | Cougar (*Puma concolor*) | Brazil |            |
| Lemuridae      | Ring-tailed lemur (*Lemur catta*) | Chile (zoo) | Zordan et al. (2012) |
|                | | ??? Zoo | Mentioned in Redrobe and Patterson (2005) |
| Cercopithecidae| Vervet monkey (*Chlorocebus pygerythrus*) | South Africa | Fripp and Kaschula (1974) |
|                | Grivet (*Chlorocebus aethiops*) | South Africa | Fripp and Kaschula (1974) |
|                | Rhesus macaque (*Macaca mulatta*) | South Africa | Brack (1987) |
|                | Crab-eating macaque (*Macaca fascicularis*) | UK (wild-caught laboratory-maintained primates) | Abbott and Majeed (1984) |
|                | Celebes crested macaque (*Macaca nigra*) | England (zoo) | Pizzi et al. (2008) |
|                | | England (zoo) | Stidworthy et al. (2009) |
**C. hepaticum** in the livers of 0.23 % of 3,927 dogs and 1.38 % of 435 cats examined in Brazil.

### Dispersal by animals and spurious infections

With the death of the animal host (cannibalism, predation, or decay), the eggs of *C. hepaticum* are released into the environment. The dissemination of eggs by ground beetles and rain worms had been reported, but their role in the importance of maintaining the life cycle of this parasite is unclear (Mobedi and Arfaa 1971; Schmidt 2001).

In humans, spurious infections are associated with the consumption of unembryonated eggs in soil or infected game (Fuehrer et al. 2011). The same can be considered for other carnivore and omnivore animals (Reperant and Deplazes 2005). Gonzalves et al. (2012) described the first case of a spurious infection in a dog in Brazil (Amazonas) after the dog was fed with raw game meat. In the Zoological Garden of Vienna, eggs of *C. hepaticum* were found in the feces of a Pallas's cat (*Otocolobus manul*) (Basso et al. 2005). Spurious infections have also been observed in Norway rats (6 %) and black rats (20 %), where cannibalism might be the mode of intake of unembryonated eggs (Firlotte 1948; Promkerd et al. 2008). In Madagascar, eggs from *Capillaria* sp. with the shape of *C. hepaticum* have been found in the feces of gray mouse lemurs (*Microcebus murinus*), greater hedgehog tenrecs (*Setifer setosus*), and black rats (*R. rattus*).

Furthermore, eggs of *C. hepaticum* were found in the feces of non-mammalian animals. In Malaysia, 2.83 % of large-billed crows shed eggs of this parasite with the feces (Lee et al. 2008). Eggs of *C. hepaticum* were also documented in fecal samples from reptiles fed with infected rodents (Pantchev and Tappe 2011). In an analysis of the intestinal content of two timber rattlesnakes (*Crotalus horridus*), eggs of *C. hepaticum* were documented (Solomo 1974).

Although many authors described spurious infections in animals, care should be taken to exclude mix-ups with other Capillaridae or Trichuridae shedding eggs of resembling morphology (e.g., Bork-Mimm and Rinder 2011; Di Cesare et al. 2011; Stuart et al. 2013; Traversa et al. 2011). With the absence of specific molecular diagnostic tools, the classification of *C. hepaticum* in spurious infections is based on the morphology of the eggs only. Consequently, the role of spurious infections for the maintenance of the life cycle of this nematode remains unclear.

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**Table 2** (continued)

| Classification | Species | Country/countries | References |
|----------------|---------|-------------------|------------|
| Tibetan macaque (*Macaca thibetana*) | China (Huangshan mountain of Anhui) | Mentioned in Wang et al. (2013) |
| Northern plains gray langur (*Semnopithecus entellus*) | Belgium/Sri Lanka | Kumar et al. (1983) |
| Gelada (*Theropithecus gelada*) | USA (zoo) | Jensen and Huntress (1982) |
| Atelidae | Mexico (Chiapas) | Cavallero and Grocott (1952) |
| Mexican spider monkey (*Ateles geoffroyi velerosus*) | Panama | Foster and Johnson (1939) |
| Geoffroy's spider monkey (*Ateles geoffroyi*) | Brazil | Soares et al. (2011) |
| Red-faced spider monkey (*Ateles paniscus*) | Germany | Brack (1987) |
| Humboldts woolly monkey (*Lagotrix lagotricha*) | England (zoo) | Pizzi et al. (2008) |
| Pitheciidae | Red bald-headed uakari (*Cacajao calvus rubicundus*) | Brack (1987) |
| White-faced saki (*Pithecia pithecia*) | Worldwide | Reviewed in Fuehrer et al. (2011) |
| White-faced capuchin (*Cebus capucinus*) | Panama | Foster and Johnson (1939) |
| Hominidae | Mountain gorilla (*Gorilla beringei beringei*) | Rwanda (Parc National de Volcans) | Graczyk et al. (1999) |
| Common chimpanzee (*Pan troglodytes*) | Worldwide | Troiser et al. (1987) |
| (Gorilla gorilla) | Poland (spurious infection/zoo) | Paciennik (1976) |
| Free ranging | USA (lab animals originated from West Africa) | de Gasperi (1913) |
| Common chimpanzee (*Pan troglodytes*) | Worldwide | Sadun et al. (1970) |
| Callitrichidae | Pied tamarin (*Saguinus bicolor*) | UK (zoo) | Stidworthy et al. (2009) |
| Red-handed tamarin (*Saguinus midas*) | Portugal—Lisbon Zoo | Correia et al. (2011) |
| Goeldis monkey (*Callimico goeldii*) | Portugal—Lisbon Zoo | Correia et al. (2011) |
| White-headed marmoset (*Callithrix geoffroyi*) | Portugal—Lisbon Zoo | Correia et al. (2011) |
| 1 case each in 3 zoos | UK (zoo) | Stidworthy et al. (2009) |
| Spain | Spain | Fernández-Bellon et al. (2001) |

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Conclusions

*C. hepaticum* is a worldwide-distributed zoonotic parasite with a high affinity to the liver and low host specificity. The main definite hosts are Murinae and Arvicolinae, but it has also been found in various other mammals of different families. Eggs are released into the environment after the death of the host only (decay, cannibalism, and predation). It is unclear which method of egg dispersal is the most effective one but it can be hypothesized that:

(a) Cannibalism is the most effective method of transmission in the case of rodents with a tendency to cannibalism and egg shedding in the burrow.

(b) Dispersal of unembryonated eggs by egg-shedding in feces (after cannibalism, predation by omnivores and carnivores, scavengers, dissemination by insects and earth worms) leads to the most infections in other mammals after the embryonation of the eggs.

Diagnosis is now based on liver biopsy and necropsy, and it can be suggested that the true burden of this parasite is underrepresented. Novel molecular diagnostic tools are needed to allow species determination in cases of hepatic capillariasis and spurious infections.

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