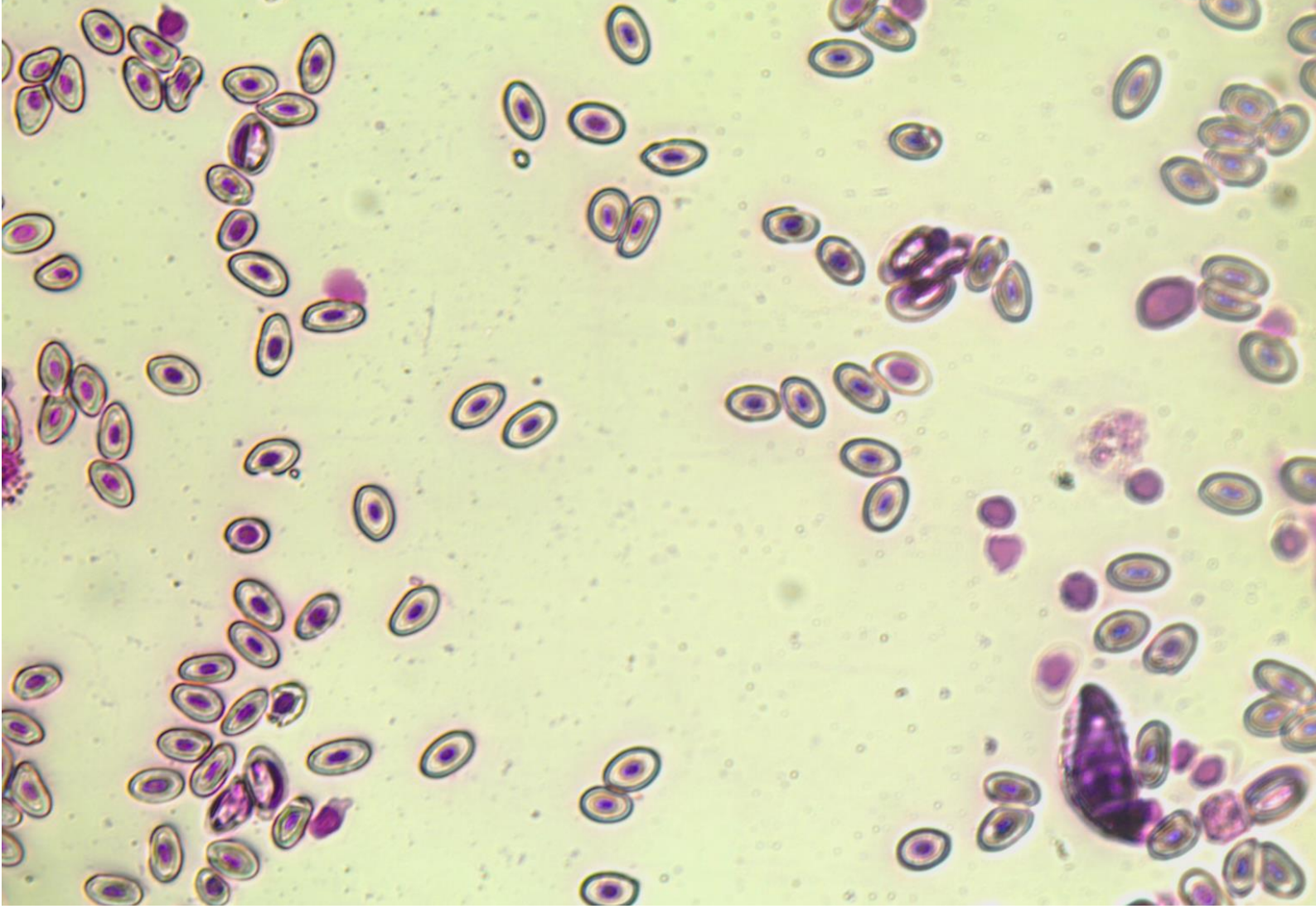

A deeper dive into *Hepatozoon* species

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

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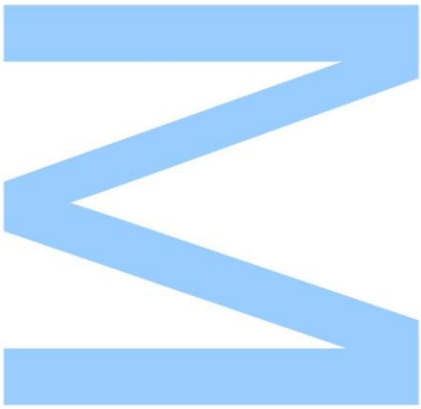

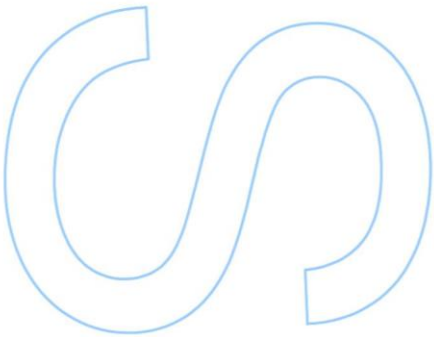

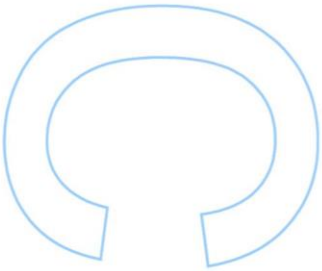

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Abstract

Parasitism is one of the main components of biodiversity, and parasite communities are affected by various factors. Parasites can be external or internal; in this study we focus on *Hepatozoon* (Apicomplexa, Adeleorina, Hepatozoidae), an endoparasite that infect the blood cells of the hosts. They have an heteroxenous lifecycle, meaning they need more than one host species to develop – a typical lifecycle they pass through two vertebrate hosts and an invertebrate host. Transmission can be vertically or horizontally, and this complexity of life cycle and hosts, along with a simple morphological aspect, has greatly limited understanding of these important parasites. Furthermore, the study of *Hepatozoon* is not equal for every host species, with a main focus on mammals and birds, and a lack of information regarding endoparasites infecting reptiles.

Hepatozoon species can be identified and studied using microscopy and genetic tools. Classically, microscopy has been used to identify and quantify the amount of endoparasites present, and identify if the host has more than one parasite infection. The genetic markers are used to identify and perform phylogenetic analyses. Most studies rely on only the 18s rRNA region as a molecular marker which greatly limits attempts to reconstruct phylogenies and to delimit species.

In order to better understand *Hepatozoon* diversity we divided this thesis in two parts: the first one where we focus on the development of new markers for different regions of the mitochondrial, the apicoplast and the nuclear genomes as well as testing primers already develop by other authors from different hosts to see if they would work in the reptile host. In the second part of this thesis, we focus on the *Hepatozoon* species that infect *Podarcis erhardii* from four different Greek islands, to understand the different host-parasite interactions and what factors play an important role in the phylogeographic of this parasite within a simplified island system.

Concerning our first aim, we were unable to develop new markers. While this is a negative result, it can still be useful to other researchers so that they appreciate the difficulties of employing some published primers.

In the second part of this thesis, we found that lizard size varied significantly between islands, as did ectoparasite prevalence. Larger lizards had higher prevalence of ticks, but lower prevalence of mites, and males had higher prevalence of *Hepatozoon* than females. Presence of ticks influenced endoparasite prevalence, but not mites. Overall,

we found no significant impact of island age and area influencing parasite prevalence. The *Hepatozoon* identified were genetically part of a clade with parasites from various other lizards, including some considered as *Karyolysus*. We also identified a species of *Schellackia*, the first record of this parasite genus from this host, both using microscopy and confirmed using DNA sequencing. Our results further underscore the complexity of this parasite system, even within small islands.

Key words: *Podarcis erhardii;* endoparasites; islands; molecular markers; phylogeny; *Hepatozoon*; lizards

Resumo

Um dos principais componentes da biodiversidade é o parasitismo. Existem diversos fatores que afetam as interações entre os parasitas e os seus hospedeiros, afetando assim os ecossistemas. Os parasitas podem ser externos ou internos. Neste trabalho iremos concentrar num parasita sanguíneo, *Hepatozoon* (Apicomplexa, Adeleorina, Hepatozoidae). Este parasita possui um ciclo de vida heterogéneo, o que significa que precisam de mais de uma espécie hospedeira para se desenvolver - um ciclo de vida típico: eles passam por dois hospedeiros vertebrados e um hospedeiro invertebrado. A transmissão pode ser vertical ou horizontal, e a complexidade do ciclo de vida e dos hospedeiros assim como o aspeto morfológico simples, tem limitado a importância da compreensão destes parasitas. Além disso, o estudo do *Hepatozoon* não é igual para todas as espécies hospedeiras, com foco principal em mamíferos e aves, e falta de informações sobre endoparasitas que infetam répteis.

As espécies de *Hepatozoon* podem ser identificadas e estudadas usando microscopia e métodos genéticos. A microscopia tem sido usada para identificar e quantificar o número de endoparasitas presentes assim como identificar se o hospedeiro tem mais do que uma infeção parasitária. Os marcadores genéticos são usados para identificar e realizar análises filogenéticas. A maioria dos estudos baseia-se apenas na região do gene 18S rRNA como um marcador molecular o que limita muito as tentativas de reconstruir filogenias e delimitar espécies.

Para compreender melhor a diversidade do género *Hepatozoon*, dividimos esta tese em duas partes: a primeira onde nos focamos no desenvolvimento de novos marcadores genéticos para diferentes regiões do genoma mitocondrial, apicoplastidial e nuclear, além de testar primers já desenvolvidos por outros autores de diferentes hospedeiros para ver se eles funcionam em répteis. Na segunda parte do nosso trabalho, vamos nos concentrar nas espécies de *Hepatozoon* que infetam *Podarcis erhardii* de quatro ilhas gregas, para entender as diferentes interações parasita-hospedeiro e quais os fatores desempenham um papel importante na filogeografia deste parasita dentro de um sistema de ilhas simplificado.

Quanto ao nosso primeiro objetivo, não fomos capazes de desenvolver novos marcadores genéticos. Embora este resultado seja negativo, ainda pode ser útil para outros investigadores, para que avaliem as dificuldades de empregar alguns dos primers publicados.

Na segunda parte desta tese, descobrimos que o tamanho dos lagartos varia significativamente entre as ilhas estudadas, assim como a prevalência de ectoparasitas. Lagartos maiores tiveram maior prevalência de carraças, mas menor prevalência de ácaros, e os machos tiveram maior prevalência de *Hepatozoon* do que as fêmeas. A presença de carraças influenciou a prevalência de endoparasitas, ao contrário dos ácaros. Em geral, não detetamos um impacto significativo por parte da idade da ilha e da área que influencie a prevalência do parasita. Os *Hepatozoon* identificados faziam parte geneticamente de um grupo com parasitas de vários outros lagartos, incluindo alguns considerados cariólise. Também identificamos uma espécie de *Schellackia*, é o primeiro registo deste gênero de parasita neste hospedeiro, tanto por microscopia quanto confirmado por sequenciamento de DNA. Nossos resultados ressaltam ainda mais a complexidade deste sistema parasítico, mesmo em pequenas ilhas.

Palavras-chave: *Podarcis erhardii;* endoparasitas; Ilhas; marcadores moleculares; filogenias; *Hepatozoon*; lagartos.

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Abbreviations

rRNA- Ribosomal ribonucleic acid
SVL- Snout-vent length
PCR- Polymerase Chain Reaction
DNA- Deoxyribonucleic acid

Chapter 1

Introduction

1.1. Parasites

In an ecosystem, most organisms interact with each other; these interactions are the result of natural selection that occur during million years. Parasitism is one of the most successful interactions known (Poulin, 2007), and is defined as a relationship between two species in which one benefits at the expense of the other.

Parasitism is currently considered one of the main components of biodiversity and one of the most efficient lifestyles (Combes 2001; Poulin & Morand 2000), as the importance of parasites in the ecosystem has increasingly been recognized (Thomas et al., 2000; Damas, 2013; Maia, 2015). The diversity of parasite communities present in an ecosystem can help understand the health of the ecosystem (Hudson et al., 2006).

Parasite communities are influenced by a variety of factors such as population size, habitat, host migration, and anti-parasite defences of the hosts. Various factors within a host community play a role, for example in some cases male hosts have lower resistance to infection and immune response than female hosts (Schmid-Hempel, 2003) due to the testosterone values, since males with higher testosterone contain a weaker immune system (Amo et al., 2005). The parasites can be ectoparasites, parasites that install themselves in the outside of the hosts body (like ticks and mites) feeding on the host's blood, or endoparasites, parasites that live inside of the host body (like various blood parasites and parasitic worms).

Parasite diversity also depends of the phylogenetic, geographic history and host specificity of each parasite species (Combes, 1996; Maia, 2015; Papkou et al., 2016; Poulin, 2007). In the case of islands, the phylogenetic history is one of the main factors driving parasite communities diversity because after the islands are separated from the mainland/ other islands or are formed the host and parasite genetic variability typically decreases (Fornberg & Semegen 2021). Parasites can be lost during the colonization events or find novel hosts.

Just as the hosts characteristics can affect parasitism, parasites can also, indirectly, affect the biology of their hosts (Schmid-Hempel, 2003) by, for example, making them spend more energy; with less energy available they are more vulnerable to predators and less competitive, potentially reducing their ability to reproduce. However, most

parasite species do not directly cause diseases on their hosts, because they depend on their survival to reproduce and live (Combes, 2001).

Despite all this, and even though parasites represent a huge part of the global biodiversity and the knowledge available about them is improving, most parasite species remain undescribed (Bouattour et al., 2021). From all this vast diversity of parasites, in this work we will be focusing on the phylum Apicomplexa.

The phylum Apicomplexa is one of the largest unicellular clades. Even though the total diversity within this group is poorly known, it includes many obligate endoparasites and some of the best known pathogenic parasites, and its members are present in a variety of species, both vertebrate and invertebrate (Votýpka et al., 2017). Studies suggest this phylum has evolved from free living, photosynthetic organisms (Mathur, 2016). This organism may have originated 800 My ago, which means they are expected to be very different from other organisms. Dinoflagellates seem to be the closest relatives. This may have repercussions on the usefulness of available markers (Escalante & Ayala, 1995).

This phylum can be divided into 7 groups: gregarines, cryptosporids, adeleorinids, piroplasms, haemosporinids, sarcocystids and eimeriids; however, this division does not include all known species from this phylum (Barta et al., 2012). As there is currently little data available, new information is always emerging, and this can easily change the estimates of phylogenetic relationships. Nevertheless, study effort on this phylum has increased, as some important pathogenic organisms —capable of causing diseases on human, livestock, and pets— are present in it; still, most of its members are non-pathogenic.

Parasites present in this phylum are protozoa with an alveolate format, but there is minimal information available regarding their distribution and phylogeny. Most species possess a nuclear genome —organized in chromosomes inside of the nucleus, with a variable number of chromosomes between species —, a mitochondrial genome —small and variable and typically containing three protein coding regions, the COI (Cytochrome c oxidase subunit I), COIII (Cytochrome c oxidase subunit 3) and CytB (Cytochrome b), it also codifies the LSU (rRNA large subunit) and SSU (rRNA small subunit) (Hikosaka et al., 2012)—, and an apicoplast genome —typically circular and around 35 kilobases, it is housed in the apicoplast, a unique organelle from which the group name derives (Campo et al., 2019). They also have other characteristics that make them unique, such as the apical complex. This complex is formed by the apical cap, the conoid and the

micronemes and rhoptires (Frénal et al., 2017). Inside of these phylum different groups utilize this mechanism in different ways to enter the host cells.

Apicomplexan parasites lifecycles all have three main development stages: gametogony, sporogony and merogony.

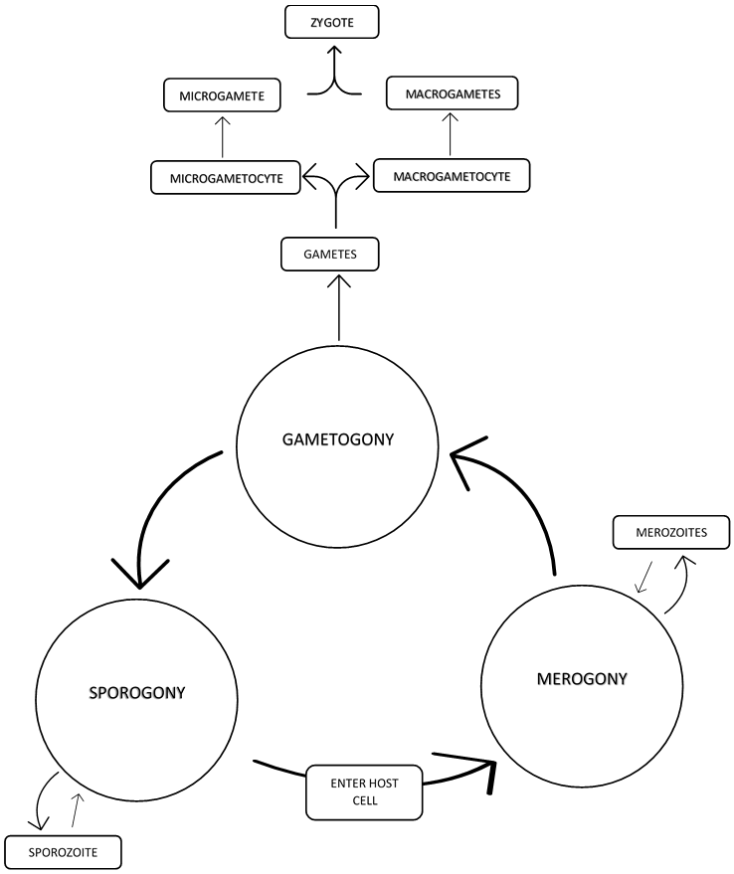

Figure 1- Generalized Apicomplexa lifecycle.

The lifecycles are generally heteroxenous, requiring interaction with two or more hosts to complete all three developmental stages, but can also be monoxenous, relying on a single host to complete their lifecycle. To form a zygote, it is necessary that macrogamonts (female) and microgamonts (male) undergo gametogony to generate macro- and microgametes. These then fuse and form the only diploid stage, the zygote. After the zygote is formed, it develops into an oocyst and then into a sporocyte.

Regarding the ones that cause diseases in humans, the best known are from the genera *Plasmodium* and *Toxoplasma*. The first is responsible for up to 500 million clinical cases of malaria and the death of 1 to 2 million people, mostly children, per year; while the last one infects people worldwide, but generally only those that are immunocompromised develop symptoms. Likewise, Apicomplexa that affect livestock

are responsible for causing economic distress, since they cause diseases that may lead to weight loss and even death. Most of these parasites are resistant to drugs (Frölich et al., 2012) and it is difficult to prevent infections as they can be transmitted in a variety of ways. On the other hand, most apicomplexan endoparasites that infect animals — especially wildlife — are still poorly known and should be the target of more study, to better understand them and their impact on their hosts (Becker, 2011).

In wildlife the study of *Hepatozoon* is not equal for every host species: there is a main focus in groups such as birds and mammals, so for reptiles hosts there is a lack of available information. Although there are some species of *Plasmodium* already known in lizards hosts, for example the malarial infections that are caused by *Plasmodium mexicanum,* and infected hosts are less apt to interact with their conspecifics (Schall & Dearing, 1987) so they have less opportunities to reproduce (Beldomenico & Begon, 2010; Howard & Minchella, 1990).

As mentioned before, the Apicomplexa phylum can be divided in seven main groups, in this study we will be focus on the suborder of Adeleorina (Hemogregarines): this can be divided into the groups *Haemogregarine, Hepatozoidae, Karyolysidae* and *Dactylosomatidae.* All species from this suborder produce gamonts by syzygy, pairing of the gametes prior to fertilization.

Hemogregarines can be transmitted by a variety of invertebrates, such as ticks, mites, leeches, and mosquitoes to the vertebrate host through ingestion. They can cause mortality and severe complications in some vertebrates, but this is rarely reported in their natural vertebrate hosts (Barta et al., 2012; Telford, 2009).

In lizards, it has been shown that these endoparasites can reduce the number of erythrocytes, reducing the capacity to transport oxygen. Because of that, and the energy spent to fight the infection, the hosts have a reduction in interactions (Lochmiller & Deerenberg, 2000), the range of their homes (Bouma et al., 2007), the body condition of the hosts, the speed that they move or the rate of tail regeneration (Oppliger & Clobert, 1997). In general, the impact that these parasites have in their hosts depends on their history and the conditions that the hosts are.

Hepatozoon is one of the most well distributed and common protozoans found in reptiles, it is also present in other vertebrate hosts including amphibians, birds and mammals. Some species of *Hepatozoon* can significantly be harmful to other species, for example cats and dogs, increasing the veterinary research made (Criado-Fornelio et al., 2009).

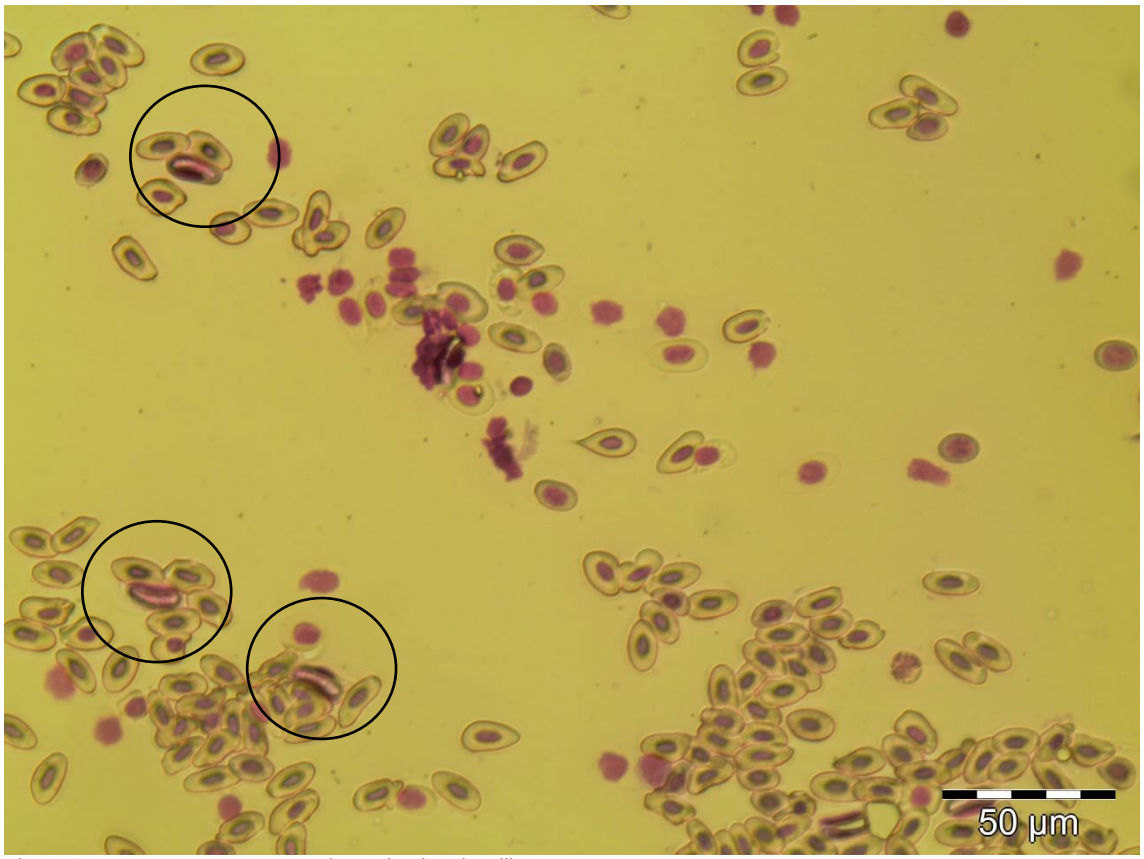

Figure 2- *Hepatozoon sp*. present in *Podarcis erhardii.*

In lizards, the most widely identified endoparasites are species of the genus *Hepatozoon. Hepatozoon* were first described by Miller in 1908; since then, the knowledge about it is improving but various aspects remain poorly known.

Hepatozoon lifecycles varies between species.

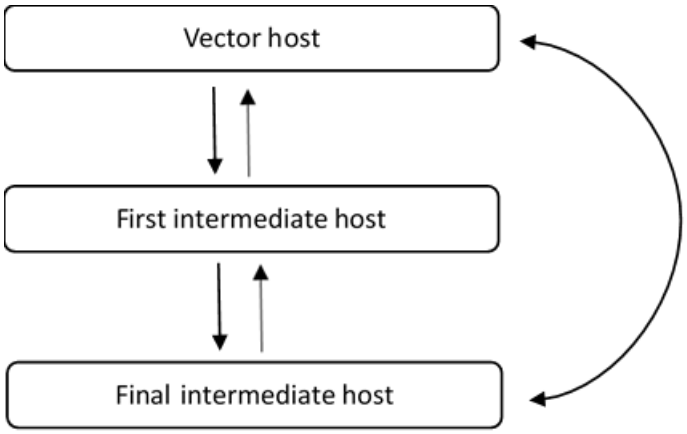

Figure 3- Generalized *Hepatozoon* lifecycle.

Some lifecycles are more complex than others: the lifecycle can have vertical transmission and/or horizontal transmission, vertical occurs from an effected animal to

their descendants and horizontal occurs between species. For the *Hepatozoon* spp. that infect reptiles (as the first intermediate host), their lifecycle normally contains one invertebrate (final) host and two vertebrate host, the first one is normally a small mammal, bird, reptile, or amphibian that transmit the parasite to the second vertebrate host, typically a bigger animal, when the latter ingests the former. The first vertebrate host is infected by ingestion of the invertebrate or when the invertebrate feeds on the vertebrate blood, the transmission can also occur vertically by transovarial transmission in the definitive host, especially in mammals, but it is a topic that need more research. In viviparous reptile species this transmission is also possible but is unlikely in most species that lay eggs. (Barta et al., 2012; Combes, 1996; Damas, 2013; Kopena et al., 2021; Maia, 2015; Smith et al., 1999; Smith & Desser, 1997).

The genus *Hepatozoon* is heteroxenous, it needs more than one species of host to develop, and normally this genus is characterized by the formation of large polysporocystic oocyst found in the definitive host. Considerable uncertainty concerning the definitive host for many *Hepatozoon* species remains, because different species have different definitive hosts (Léveillé, 2019; Smith & Desser, 1997). In lizards the definitive hosts are thought to be predominantly ticks or mites.

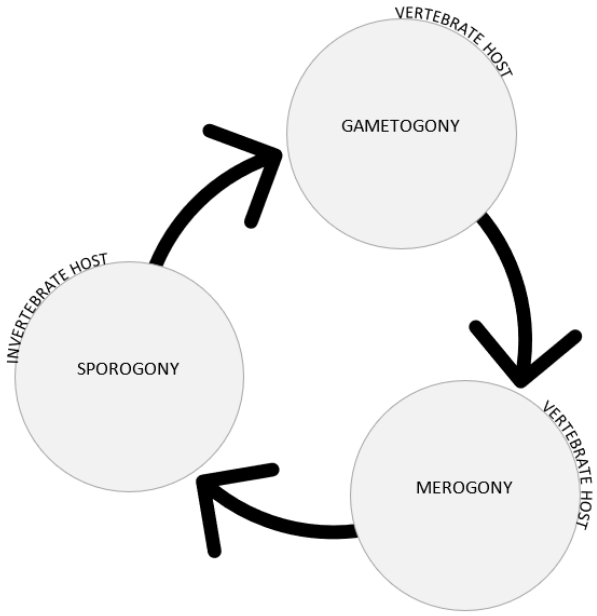

Figure 4- Stages of the lifecycle of *Hepatozoon.*

The sporulation phase occurs in the invertebrate, in this phase the sporozoites are produced. After they are transmitted to the first vertebrate host, the sporozoites penetrate the cells of the lungs or liver where occurs the cystic production. Subsequently two of

the phases can take place, merogony or gametogony (Barta et al., 2012; Combes, 1996; Damas, 2013; Maia, 2015; Smith et al., 1999; Smith & Desser, 1997).

Merogony is the stage in which the asexual reproduction occurs, in other words, when the sporozoites goes thought numerous fissions to generate meronts; after developing they become merozoites. The latter can enter the bloodstream and infect the erythrocytes (and becoming gamonts), and then pass either to the second vertebrate host or to the invertebrate host (Damas, 2013; Maia, 2015; Smith et al., 1999; Smith & Desser, 1997).

These parasites are typically detected either by microscopy and/or by genetic analyses. These different approaches will be discussed next.

1.2 Microscopy

The first microscope techniques were developed in the 15th century by Antonie van Leeuwenhoek, and it remains the traditional and standard method for detection, identification and quantification of parasites though the examination of blood smears stained with Giemsa (Telford, 2009; Valkiūnas, 2005). Microscopy has several positive features, such as the capacity to observe the parasite morphology during the different life stages and understanding the course of infection, the possibility to quantify the parasite intensity, number of parasites present in one host, what type of blood cell are infected and if there are multiple infections in the same host. Another advantage of this technique is the fact that it is inexpensive and available in most laboratories, however this technique is susceptible to false negatives due to the number of erythrocytes counted, for example if there are counted 2000 erythrocytes and none of them is infected that does not guarantee the sample does not have endoparasites as they could have simply have not been observed (Maia, et al., 2014).

As mentioned before the parasite intensity can be quantified using the microscope, and to perform this there are two ways: the first one is counting the number of infected cells in a determined amount of time, while the more widely used alternative is counting the number of infected cells, for example per 2,000, 5,000 or 10,000 erythrocytes cells. The amount of the erythrocytes counted varies according to the studies needs and the quality of the samples.

1.3 Genetic analyses

To have a better understanding of the parasites present in the samples, an integrated approach is used, combining microscopy techniques with genetic techniques. This latter

technique can be used for specie identification, assessing parasite diversity and the population differentiation, and to estimate phylogenies.

There are mainly two molecular techniques used, conventional polymerase chain reaction (PCR) and the quantitative PCR (qPCR), or Real time PCR. Both techniques have advantages and disadvantages.

Conventional PCR was developed by Kary Mullis, and it consists of three phases: first the denaturation where the DNA chain open, annealing where the primer connects with the sequence, and extension. This is then repeated to exponentially amplify the desired region. The main advantage is the capability of getting genetic information with more length and being cheaper, the main disadvantage is the impossibility to measure the intensity. The real time PCR is a much expensive methodology, but it allows to quantify the parasite gene copies (intensity of parasites).

For the genetic analyses of *Hepatozoon* and related parasites, few genetic markers have been developed. Indeed, most studies have relied on a single molecular marker, and the most common primers are the HepF300 and HepR900, targeting part of the 18S rRNA region, (Ujvari et al., 2004) and HEMO1 and HEMO2 (Perkins & Keller, 2001) for the same gene but different zones. Recently several primer pairs were designed for *Hepatozoon* species found in amphibians, so in this work one of our aims will be to try to make them work for our samples. The primers used for the cox3 in dinoflagellates because it has a faster evolution rate and the results could be combined with the 18S rRNA gene region (John et al., 2019).

All the genetic information available from GenBank for *Hepatozoon* is in annex 1. As can be seen, other than 18S rRNA sequences there is very little data, such as apicoplast sequence obtain from parasites infecting *Canis lupus familiaris.* Apicoplast sequence from other hosts (Calil et al., 2019) was later shown to be contaminants (Harris, 2020), which demonstrates the difficulty of utilizing other gene regions. This is particularly problematic given that the 18S rRNA region is considered to have a slow evolution rate, so distinguishing closely related parasite species may not be possible with this marker.

There is limited molecular information available about blood parasite communities that infect *Podarcis*. Most information available for *Hepatozoon* infecting *Podarcis* are for *Podarcis bocagei, Podarcis lilfordi* and *Podarcis vaucheri* (Harris et al., 2012; Maia et al., 2011; Maia et al., 2012). Regarding *Podarcis erhardii,* there is one recent study of particular importance which assessed how the time of separation of the islands and other

characteristics could affect prevalence, number of infect animals in the population and intensity, number of parasite per host (Fornberg & Semegen, 2021).

In this study the focus was on endoparasites specially in *Hepatozoon* (including some forms identified as *Karyolysus*, but for which taxonomic identification is unclear, given that *Karyolysus* as typically recognized is paraphyletic with *Hepatozoon* (Haklová-Kočíková et al., 2014; Maia, 2015). Other endoparasites can also be found in the blood smears of *Podarcis* species, such as species from the genus *Schellackia*.

The genus *Schellackia,* another endoparasite, a type of haemococcidian, first described and identified in European lizards by analysis of blood smears via microscopy (Telford, 1993). It infects mainly erythrocytes, but it can be also found in lymphocytes and monocytes. This genus contains 12 species described worldwide, infecting birds, lizards, and frogs. In lizards it is now considered that infection due to *Schellackia* only occurs in species from the Old World, and that species that infect lizards in the New World (previously considered *Schellackia*) are now considered part of *Lankesterella* (Megía-Palma et al., 2017). *Schellackia* parasites have a high host-parasite specificity (Bristovetzky & Paperna, 1990). Co-speciation between reptile hosts and *Schellackia* species may also occur (Megía-Palma et al., 2018).

The lifecycle of *Schellackia* is heteroxenous, it contains more than one host, on their life cycle once in the invertebrate host, the sporozoites a turn into an dormant state when the blood cell is digested (Megía-Palma et al., 2018; Upton, 2000).

In lizards these parasites are typically found in low prevalence and parasitaemia (Olsson et al., 2000; Psaroulaki et al., 2006; Zechmeisterová et al., 2021). These endoparasites are also present in other reptile species such as *Chelonia mydas;* in this specie *Schellackia* can cause diseases and organ failure (Pedroso et al., 2020).

The different species from this genus are hard to identify using only morphologic data due to the lack of morphologic descriptions available on their gamonts development and fertilization. Transmission of this parasites occurs via predation of infected hosts or by hematophagous vectors (Megía-Palma et al., 2018).

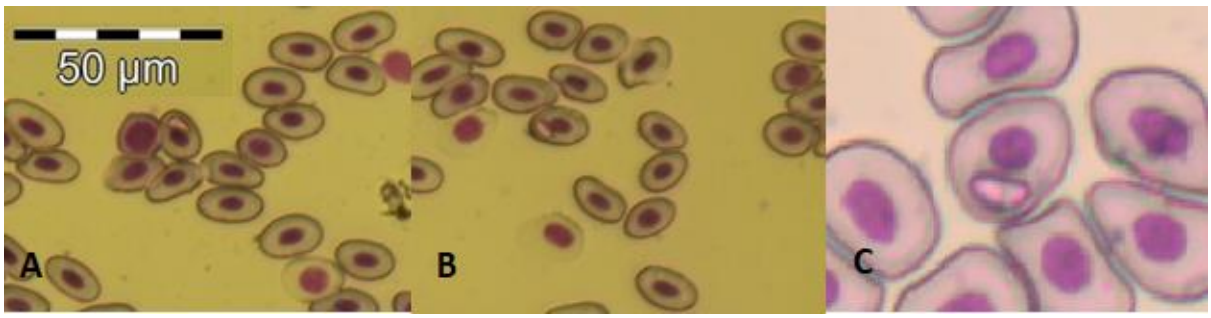

Figure 5- *Schellackia* sp. present in *Podarcis erhardii*. Image A and B at scale, image C with zoom.

1.4 Reptiles

Reptiles belong to the phylum Chordata, class Reptilia (this class is commonly considered paraphyletic), order Squamata. The genus *Podarcis* has 26 species known in the southern European region and is one of the most predominant reptiles. This genus is a monophyletic group, and while until recently the relationships inside this group were poorly understood (Faria, 2019; Lymberakis et al., 2009; Salvi et al., 2021; Speybroeck et al., 2020; Uetz, 2021), recently many subgroups have been defined (Salvi et al., 2021).

Podarcis was first described as a genus in 1830 by Wagler (1830), although it was generally relegated to a subgenus, prior to the work of Arnold (1973). This genus is widely use in phylogeographic and evolutionary studies due to the high endemism of this genus, with species restricted to specific areas, with one main exception, *Podarcis muralis.* It is thought that the genus *Podarcis* has divided and spread giving rise to most of the species known during the Pleistocene glaciations (Poulakakis et al., 2005; Yang et al., 2021). It is thought that multiple glacial refugia occurred within the Mediterranean peninsulas (the Balkans, the Italian Peninsula and the Iberian Peninsula) and various studies have determined how changes in the sea level in the coastal and island settings impacted diversity within and between species (Salvi et al., 2021).

In this thesis, I will be focusing on one of the species, the Aegean wall lizard, *Podarcis erhardii.* This is a diurnal, medium-sized lizard (snout-to-vent length in adulthood 49–78 mm), ground-dwelling lacertid. It can be found from sea level up to 2000 meter of altitude. The colour and pattern of these species vary a lot with the place where they are found. Males are usually bigger than the females (Brock et al., 2020; Marshall et al., 2015; Zabalaga, 2008; Zhao, 2018). *Podarcis erhardii* is widely distributed in Albania, Bulgaria, Greece, North Macedonia, and Serbia (Lymberakis et al., 2009), and is present in mainland and in many islands. It can be found in various habitats, but they are more common in areas with dry stone walls and/or shrublands (Lymberakis et al., 2009). It is listed as Least Concern under the IUCN Red List of endangered species (Lymberakis et al., 2009).

The diet of the Aegean Wall Lizard consists mainly of arthropods (Brock et al., 2020). They can also consume snails and some fruits, although it is not reported that they consume specifically nectar or vegetables. Occasionally they demonstrate cannibalism tendencies (Adamopoulou et al., 1999; Zhao 2018). The lizards that live in rock walls are more sedentary and ingest highly mobile prey. On the other hand, the ones that are more active tend to eat more sedentary preys and some plant material (Donihue, 2016).

This species can be divided in 28 subspecies, with different evolutionary histories that have promoted differences in size, colour, and different environments where they live. As *Podarcis erhardii* live in so many different places it can be consider a good indicator to study the historical biogeography of the islands due to poor over-water dispersal abilities.

1.5 Islands

A significant part of the earth's biodiversity consists of the species endemic to islands, and these island endemics represent a large part of the world's endangered species (Spatz et al., 2017). There are different types of islands, such as continental island that were once connected to the continent, tidal islands, barrier islands made of sediments or corrals, and oceanic islands or volcanic islands that were made by the eruption of volcanos on the ocean floor, and never connected to continents.

On environments like islands, gene flow is restricted so the populations typically have low genetic variability (Fornberg & Semegen, 2021; Foufopoulos et al., 2017).

There are a lot of behaviour and structure differences between *Podarcis erhardii* in the mainland and in the islands, and these changes are thought to be a result of differences in the temperature, that affects indirectly with animal behaviour, in the number of predators that affects the size of the lizards and the populations density; and the quantity and variability of food available that also can change their behaviour. Lizards that live in islands tend to be bigger due to a reduction in potential mammal predators, and this can also result in a higher density population (Aguiar et al., 2020; Lomolino, 2005; Meiri, 2008). When the populations have higher densities there are more competitions between conspecifics for the resources available (Lymberakis et al., 2018).

Lizards populations from younger islands often have a higher occurrence of parasites than older ones (Foufopoulos et al. 2017; Frankham et al., 2003; Roca et al. 2009), possibly since the populations from older islands had longer periods of co-evolution and in some cases parasite populations were unviable and went extinct. On the other hand, it has been proposed that larger islands tend to have more numerous reptile's

populations, so they can keep more considerable parasite populations, leading to higher parasite intensity (Foufopoulos et al., 2017).

In this work we focus on islands from Greece, more specific the Cyclades archipelago. These islands have a classic Mediterranean climate, where the summers are warm and torrid, and the winters are mild and wet.

These archipelago has about 220 islands (Knodell et al., 2020) where most of them are volcanic or continental.

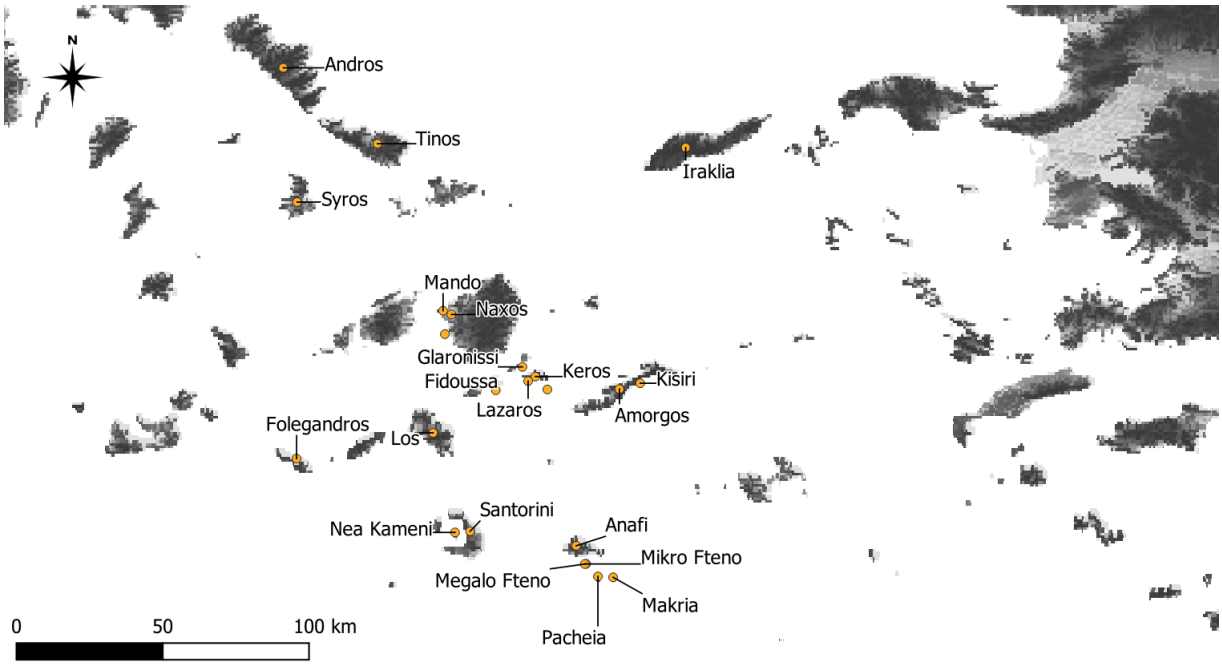

Figure 6- Map of Greek islands sampled for *Hepatozoon* and their host, *Podarcis erhardii*

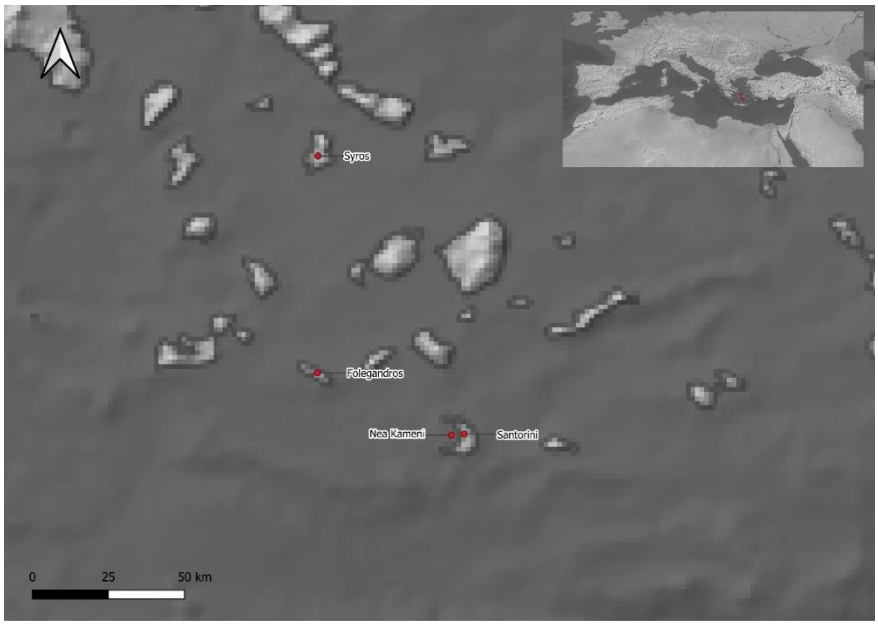

Figure 7- Map of the islands that are the focus on the second manuscript for *Hepatozoon* from *Podarcis erhardii*

The island we focus on in this study were Santorini (also known as Thira), Nea Kameni, Folegandros and Syros. The island of Santorini has a shared history with the Protocycladic block, meaning it has a continental connection but it separated from the block at least 200,000 years, but recently (3500 years ago) the volcano present in the island erupted causing a catastrophic tsunami (Andel & Shackleton, 1982; Driessen & Macdonald, 2000). Nea Kameni origins are volcanic and the most recent explosion that impacted the island was 400 years ago (Cita & Aloisi, 2000).

The age considered for Syros and Folegandros were the age that they separate from the adjustment landmass, 12800 and 11650 years, respectively (Foufopoulos & Ives 1999; Marshall et al. 2015; Poulakakis et al. 2003).

For Apicomplexa parasites in these islands, *Hepatozoon* species were described affecting dogs, cattle, sheep, goats, cats, ticks and reptiles (Efstratiou, et al., 2021; Latrofa et al. 2017; Morelli et al. 2021). As for *Hepatozoon* that infect *Podarcis* in these islands having a 95% prevalence of blood parasites (Garrido et al., 2013).

Table 1- Main differences between islands

Island	type of habitat	Area in km^2	number of inhabitants	Historical connections	number of avian predators
Folegandros	Rocky shrubland	32.38	800	Syros, Santorini	2
Santorini	Rocky shrubland	76.19	13500	Folegandros, Syros	5
Nea Kameni	Lava dome	3.4	0	volcanic eruption	5
Syros	Rocky shrubland	101.9	21507	Folegandros, Santorini	5

The main type of *Podarcis* habitat in Santorini, Folegandros and Syros is rocky shrubland, and in Nea Kameni is lava dome (Marshall et al., 2015). Even though some *Podarcis* can exhibit behaviour preference for darker subtracts, the volcanic ash negatively affects the locomotor performance of the reptiles (Zabalaga, 2008).

Objectives

In this study we have two main goals, the development of genetic markers for *Hepatozoon*, and the understanding what variables influence the prevalence and intensity of parasites, using a group of small islands as a model system.

The molecular markers used to study the genus *Hepatozoon* have until now been almost without exception the 18s rRNA gene region. To be able to better understand these parasites phylogenetics our first goals were to develop and test new genetic markers from different parts of the genome, and in particular to identify markers that had a higher mutation rate.

At the same time, we decided to study the *Hepatozoon* that were infecting *Podarcis erhardii* to understand the factors that influence their prevalence and intensity, using microscopy to identify cases of multiple parasite infection and molecular markers to identify species and to place these in a phylogenetic framework.

Chapter 2

Manuscript I

In the blood: developing genomic resources for endoparasites- *Hepatozoon*

Abstract

The phylum Apicomplexa contains the most common blood parasites, and within this phylum, the genus *Hepatozoon* is one of the most diverse and prevalent. As this genus has both a complex lifecycle and many described species, the taxonomic evaluation is difficult. Historically the parasite was identified using microscopy, but more and more genetic analyses are employed. However, most studies use only one gene for phylogenetic analyses, the 18S ribosomal RNA gene, which has a slow mutation rate. Genes from the mitochondrial (smaller and with three main genes) and/or the apicoplast genome would be ideal to incorporate into the phylogenetic analyses, but they also are harder to amplify and sequence. We designed and tested multiple primers with the aim of developing new markers for *Hepatozoon*, from various vertebrate hosts. Unfortunately, none of these that amplified gave identifiable parasite sequences. Extremely high diversity, coupled with gene rearrangements, may explain the difficulty in developing markers in this poorly known group.

Key words: *Hepatozoon;* primer-design; mitochondrial genome; reptile; PCR

Introduction

Hepatozoon species belong to the Apicomplexa phylum, suborder Adeleorina. The phylum Apicomplexa contains some of the most common blood parasites, consisting of unicellular intraerythrocytic parasites. Most of these endoparasites have an heteroxenous lifecycle, which means they need more than one host; normally they have one invertebrate definitive host (ticks, mites, fleas, lice and some dipteran flies), and one or more intermediated vertebrate hosts (mammals, amphibians, reptiles and birds) (Criado-Fornelio et al., 2009). The transmission in most cases occurs via ingestion of the invertebrate or vertebrate host/ vertebrate host blood per another vertebrate or by the invertebrate.

Hepatozoon was first described by Miller in 1908, and since then many different species have been described, while the monophyly of the group has been called into question (Barta et al., 2012), Many new species have been discovered during screening of herpetofauna (Tomé et al., 2018), and currently this genus is considered paraphyletic (Zechmeisterová et al., 2021), with *Karyolysus* being sister taxa to a lineage of *Hepatozoon* primarily from carnivores. The position of *Hemolivia* is unclear but may also fall within *Hepatozoon*.

Species from this genus contain a nuclear, an apicoplast and a mitochondrial genome. The nuclear genome consists in chromosomes inside of the nucleus. The mitochondrial genome is small (6-7 Kb), but functional in a single mitochondria and variable, typically contain three protein coding regions, the COI, COIII and Cyt b, and the structure and order varies between species (Hikosaka et al., 2012). The apicoplast genome is typically circular and has 35 kilobases (Cai et al., 2003).

The lifecycle of *Hepatozoon* species is variable and complex, and since being first described by Miller in 1908, more studies have clarified the different species lifecycle. Most of them have three main phases: gametogony, sporogony and merogony. The gametogony and merogony phase can be found in the vertebrate hosts but the sporogony phase is more often found in the invertebrate host (Barta et al., 2012; Harris et al., 2015; Smith & Desser, 1997).

To verify the prevalence and intensity of *Hepatozoon* in different samples, normally blood smears are examined under the microscope. The number of infected erythrocytes per 2,000, 5,000, or 10,000 erythrocytes is counted. Different species of *Hepatozoon* are hard to tell apart in some stages in the microscope, and so genetic analyses are

invaluable both to separate morphologically similar species, and to reconstruct phylogenetic relationships.

In most studies, the primers used to perform the genetic and phylogenetic analyses amplify a part of the 18S rRNA gene region. The primers used in most studies are HepF300 and HepR900 from Ujvari (2004) (Ujvari et al., 2004) or HEMO1 and HEMO2 from Perkins and Keller (2001) (Perkins & Keller, 2001). These primers are the most widely used because the nuclear region has a low mutation rate, so they are specific enough to work on most *Hepatozoon* species described. For the same reason the 18S is not the best region to be used in phylogenetic analyses, as closely related species may be identical with this marker. Furthermore, it is well known that a gene tree may not reflect the species tree, so, when possible, it is important to assess multiple, independent genes. Therefore, the aim of this study was to design and test primers for other regions that contain a more rapid evolution rate, with a focus on the mitochondrial and apicoplast genomes.

Léveille in 2014 and 2019 developed some primers for *Hepatozoon* that infect amphibians and mammals for the mitochondrial genome, as well as some primers for the apicoplast genome (Léveillé et al., 2014; Léveillé et al., 2020). Therefore, our approach was both to test these published primers in Hepatozoon from reptiles, and also to design new primers based on the limited sequences currently available that we hoped would amplify across various parasite lineages.

Materials and methods

Test of available primers

Our first approach was to determine if the available primers for mitochondrial and apicoplast genome worked in the *Hepatozoon* present in reptiles hosts. First, we took samples of reptiles and some mammals that were positive, re-extracted them using the DNeasy Blood & Tissue Kits from Quiagen, and verified by PCR that they were positive using the hep300 and hep900 primers from Ujvari (2004). Then, we reproduced the PCR reaction mentioned in the respective articles (table 2) but with platinum taq DNA Polymerase High Fidelity from ThermoFisher or with MyTaq HS mix from Bioline. Those that amplified were send to sequence by a commercial company (Genwiz, Germany). The ones that did not amplify were repeated with different anneal temperatures, different numbers of cycles and amounts of DNA.

Table 2- Primers tested in samples from mammals and reptiles that were infected with Hepatozoon

Amplicon	Size (bp)	Primer names	Primer Sequences	Annealing Temperature	Reference
Mitochondrial amplicon	2000	Api_LSUG_R	5′-AGATAGGGAACAAACTGYCTCAA-3′	62 °C	(Léveillé et al., 2019)
		Api_LSUF_F	5′-GTWCGCCGGGGATAACAGGT-3′		
cytochrome c oxidase subunit I	1800	Hep_COI_R2	5′-TATCAGGACTCTAATTGCGACAG-3′	62 °C	(Hrazdilová et al., 2021)
		Api_LSUG_R	5′-AGATAGGGAACAAACTGYCTCAA-3′		(Léveillé et al., 2019)
Cytochrome b	1400	Hep_cytb_F2	5′-TGTCGCTGGGTAACTATTATCAC-3′	57 °C	(Hrazdilová et al., 2021)
		Hep_cytb_R2	5′-AACTAGTCCATCCACACAATTGT-3′		
apicoplast 23S rDNA	630	ApiPL23SF/ Api_PL_23S_2414F	5′-TAACGGTCCDAAGGTAGCG-3′	61 °C	(Léveillé et al., 2019)
		ApiPL23SR/ Api_PL_23S_3135R	5′-TTYTGAACCCAGCTCACGT-3′		
apicoplast 23S rDNA	500	ApiPL23SF/ Api_PL_23S_2414F	5′-TAACGGTCCDAAGGTAGCG-3′	62 °C	(Léveillé et al., 2019)(Léveillé et al., 2019)
		ApiSPPLR/ Api-Sp-PL_23S_R	5′- GATHAGCCTGTTATCCCTAGAGTAAC -3′		

Primer design

To perform the design of new markers we started by downloading and aligning the available published data for *Hepatozoon*, (annex 1), using the programs BioEdit and Geneious, and separated them by the genes available (all, COI, COIII and Cytochrome b). To align the sequences, we use the clustalW Multiple alignment in Geneious. Then we look for zones that were invariable enough to be able to anneal to a primer. To design

the primers, we follow some standard rules, such as to not have mismatch in the last 10 pb in the 3' extremity, avoiding zones with a lot of nucleotide repetitions, making the melting temperature vary between 55º C and 70º C, and calculating the primer-dimer probability and choosing the ones that had a lower probability.

From 23 possible primer pairs designed, we chose the best 14 to test (table 3). These were chosen by verifying the difference of annealing temperatures between the forward and reverse primers, the percentage of GC and the self-complementarity values. At the same time, we compared the possible new primers against typical vertebrate (host) gene sequences, to try to ensure that the primers will amplify parasite, but not host DNA.

Table 3-Primer's design to amplify via PCR

Amplicon	Size (bp)	Primer names	Primer Sequences	Annealing Temperature
Mitochondrial amplicon	400	400F	5′-TGGGACGACAGTCTACTCAA-3′	55 °C
		400R	5′-ATGGCCTCACCATAAAGGA-3′	
Small subunit ribosomal RNA gene	195	195F	5′-TAGATGTTCTGGGCTGCACG-3′	55 °C
		195R	5′-TGTGTACAAAGGGCAGGGAC-3′	
Small subunit ribosomal RNA gene	346	346F	5′-ATTGGAGGGCAAGTCTGGTG-3′	51 °C
		346R	5′-ATGCCCCCAACTGTCCCTAT-3′	
Cytochrome b	172	172F	5′-AAACCTTCCTGAGCGACTCG-3′	55 °C
		172R	5′-AAGGCGAGAAGGGAAGTGTG-3′	
Mitochondrial amplicon	456	456F	5′-TTACAGCTACCAGGCACAGC-3′	55 °C
		456R	5′-AGTTACCCAGCGACACCAT-3′	
cytochrome c oxidase subunit I	304	304F	5′-TTGATACGGGGGAATGCGAC-3′	55 °C
		304R	5′-TGGCACTAGCACCTTCCTTC-3′	
Cytochrome b	302	302F	5′-TCGCAAAGTGAAAACAGGCG-3′	55 °C
		302R	5′-CACCAGACTTGCCCTCCAAT-3′	
cytochrome c oxidase subunit I	156	156F	5′-TCGCATTCCCCCGTATCAAC-3′	55 °C
		156R	5′-ATGCAAAGGGGCTAGCCATT-3′	

Amplicon	Size (bp)	Primer names	Primer Sequences	Annealing Temperature
cytochrome c oxidase subunit III	763	763F	5′-AGATGTTAGTATAGGTACGG-3′	51 °C
		763R	5′-GGCCTCACCATAAAGGA-3′	
cytochrome c oxidase subunit I	1177	CO1177F	5′-TCCTGTAGCGTTTCTGTTGGT-3′	54 °C
		CO1177R	5′-CAGGTACAGCCGAGTGTTATC-3′	
cytochrome c oxidase subunit I	760	CO760F	5′-TCTGGTTCTTCGGTCATCC-3′	49 °C
		CO760R	5′-GTAACCAGGCGTCAATAGCG-3′	
cytochrome c oxidase subunit I	174	CO174F	5′-TTTCACCGCGGTCACAATCT-3′	50 °C
		CO174R	5′-GCATTGCCTAACACCACACC-3′	
Cytochrome b	519	CB519F	5′-GGGTCAGATGAGTTTCTGGGC-3′	55 °C
		CB519R	5′-TTCGTATTTACTTGACGCTGCT-3′	
Cytochrome b	423	CB423F	5′-GGGTCAGATGAGTTTCTGGGC-3′	56 °C
		CB423R	5′-AGCATCGCATAGAATGGTAGGAA-3′	

As “in silico” design is difficult to produce, primers that look good in theory sometimes do not amplify, while those which look less good sometimes amplify, so we rely on “in vitro” primer testing in the laboratory.

The samples used were already collected (as part of the Cibio/InBio collection) and were already known to be infected with endoparasites, confirmed using 18S rRNA primers from Ujbari (2004) (Ujvari et al., 2004) or through examination of blood cells from direct observation of parasite gamonts in the microscope. To extract the positive samples we use high-salt approaches (Maia et al., 2014; Sambrook et al., 1989) or the DNeasy Blood & Tissue Kits from Quiagen.

The PCR technique uses a mix that contain enzyme (Taq polymerase), dNTP’s, MgCl2, buffer and primers. These can be added separately or be present in a “master mix” so that all that is added are the primers. The Taq polymerase used was Platinum™ from thermofisher or MyTaq™Mix by Bioline, which comes with a “master mix”. We adjusted conditions such as magnesium concentration, annealing temperatures and other standard approaches until positive PCR occurs.

Any markers that amplified were then sequenced from different host species so we can determine if that gene shows some variability. Ideally, we would then select primers that amplify across many different lineages of parasites.

Results

From the primers tested in table 2 we were able to amplify Api_PL_23S_2414F and Api_PL_23S_3135R for samples from mammals (lion, serval, cat, and seals) and reptiles (snakes). We perform these PCR with the recommend temperatures from the original article, except we used MyTaq™Mix. Then we run the second primer pairs (Api_PL_23S_2414F and Api-Sp-PL_23S_R) with the PCR product obtain from the first ones (Api_PL_23S_2414F and Api_PL_23S_3135R), when this failed, we tried 95 ºC 10 min, 35 cycles – 94 º C 3 min, 55 ºC 30 sec and 72 ºC 40 sec follow by 72 º C 10 min. The samples from the seals did not amplify, the samples of the lion and the serval amplified (figure 1), the sample from the reptiles amplified two bands. Despite changing annealing temperature, the amount of DNA and the number of cycles, this did not improve.

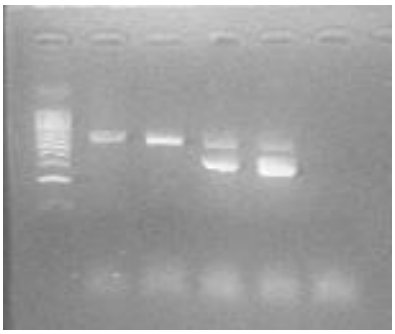

Figure 8-Results from the electrophoresis with the Api_PL23S primers

Concerning the other primers from table 2, none of them worked consistently. From table number 3, one of the primers worked, the 195 and was sent to sequence to know if it amplifies the parasite.

Unfortunately, none of the sequences were satisfactory. Most were unreadable, except for an apparent *Methylobacterium* (Apicoplast primers, cat host) and apparent large subunit rRNA algal sequences (seal host). However, even these were poor quality sequences and with no close matches.

Conclusion

The work perform did not go as expected, since none of the primers amplified without unspecificities the samples obtain from reptile hosts. It seems likely that this is a general

problem – for example primers for apicoplast have been available for some time (eg Obornik et al. 2002). However, these have not been used within *Hepatozoon*, except for in one case (Calil et al. 2019), but these were later shown to be contaminants (Harris 2020). Similarly, some of the mtDNA primers have been available for some time (eg those from Léveillé et al. 2014), and yet there have been few successful attempts to employ these primers in later studies (Hrazdilová et al. 2021), despite several studies highlighting the need for sequences of this organelle. It seems likely that high variability in gene order may cause some problems. The phylum Apicomplexa is an extremely ancient group (800 million years ago), and therefore designing primers to amplify across such a long evolutionary history will always be complex. In our case, presence of other microorganisms, such as bacteria or fungi, might co-amplify and thus prevent the sequences from being usable. Cloning the obtained PCR products might be a potential way forward to overcome this problem.

To improve our knowledge more studies should be performed using the genomic approach, and the primer design should be made with more sequences. Changing the Taq used might be useful. Léveillé (pers. comm.), who successfully amplified the mtDNA genes in amphibians (Léveillé et al. 2014) suggests using High Fidelity Phusion Taq. After this thesis was nearly completed, we attempted to use this Taq, but still unsuccessfully. More mtDNA sequence data have also recently become available from related species of the genus *Haemogregarina* (Attia et al. 2021). As more data becomes available for other related groups, designing primers for use in *Hepatozoon* infecting lizards should, we hope, become an obtainable goal in the near future.

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Manuscript II

What factors influence prevalence and intensity of *Hepatozoon* infection in *Podarcis erhardii* from different Greek islands?

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Abstract

Island biogeography theories predict that characteristics such as island size, age, and isolation interplay in host-parasite dynamics. In this study, we analyse the Aegean wall lizard *Podarcis erhardii*, and blood parasites of the genus *Hepatozoon* (Apicomplexa: Adeleina: Hepatozoidae) to investigate how island characteristics related to parasite prevalence and intensity. A previous study on Greek islands suggested that isolation time and host population density were key predictors of parasitism. In our study we increase this previously published dataset by including data from four additional islands, Santorini, Syros, Nea Kameni and Folegandros, and by collecting data for the prevalence of ectoparasites (ticks and mites), definitive hosts for *Hepatozoon*. Furthermore, we employed partial 18S rRNA gene sequences to confirm parasite identities.

Lizard size varied significantly between islands, as did ectoparasite prevalence. Larger lizards had more ticks, but less mites, and males were more frequently infected by haemogregarines than females. Presence of ticks influenced endoparasite prevalence, but not mites. The additional data, when joined with that from Fornberg and Semegen (2021), showed no significant impact of island age and area influencing parasite prevalence. All the *Hepatozoon* identified were genetically part of a clade with parasites from various other lizards, including some considered as *Karyolysus*. We also confirmed by microscopy and DNA sequencing the presence of *Schellackia*, the first record of this parasite genus in this host. Our results further highlight the complexity of host-parasite systems, even within small islands.

Keywords: Insularity; Host-parasite interactions; 18S rRNA; Aegean wall lizard; Apicomplexa; *Karyolysus*; *Schellackia*.

Introduction

Parasites represent a huge proportion of biodiversity, and have an important role in the ecosystems, influencing the dynamics and structure of host populations (Combes, 2001; Hudson et al., 2006; Poulin & Morand, 2000). Islands are classic models in evolutionary studies, due to the simplicity of the system when compared to continental regions, and, in particular, host-parasite interactions have received little attention in assessments of island ecology (Fornberg & Semegen, 2021). It is expected that island size, age, and isolation all interplay to impact host-parasite dynamics, but the relative importance of the different factors is still not clear (Fornberg & Semegen, 2021; Foufopoulos et al., 2017; Patiño et al., 2017).

In islands, animal populations in the initial stages of colonization tend to be smaller, with high levels of inbreeding and lower genetic variability (Fornberg & Semegen, 2021). During the process of isolation, parasites can decrease in numbers or even be lost entirely due to the reduction of host abundance and dispersal and through the process of "bottlenecks" associated with each colonization event and shifting the hosts is also possible (Tomé et al., 2018). On the other hand, due to the lack or reduced amount of predators, insular systems can have very dense populations, and in particular the smaller islands generally can have more dense populations than the bigger ones (Rodda & Dean-Bradley, 2002). Given that, insular species can be more susceptible to diseases and parasitism (if they are new to the insular environment) (Fornberg & Semegen, 2021; Papkou et al., 2016).

Lizards are good model systems to study the variation of parasitism on island populations given their low mobility, high densities, and easiness of sampling. This is particularly true for the Aegean Wall Lizard, *Podarcis erhardii*, a diurnal medium-sized lizard, widely distributed in mainland Greece and many Aegean islands (Lymberakis et al., 2009). Moreover, *Podarcis erhardii* can be found in different habitats and types of islands (Lymberakis et al., 2009), being primarily insectivorous (Brock et al., 2020), although diet varies considerably according to habitat (Foufopoulos & Ives, 1999; Zhao, 2018). Recently, Fornberg and Semegen (2021) carried out an extensive assessment of parasite diversity within *P. erhardii* in the Cyclades islands, 19 islands, (which are part of the Aegean islands, Greece). They found that islands with greater host density and islands that had been isolated for less time generally had higher hemogregarine prevalence, which they hypothesised was associated by insular density compensation, when a island support a large number of species and they occupy a familiar habitat their populations tend to be more dense. Islands that were temporally and spatially isolated

also showed a trend towards higher prevalence and parasitaemia levels. However, Fornberg and Semegen (2021) only used morphological identification of the parasites, and as such, they could not be certain of the identity, ascertain if distinct parasites were present nor place them within a phylogenetic framework.

In this study, we aim to extend the work of Fornberg and Semegen (2021) by sampling four additional islands within the Cyclades, that were not sampled before: Santorini, Nea Kameni, Folegandros and Syros (Figure 9). These islands have notable differences in size (from 3.4 Km^2 to 101.9 Km^2) and ages since separation (between 400 years and 12,800 years) (Perkins & Keller, 2001).

The genus *Hepatozoon* (Apicomplexa: Adeleina: Hepatozoidae) consists of a variety of unicellular obligate endoparasites. These parasites are present in almost every group of terrestrial vertebrates, being one of the most abundant and widespread hemoparasites, especially in reptiles (Telford, 2009). The lifecycle of *Hepatozoon* species is heteroxenous, employing intermediate hosts- vertebrates, and definitive hosts- invertebrates, typically mites and ticks (Barta et al., 2012; Harris et al., 2015; Smith & Desser, 1997).

Hepatozoon are transmitted to the vertebrate hosts primarily through ingestion of an infected invertebrate (or another infected vertebrate) or when the invertebrate feeds on the vertebrate blood. One of the most common lizard host species in the Greek islands is the Aegean Wall lizard, *Podarcis erhardii.* These lizards can be found in different habitats being more common in areas with dry stone walls and/or shrublands (Lymberakis et al., 2009).

Hepatozoon definitive hosts present in these Greek islands are thought to be ticks (the genus *Dermacentor, Hyalomma*, and *Ixodes* are present (Allain & Bateman, 2018)) and mites from the family Trombiculidae (Garrido & Pérez-Mellado, 2015). Ectoparasite load is generally affected by the type of vegetation present and the presence of ruminants (Allain & Bateman, 2018), with males often having a higher ectoparasite load (Amo et al., 2006; As et al., 2020).

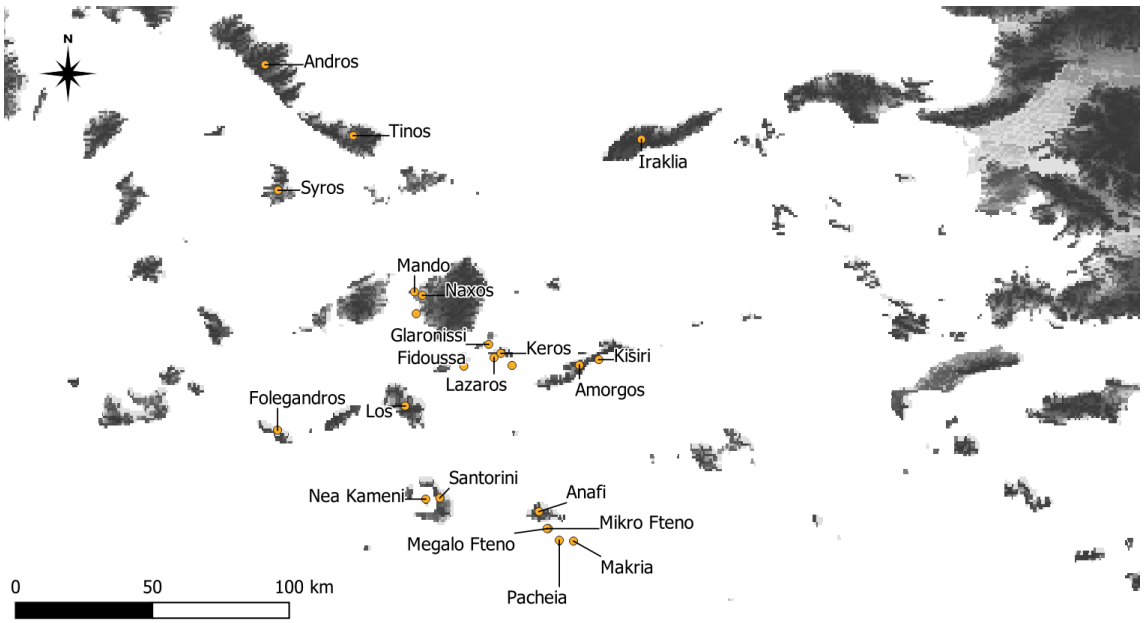


Figure 9- Map of Greek islands sampled in this study and in the Fornberg and Semegen 2021 for *Hepatozoon* and their host, *Podarcis erhardii*. The island included in this study are named. The islands from our study were Santorini, Nea Kameni, Folegandros and Syros

Material and methods

We collected blood samples from 195 adult *P. erhardii* lizards between April and June 2014. After lizards were caught, we cut the tail tip, and we performed blood smears from the blood dropped naturally from this cut. The tip of the tail was then immediately stored in 96% ethanol. We also sexed them by seen the format and size of the femoral pores and measured lizards' snout-to-vent length (SVL) and weight using digital callipers and a small scale (± 0.01mm/g respectively). Sex was recorded, as well as the number of ticks and mites present. The lizards were after released in the place where they were captured. Blood smears were fixed with methanol and air dried in the same day. Once in the laboratory, they were stained with Giemsa for 45 min.

Blood smears were examined under an Olympus CX41 microscope using x400 optics, and pictures were taken with Cell^B 3.4 Olympus® software. Pictures were inspected using the ImageJ 1.46® program. For each individual, we counted 2000 erythrocytes, and scored how many were infected with parasites. Like this, we could assess the parasite prevalence (percentage of individuals infected in the population) and intensity (number of parasitized cells per individual) (supplemented material s3).

The variables included were prevalence and intensity of parasites (ectoparasites and haemogregarines), sex, body size and weight of the *Podarcis erhardii*, and the island where they were captured. We determined if the variables followed a normal distribution

using the Shapiro-Wilk normality test and checked the homogeneity of variances among groups (sexes, islands) using Bartlett test.

Since the variables did not follow a normal distribution, we used non parametric approaches. We checked for correlation between the transform data to logarithms of lizard weight and SVL using a Spearman rank correlation. Since logSVL and logweight were correlated only SVL was used.

We employed generalized linear models with a binomial distribution to compare and understand if the ectoparasites and hemoparasites prevalence is influence by the different islands where they are present and sexes of the hosts.

For the intensity of parasites, we employed two different methods (Negative Binomial Models and Binomial Models) to try to understand if any of the variables influence the endoparasite intensity. We start by using a permutational analysis of the variance using the function adonis, package vegan (Permanova), then we run a permutational Ancova (Anova with covariance) to see if this statistic analysis would change our results once it creates a distribution curve based on our real data. We also use negative binominal models to check if it would change the results.

Then we combined the data from the four islands sampled with the data from Fornberg and Semegen (2021) using permanova analysis follow by permutational pairwise a-posteriori contrasts to know which haplogroups were different (function pairwisePermutationTest, R package rcompanion), we could also use a structural equation (path analysis) but as our main focus was the influence of the island age and area in the prevalence and intensity of endoparasites, so we chose the permutational analysis of the variance. All statistical analyses were performed in Rstudio 1.4.

Table 4- Statistic results obtain, and models used

	Podarcis erhardii SVL	*Hepatozoon* prevalence	*Hepatozoon* intensity
SVL	-	p<0.001	F= 0.151, p= 0.723
Sex	F= 21.807, p<0.001	p= 0.01	F= 0.060, p= 0.821
Island	F= 23.782, p<0.001	p<0.001	F= 0.980, p= 0.332
Number of mites	F= 16.857, p= 0.001	p= 0.119	F= 0.047, p= 0.799
Number of ticks	F= 3.1047, p= 0.046	p= 0.011	F= 0.171, p= 0.634

Island age*	-	F= 0.991, p= 0.334	-
Island área*	-	F= 0.018, p= 0.901	-

In order to confirm the identity of the parasites present in the four islands analysed DNA from six tail-tip samples were extracted (n=195) using standard High Salt methods (Sambrook et al., 1989). Following extraction, we performed a PCR to amplify part of the 18s rRNA gene, using the Hep300 and Hep900 primers from Ujvari (2004) and the conditions proposed in Maia et al. (2011). Positive PCR products were cleaned and sequenced by a commercial company (Genewiz, Germany). The sequences generated were compared with the data from GenBank using BLAST to confirm parasite identify. The sequences were aligned in Geneious using clustalW, with representative sequences from GenBank with 104 (Supplementary Material, Table s1). We used Bayesian inference (BI) to estimate the phylogeny with the most appropriate model of molecular evolution identified using PartitionFinder2 (Lanfear et al., 2016). BI was implemented using Mr. Bayes v.3.1 (Huelsenbeck & Ronquist, 2001). The analysis was run for 10^7 generations, saving one tree each 1000 generations. The log-likelihood values of the sample points were plotted against the generation time and all the trees prior to reaching stationarity (25%) were discarded. Remaining trees were combined in a 50% majority-rule consensus tree (Huelsenbeck & Ronquist, 2001). Phylogenetic relationships within haplogroups were also inferred using a network approach, which is particularly appropriate when few characters for phylogenetic analysis are available due to limited divergence (Posada & Crandall, 2001). We used the statistical parsimony network approach implemented in TCS 1.21 (Clement et al., 2000) with a connection limit of 95%. Networks were visualised and edited in TCSbu (Santos et al., 2015).

Results

Significant differences were identified in SVL between islands (F= 23.782, df=3, p<0.001) and between sexes, with males being larger than females (F= 21.807, df=1, p<0.001). Interaction between these factors was not significant (F= 1.295, p= 0.283). The lizards from Syros were largest, follow by Folegandros and then Santorini and Nea Kameni (Figure 10)

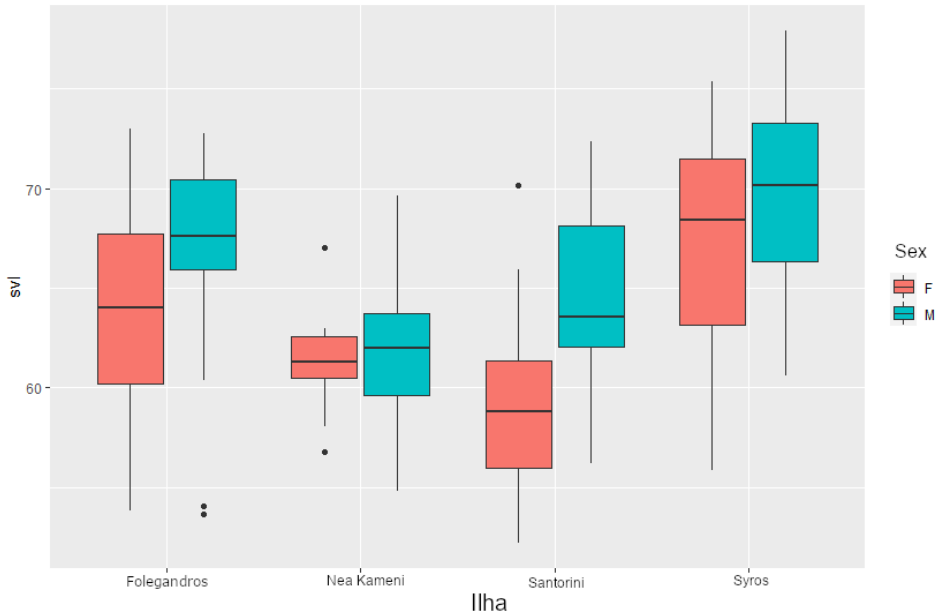


Figure 10- Variation of *Podarcis erhardii* SVL (mm) between islands.

The number of ticks (df=1, p=0.046) and mites (df=1, p= 0.001) present in the lizards were both correlated with SVL (Figure 11), with larger *Podarcis* hosting a higher number of ticks, but inversely a smaller number of mites.

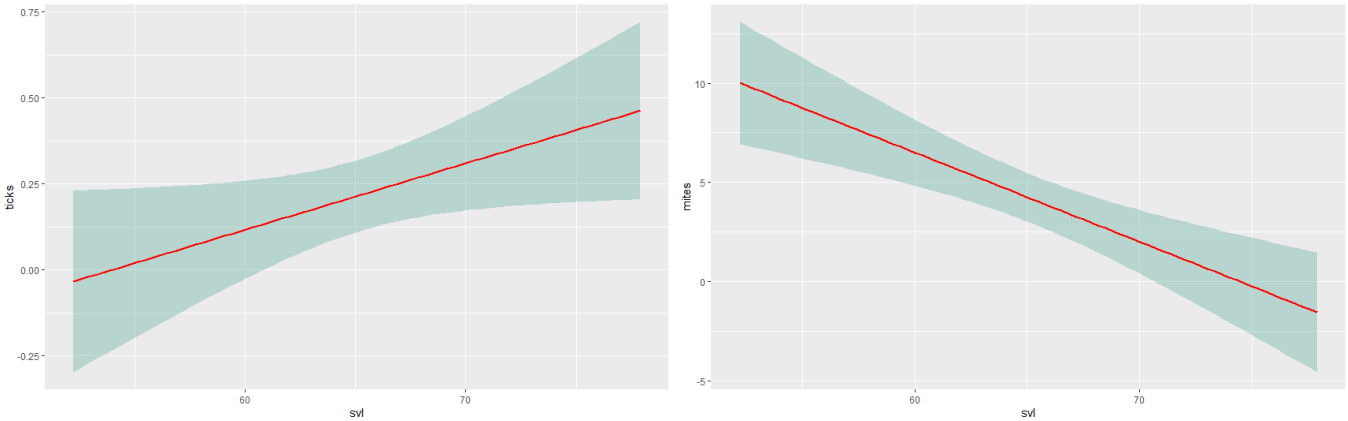


Figure 11- Variation of SVL of *Podarcis erhardii* in comparison with the number of ticks present (A) and the number of mites present (B).

Hepatozoon prevalence varied between islands (df=3, p=2.525e-07) and between sexes (df=1, p=0.012), with males having higher prevalence than females. The

differences found in prevalence between islands were between Syros, Folegandros and Santorini and Nea Kameni. There were no significant differences between these last two.

Regarding whether the numbers of mites and ticks on a lizard influenced the prevalence, the number of ticks present on the lizard did influence prevalence (df=1, p=0.011), while the number of mites and the interaction of both did not (df=1, p= 0.119; df=1, p= 0.845, respectively), during this statistic part the islands where the samples were caught were not considered.

Table 5- Percentage of the prevalence of *Hepatozoon, Schellackia*, ticks and mites present in each island. The percentage for total/ for the number of males/ for the number of females

Island	N/ N males/ N females	*Hepatozoon* (%)	*Schellackia(%)*	*Ticks (%)*	Mites (%)
Folegandros	64/38/26	70/ 84/ 57.7	5/ 2.6/ 7.7	34.4/50/ 11.5	20.3/ 23.7/ 15.4
Syros	57/35/22	46/54.3/31.8	10.5/14.3/4.5	0/0/0	0/0/0
Santorini	51/ 26/25	67/69/64	37.3/38.5/36	0/0/0	90.2/92.3/48
Nea Kameni	21/11/10	9.5/9/10	19/ 27.3/10	0/0/0	0/0/0

Table 6- Average intensity of *Hepatozoon* in each island (per 2,000 erythrocytes)

	Hepatozoon		
Island	average intensity (total)	average intensity (males)	average intensity (females)
Folegandros	8.2	8.5	8.2
Syros	6.2	6.1	6.2
Santorini	4.6	4.7	4.6
Nea Kameni	0.5	0.5	0.6

Table 7- Average intensity of ticks and mites in each island

	Ticks			Mites		
Island	average intensity (total)	average intensity (males)	average intensity (females)	average intensity (total)	average intensity (males)	average intensity (females)
Folegandros	0.66	0.68	0.65	1	0.87	1
Santorini	0	0	0	10.7	12	11

Combining our results with those from Fornberg and Semegen (2021), we found that prevalence was not significantly influence by island age (p=0.295), while in Fornberg and Semegen (2021) younger islands had a trend towards higher percentage of infected animals. Concerning island size, our results showed it was not significant on the *Hepatozoon* prevalence (p=0.900). Regarding parasite intensity in different islands, sexes and ectoparasite quantities, we conclude that there were not significant differences (p>0.05). There was also no significant correlation between parasite intensity and the islands age (p=0.506) and area (p=0.249).

As for intensity none of our variables had a significant influence in the intensity of the *Hepatozoon,* with SVL, sex and island containing a probability of p= 0.710, p= 0.06010, p= 0.98076 respectively.

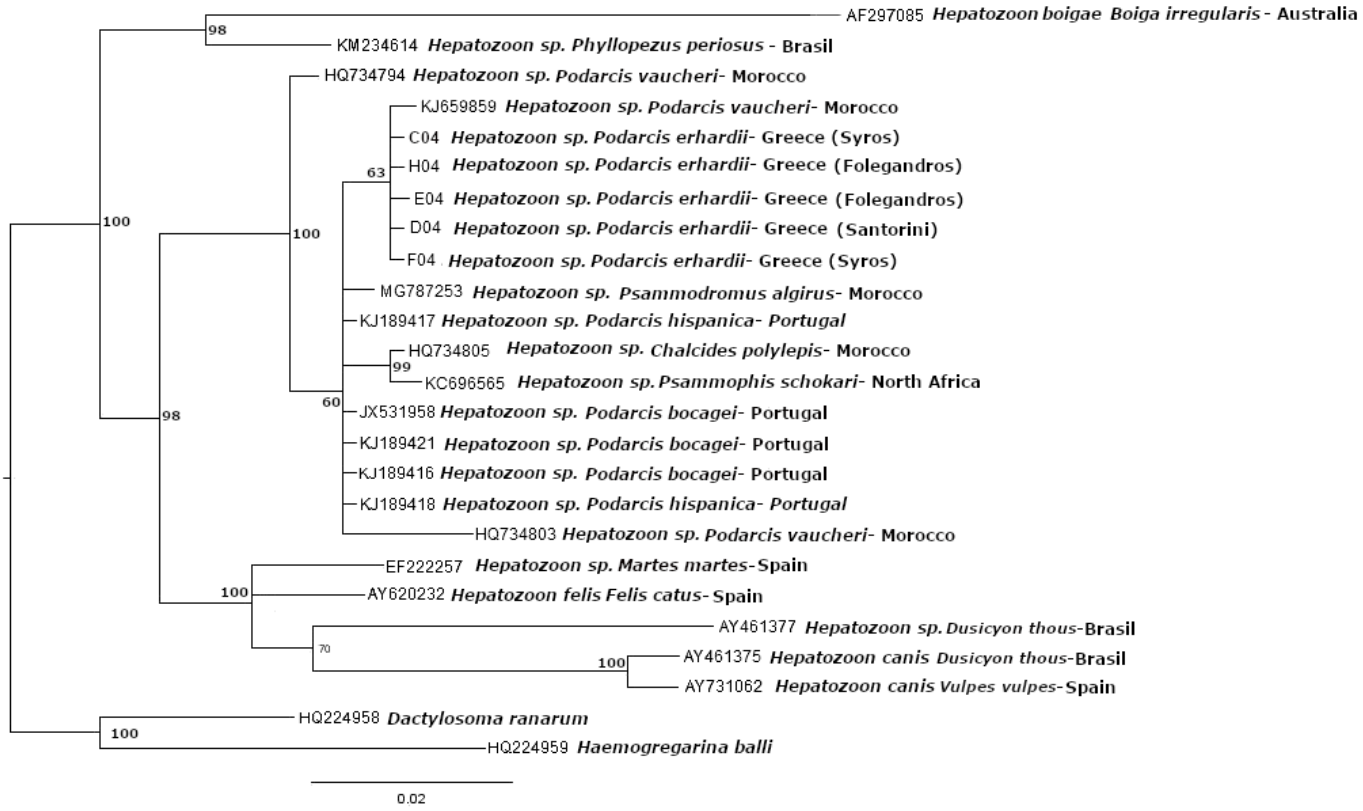


Figure 12- Estimate of relationships of *Hepatozoon* species based on 18S rRNA gene fragments. Numbers near to nodes are Bayesian posterior probability values. The tree was rooted using *Dactylosoma ranarum* and *Haemogregarina balli.*

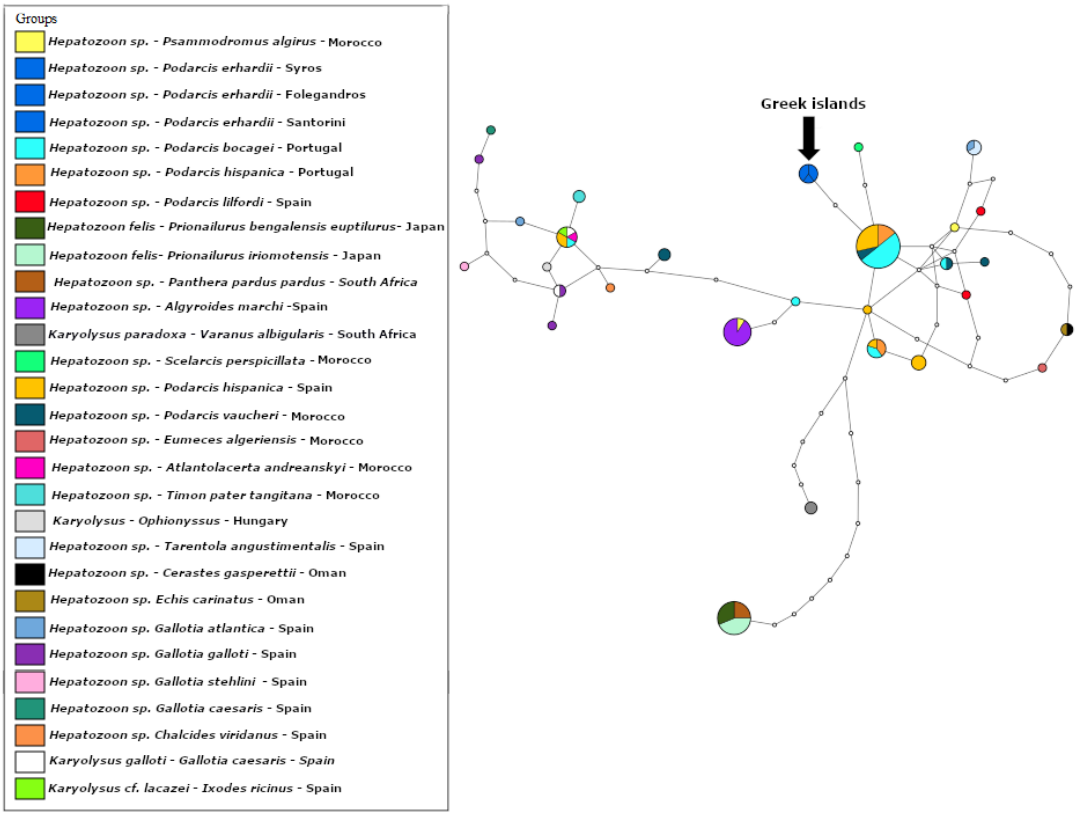


Figure 13- Estimate of the relationships from *Hepatozoon*, using a network approach employing TCS and TCSbu. All available sequences related to those from *P. erhardii* were included.

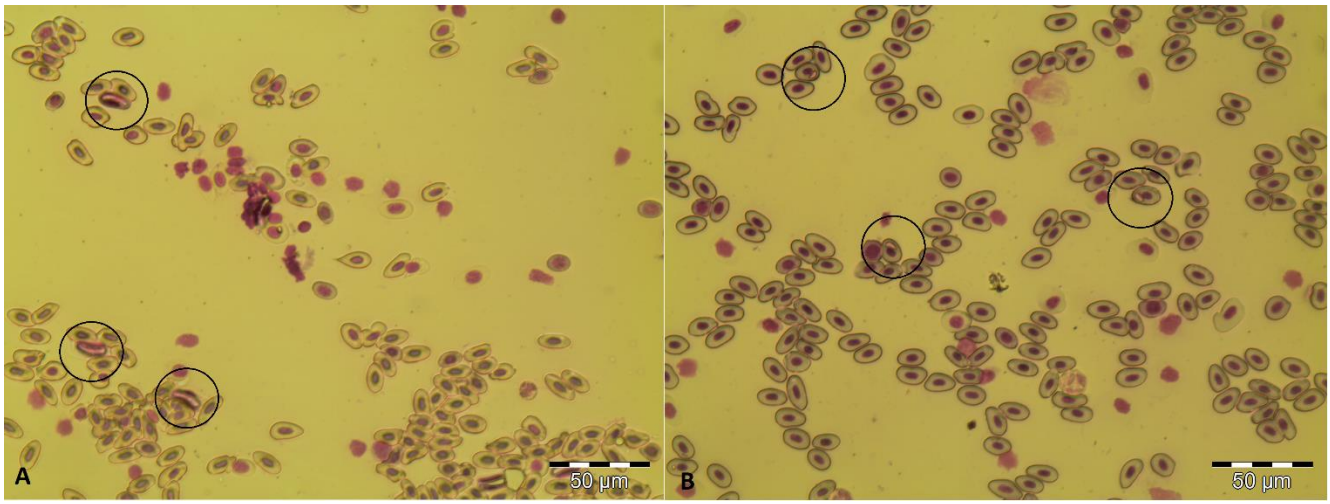
We amplified a fragment of the 18S rRNA gene region from the *Hepatozoon* of five infected *Podarcis erhardii* individuals (two individuals per island (Syros and Folegandros) and one individual from Santorini) and aligned these sequences against those from GenBank (aligned length 553 bp). All the new sequences were closely related (maximum of 30 nucleotide differences) and formed a clade with other lizards haemogregarines, which includes many samples identified as *Karyolysus* and *Hepatozoon*. Taxonomic reassessment of this group still needs to be fully reassessed.

From the haplotype network (Figure 13) it is possible to observed that the *Hepatozoon* species from the Greek islands are more similar to the ones from similar hosts, primarily other lizard species, particularly from Portugal and Spain.

Under microscopy, as well as typical haemogregarine parasites from the genus *Hepatozoon*, several lizards appeared to be infected with *Schellackia* (Figure 14). We successfully amplified one of these (from *Podarcis erhardii* from the Greek island of Nea Kameni) using the same conditions and primers as those used for the *Hepatozoon* parasites.

The sequence quality for *Schellackia* was suboptimal, but a BLAST search with 253bp of sequence showed a 100% match with MG775272 sequence from GenBank, from *Schellackia* species infecting a *Timon lepidus* collected in Spain.

Figure 14- Endoparasites found in samples from the Greek species- *Podarcis erhardii.* Figure A is a species of *Hepatozoon*, Figure B is a species of *Schellackia.*



Discussion and conclusion

Unravelling the dynamics of host-parasite relationships is a major aim of evolutionary ecology but is extremely complex, with multiple factors influencing the interactions (Megía-Palma et al., 2021). In such situations, islands are ideal models, simplifying the system while allowing the impacts of population fragmentation to be determined within known time frames.

In this study we detected the presence of two different blood parasites: haemogregarines belonging to the genera *Schellackia* and *Hepatozoon/Karyolysus*. This is, as far as we know, the first report of *Schellackia* parasites in *P. erhardii*, and the factors that are influenced by the size of the lizard (number of ectoparasite) or influence (island and sex), the *Hepatozoon* prevalence (sex and island). The *Hepatozoon* average intensity was significantly higher that the *Schellackia* average intensity in Santorini, Syros and Folegandros, but not in Nea Kameni. *Hepatozoon* intensity was not significantly affected by the sex of the host, the island where they were present or by the size of the host. *Hepatozoon* prevalence was higher in males than females, probably due to their higher susceptibility and their behaviour (Olsson et al., 2000), except for Nea Kameni, where the overall prevalence of *Hepatozoon* was significantly lower, presumably associated with the type of habitat there.

Recent applications of molecular tools have highlighted the diversity of parasites infecting Mediterranean lizards. The most common parasites infecting lacertids are haemogregarines, typically considered to be transmitted by mites and ticks (Allain & Bateman, 2018). Less common are haemococcidians, including *Schellackia*, which are regarded as more host specific (Megía-Palma et al., 2018). Our identification of *Schellackia* sp. in all four studied populations, with molecular represents an interesting finding and the first record for *P. erhardii*. That this parasite was not reported by Fornberg and Semegen (2021) in the other Greek islands. This genus of parasites has in general, lower prevalence, but morphologically might be mistaken by other parasites. In our case, molecular tools were helpful to detect the presence of these parasites and confirm their identity. Assessment of more islands particularly for the presence of *Schellackia* would be needed to confirm this.

We detected both *Hepatozoon/Karyolysus* and *Schellackia* parasites in all four studied populations. Interestingly, ticks were only present in one and mites on two of the four populations, and the prevalence of mites in these two islands was higher in males. Infection with mites and ticks in *Podarcis melisellensis* was more severe at the end of the reproductive season (Huyghe et al., 2010). On the other side, tick prevalence was

significantly associated with past grazing practices in the islands occupied by *P. erhardii* (Hurston, 2007). It seems like that temporal variation combined with contrasting habitat characteristics and use may explain the differences in ectoparasite prevalence in our study, although this aspect clearly needs further assessments.

Not unexpectedly, average sizes of *P. erhardii* vary across populations. Body size often evolve rapidly in island lizards (Poulakakis et al., 2003). These island populations also show colour differences that apparently match background colours as anti-predator avoidance (Marshall et al., 2015), with body size differences also associated with anti-predator defence mechanisms. Unexpectedly, we found an inverse relationship between ticks and mites, with larger lizards having more ticks but less mites. Previous studies found that mites intensity was not associated with body size in *Podarcis muralis* (Amo et al., 2005), while in a community of three lacertid lizards in the Iberian Peninsula, there was a positive correlation between SVL and mite infestation (Drechsler et al., 2021). This latter study highlighted that each host-parasite system showed unique particularities, despite being related hosts in similar environments. An inverse relationship was also described with different habitats both parasites, mites being more present in areas with dry grasslands and little disturbance, and ticks in areas with higher plant cover and disturbance by livestock (Hamilton et al., 2021). Our results corroborate this – even in a simplified island system, unique particularities are seen between different ectoparasites and endoparasites. Such singularities highlight the difficulties in generalizing patterns of host-parasite dynamics, and the need for more studies to try to understand these complex relationships, however traits like island size and distance to continent should not be relevant.

As expected, the haemogregarines prevalence was much higher in males than females, due to their higher susceptibility (due to higher values of testosterone values and immunosuppression) and their behaviour, the fact that males have a more bolder behaviour make them more expose to the parasites because they have more interactions with other individuals and different species (Olsson et al., 2000), except for Nea Kameni. The overall prevalence of these parasites in this island was significantly lower than in the other islands, this prevalence can be influence by the type of habitat that this host live in.

As for the islands age and area, our results contradicted the findings from Fornberg and Semegen (2021) where they found that smaller islands had a higher prevalence. Our results, however, did not identify a significant relation between island age, area and

prevalence and intensity of parasitism. We think that more studies should be performed including islands with similar evolutionary histories.

Lizards were more intensely infected with *Hepatozoon* than with *Schellackia* in Santorini, Syros and Folegandros. The average intensity of both endoparasites was the same in Nea Kameni. Haemogregarines intensity was not significantly affected by the sex of the host, the island where they were present or by the size of the host.

The lack of consistency between our results and the previous study by Fornberg and Semegen (2021) highlights the need for more studies to understand how factors such as the size and age of the island, vegetation, habitat structure, and lizards' density, among others, shape parasitism. The Greek islands provide a unique framework for a better understanding of host parasite interactions in insular ecosystems.

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Supplementary Material

Table s1- Island age and area considered in this study

Island	Island age	Area km2
Amorgos	200000	123
Anafi	5000	40.37
Andros	5800	379.95
Antikeros	15150	1.05
Fidoussa	600	0.63
Glaronissi	5600	0.16
Los	11750	109.03
Iraklia	9800	18.08
Keros	9150	15.05
Kisiri	5700	0.01
Lazaros	9100	0.01
Makria	13500	0.5
Mando	4	0.3
Megalo fteno	9580	0.06
Mikro fteno	5000	0.03
Naxos	8700	448
Pacheia	11850	1.36
Parthenos	5400	0.008
Tinos	5800	194.5
Santorini	3500	76.19
Nea kameni	400	3.4
Folegandros	11650	32.384
Syros	12800	101.9

Table s2- Number of parasites per host

Island	Intensity of *Hepatozoon*	Island	Intensity of *Hepatozoon*	Island	Intensity of *Hepatozoon*
Syros	4	Nea Kameni	0	Folegandros	3
Syros	0	Nea Kameni	2	Folegandros	14
Syros	0	Nea Kameni	0	Folegandros	0
Syros	0	Nea Kameni	0	Folegandros	15

Syros	0	Nea Kameni	0	Folegandros	2
Syros	7	Nea Kameni	0	Folegandros	3
Syros	0	Nea Kameni	0	Folegandros	4
Syros	0	Nea Kameni	0	Folegandros	4
Syros	0	Nea Kameni	0	Folegandros	13
Syros	0	Nea Kameni	0	Folegandros	24
Syros	0	Nea Kameni	0	Folegandros	2
Syros	0	Nea Kameni	0	Folegandros	1
Syros	0	Nea Kameni	0	Folegandros	3
Syros	45	Santorini	0	Folegandros	11
Syros	1	Santorini	20	Folegandros	1
Syros	0	Santorini	0	Folegandros	10
Syros	0	Santorini	2	Folegandros	3
Syros	0	Santorini	1	Folegandros	31
Syros	44	Santorini	6	Folegandros	1
Syros	0	Santorini	5	Folegandros	9
Syros	10	Santorini	11	Folegandros	9
Syros	3	Santorini	9	Folegandros	8
Syros	47	Santorini	1	Folegandros	0
Syros	22	Santorini	1	Folegandros	0
Syros	0	Santorini	6	Folegandros	15
Syros	2	Santorini	14	Folegandros	0
Syros	5	Santorini	25	Folegandros	5
Syros	0	Santorini	0	Folegandros	4
Syros	0	Santorini	0	Folegandros	1
Syros	0	Santorini	0	Folegandros	9
Syros	0	Santorini	7	Folegandros	20
Syros	4	Santorini	56	Folegandros	38
Syros	4	Santorini	1	Folegandros	4
Syros	0	Santorini	0	Folegandros	33
Syros	0	Santorini	0	Folegandros	5
Syros	0	Santorini	0	Folegandros	9
Syros	7	Santorini	1	Folegandros	0
Syros	1	Santorini	5	Folegandros	0
Syros	46	Santorini	24	Folegandros	28

Syros	10	Santorini	0	Folegandros	1
Syros	0	Santorini	3	Folegandros	2
Syros	0	Santorini	0	Folegandros	0
Syros	0	Santorini	1	Folegandros	152
Syros	2	Santorini	32	Folegandros	3
Syros	17	Santorini	6	Folegandros	0
Syros	20	Santorini	5	Folegandros	2
Syros	0	Santorini	0	Folegandros	1
Syros	0	Santorini	0	Folegandros	0
Syros	4	Santorini	1	Folegandros	0
Syros	1	Santorini	9	Folegandros	0
Syros	11	Santorini	4	Folegandros	1
Syros	0	Santorini	0	Folegandros	0
Syros	7	Santorini	10	Folegandros	0
Syros	0	Santorini	12	Folegandros	0
Syros	2	Santorini	10	Folegandros	0
Syros	27	Santorini	7	Folegandros	0
Syros	0	Santorini	0	Folegandros	1
Nea Kameni	0	Santorini	4	Folegandros	1
Nea Kameni	0	Santorini	0	Folegandros	5
Nea Kameni	0	Santorini	0	Folegandros	1
Nea Kameni	1	Santorini	2	Folegandros	6
Nea Kameni	0	Santorini	0	Folegandros	1
Nea Kameni	0	Santorini	1	Folegandros	8
Nea Kameni	0	Santorini	5	Folegandros	0
Nea Kameni	0				

Chapter 3

Discussion and Final conclusions

At this moment in time, global biodiversity is decreasing due multiple factors including habitat fragmentation, climate change and human interference. These changes influence the dispersal ability of species, and in turn the parasite intensity and prevalence: the effects of habitat fragmentation and isolation on the host-parasite interactions are complex. The human interference can also increase the connectivity between hosts and parasites.

It is clear that there are still a lot of *Hepatozoon* species that remain undescribed. For those with available genetic data, this is typically limited to the 18S rRNA gene region, which is not always variable enough to distinguish between cryptic form. Therefore, we attempted to develop new genetic markers for *Hepatozoon* species. Separately, we also tried to understand what influences their prevalence and intensity in *Podarcis erhardii* from several Greek islands, which offer a simplified system to try to unravel the complex patterns observed in continental systems (eg. Maia 2015). This lizard species can help to understand the geographic history of Greece due to co-evolution of the island's final formation and the lizards (Hurston et al., 2009) and the parasites DNA could be used to track ancient contact between host species that are currently separated or extinct, and the appearance of other species for example alien species (*P. vaucheri*, *P. siculus*) that may change the host-population dynamics. The *Hepatozoon* species present can also help understand how the island separation history affect the endoparasite prevalence and intensity, making it easier to predict what will be the effect of habitat fragmentation on both the *Hepatozoon* species, and the species that they infect.

In the first part of this thesis, we designed primers to amplify several regions of the mitochondrial, apicoplast and nuclear genome. During the development of the molecular markers, we identified several challenges. There are a small number of mitochondrial sequences from *Hepatozoon* available in GenBank and none of them were from reptiles. While the design of the primers should follow some standard rules, this was hard to follow based on the limited published sequences available. Once the primers were designed and the ones that look better were tested, we conclude that most of our primers and even some primers develop by other authors have nonspecificities when used to amplify *Hepatozoon* in reptile hosts.

As for the published Léveillé primers, the Api23S did amplify in various samples but had considerable non-specificity in samples from reptiles. We also tried extracting from the gel the band of the expected length, but again this was unsuccessful. Cloning of these fragments may be the best approach to move this forward.

As the mitochondrial and the apicoplast genome generally have a faster mutation rate, the primer design for these regions is harder, and likely more specific for *Hepatozoon* species from a specific host group. The primers we develop could be tested in additional samples from very different host groups and with different PCR conditions to check if the nonspecificities are due the host DNA or due to a problem with the design. The primers were compared with the reptile's genome and did not coincidence, but they could likely amplify bacteria or even other parasites present that we did not consider.

Another approach that could be applied would be extensive datamining of published vertebrate genomes for parasite DNA and using this for primer design and the datamining of dinoflagellates to check the zones that are more similar. Various studies have shown that many published genomes incorporate parasite DNA, which can greatly increase the data available to design parasites. While designing the primers we could also try to redesign primers already developed in order to make them more specific.

Regarding the second part of the thesis, the results obtain supported our predictions that the host parasite interaction would be shaped during the island canonizations. From our results we were able to conclude that the size of the *Podarcis erhardii* caught were significantly different between the different islands, and that this difference can be due to the growth rate and longevity of the different island lizards, to the adaptations to the number of predators and background colour, as the lizards adapt to the characteristics of the islands that shape their ecology or even phenotypic plasticity acts that happened earlier.

One interesting find from this work was that ticks on lizards were only found in one island, while mites were present in two islands. These results were unexpected, since it is generally thought that *Hepatozoon* species are transmitted to the *Podarcis* though ticks, mites or an infected prey (Orkun & Emir, 2020) so we expected that, even if only in smaller quantities, these ectoparasites would be present in every island given that *Hepatozoon* were ubiquitous, this results are likely habitat-mediated. In the future, it would be informative to collect samples in different seasons to see why they were not present during the time of sampling or try to see how the *Hepatozoon* are being transmitted potentially by other final hosts such as biting flies. This would also have

taxonomic implications, as *Karyolysus* is often suggested to be transmitted by mites (Hassl, 2012). In some species it has been reported vertical transmission (eg. Inokuma et al., 2002), but in the case of this specie is unlikely, since vertical transmission was not identified in another lizard, *Lacerta schreiberi* (Kopena et al., 2021). We also notice that bigger lizards contained higher number of ticks and a small number of mites, potentially indicating a competition between mites and ticks. This clearly deserves further investigation, as it is a novel pattern not previously identified.

Another result was that the *Hepatozoon* prevalence was higher in males, as expected due to their testosterone values (Olsson et al., 2000). To make a more complete study an experiment could also be performed to see if the amount of *Hepatozoon* would affect their aggressivity, since supposedly animals with higher testosterone values would be more aggressive, although it is still unclear if the testosterone act directly or through body condition and damage, more experimentation is needed, particularly monitoring individual hosts (Oppliger et al., 2004). The only island where the prevalence was smaller was Nea Kameni, in which the population was small and mainly focused in one place with a lot of tourist interaction (Isabel Damas pers. comm.), so to have a better understanding of the prevalence of *Hepatozoon* here it would be important to study their diet, to see how this influences *Hepatozoon* prevalence.

Furthermore, in this work, we found the endoparasite *Schellackia,* a parasite which had not previously been described in this host (*Podarcis erhardii*). In future studies it would be important to perform wider sampling to try to have a better understanding of the prevalence and intensity of them, their interaction with other parasites and hosts, and try to understand why their prevalence is so small in comparison with *Hepatozoon*. This might also shed light on why they were not reported on a previous study of blood parasites of *P. erhardii* from many more islands (Fornberg & Semegen, 2021). The possibility that they were overlooked, or mistaken for stages of *Hepatozoon* needs to be assessed. It is also necessary to determine if the *Schellackia* negatively affects the hosts, and to determine if this is the same species found in other *Podarcis* hosts, or represents a new, undescribed species.

Regarding the influence of the island age and area in the prevalence and intensity of endoparasites, our results did not go as expected, partially contradicting the results from Fornberg and Semegen (2021). Our results shown no significant interaction between those variables. Part of the reason for this might be that the significance values obtained by Fornberg and Semegen (2021) were quite low. Another reason might be the slightly

differing timing of the study since strong seasonal effects are expected. Again, repeating the sampling over different seasons might help to address this.

Concerning the parasite intensities, the medium intensity of *Hepatozoon* was higher than from *Schellackia*, but none of the factor's studied in this work influenced the intensity. Why *Schellackia* is often found at low intensities clearly deserves further attention.

To conclude, the main goal of this thesis was to have a better understanding of these parasites, "diving deeper" into the still poorly known genus *Hepatozoon*, and I think that we were successful. More studies should be performed in the future because as we got answers, so we also got more questions. And for a better understanding of these parasite species, new primers need to emerge.

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Annex

Annex 1- Data available for *Hepatozoon* on GenBank (collated 29/09/2021)

Hepatozoon	***Host species***	**Class**	**Family**	**Country**	**GenBank ID**	**Reference**	**Available genes**
Hepatozoon aegypti	*Spalerosophis diadema*	Reptilia	Colubridae	Saudi Arabia	MH198742	(Abdel-Haleem et al., 2018)	18S rRNA
Hepatozoon americanum; Hepatozoon catesbianae; Hepatozoon canis	*Canis familiaris*	Mammalia	Canidae	USA	AF176836; AF176835; AF176837	(Mathew et al., 2000)	18S rRNA
Hepatozoon americanum; Hepatozoon canis	*Canis familiaris*	Mammalia	Canidae	Brazil	KU729739; KU729737; KU729738	(Gomes et al., 2016)	18S rRNA
Hepatozoon americanum	*Canis familiaris*	Mammalia	Canidae	Not available	EU249992; EU249993	(Johnson et al., 2008)	18S rRNA
Hepatozoon americanum	*Canis latrans*	Mammalia	Canidae	USA	JX415169; JX415170; JX415166; JX415167; JX415168; JX415171; JX415172; JX415173; JX415174;	(Starkey et al., 2013)	18S rRNA

					JX415175; JX415176; JX415177; JX415178; JX415179; JX415180; JX415181; JX415183; JX415182; JX415165		
Hepatozoon americanum	*Canis lupus familiaris*	Mammalia	Canidae	USA	EU146062; EU146065; EU146066; EU146067; EU146063; EU146064;	(Allen et al., 2008)	18S rRNA
Hepatozoon Americanum; sipedon; catesbianae	*Canis lupus familiaris*	Mammalia	Canidae	Not availableavailable	AF206668; AF206669; AF206670; AF206671;	(Baneth et al., 2000)	18S rRNA
Hepatozoon sp.;angeladaviesae	*Philothamnus semivariegatus*	Reptilia	Colubridae	South Africa	MG519502; MG519501; MG519503	(Netherlands et al., 2018)	18S rRNA
Hepatozoon apri	*Sus scrofa leucomystax*	Mammalia	Suidae	Japan	LC314791	(Yamamoto et al., 2017)	18S rRNA
Hepatozoon sp.; ayorgbor	*Apodemus sylvaticus; Clethrionomys glareolus;*	Mammalia	Muridae	Croatia	KT274177; KT274182; KT274178; KT274185; KT274186; KT274179; KT274181; KT274183; KT274184	Unpublished	18S rRNA
Hepatozoon ayorgbor	*Python regius*	Reptilia	Pythonidae	Ghana	EF157822	(Sloboda et al., 2007)	18S rRNA

Hepatozoon ayorgbor	*Rhombomys opimu*	Mammalia	Muridae	China	MW342705	Unpublished	18S rRNA
Hepatozoon banethi	*Ixodes tasmani*	Arachnida	Ixodidae	Australia	MG758137; MG758136; MG758133; MG758134; MG758135; MG758138;	(Greay et al., 2018)	18S rRNA
Hepatozoon caimani	*Caiman crocodilus*	Reptilia	Alligatoridae	Brazil	MF435048; MF435049; MF435047; MF435046	(Úngari et al., 2018)	18S rRNA
Hepatozoon caimani	*Caiman crocodilus yacare*	Reptilia	Alligatoridae	Brazil	MF322538; MF322539	(Bouer et al., 2017)	18S rRNA
Hepatozoon caimani	*Caiman yacare*	Reptilia	Alligatoridae	Brazil	KU495923; KU495924; KU495925	(Soares et al., 2017)	18S rRNA
Hepatozoon canis	*Amblyomma sculptum*	Arachnida	Ixodidae	Brazil	KP167594; KP167595	(Melo et al., 2015)	18S rRNA
Hepatozoon canis	*Camelus dromedarius*	Mammalia	Camelidae	Saudi Arabia	MN989311	(Alanazi et al., 2020)	18S rRNA
Hepatozoon canis	*Canis aureus*	Mammalia	Canidae	Czech Republic; Romania	KX712124; KX712127; KX712125; KX712126; KX712123; KX712128; KX712129	(Mitková et al., 2017)	18S rRNA
Hepatozoon canis	*Canis aureus*	Mammalia	Canidae	Hungary	KJ634654	(Farkas et al., 2014)	18S rRNA

Hepatozoon canis	*Canis aureus; Vulpes vulpes*	Mammalia	Canidae	Hungary	KJ572975; KJ572976; KJ572978; KJ572977	(Farkas et al., 2014)	18S rRNA
Hepatozoon canis	*Canis aureus*	Mammalia	Canidae	Austria	JX466880; JX466881; JX466882; JX466883; JX466884; JX466885; JX466886;	(Mitková et al., 2017)	18S rRNA
Hepatozoon canis; felis	*Canis aureus; Vulpes vulpes; Felis catus*	Mammalia	Canidae	Iraq	MK957186; MK957188; MK957189; MK957187; MK957185	(Otranto et al., 2019)	18S rRNA
Hepatozoon canis	*Canis aureus*	Mammalia	Canidae	Israel	KJ868814; KJ868819; KJ868815; KJ868818; KJ868816; KJ868817	(Levi et al., 2018)	18S rRNA
Hepatozoon canis	*Canis familiaris*	Mammalia	Canidae	Slovakia	KX761384	(Miterpáková et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus*	Mammalia	Canidae	Turkey	MN463030	(Orkun & Emir, 2020)	18S rRNA
Hepatozoon canis	*Canis lupus*	Mammalia	Canidae	Turkey	KY247116; KY247114; KY247112; KY247113; KY247115; KY247117; KY247111	(Guven et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Venezuela; Thailand; Spain	DQ439540; DQ439543; DQ439541; DQ439542; DQ439544; DQ519357; DQ519358;	(Criado-Fornelio et al., 2007)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris; Felis catus*	Mammalia	Canidae	Israel	KC138535; KC138531; KC138532; KC138533; KC138534; KC138540; KC138539; KC138541; KC138538; KC138536; KC138537; KC138542;	(East et al., 2008)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MH615006; MH615003; MH615004; MH615005	(Léveillé et al., 2019)	18S rRNA; 28S large subunit ribosomal; ITS1; ITS2
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MH557086	(Léveillé et al., 2019)	Apicoplast
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MK214283; MK214284; MK214282	(Léveillé et al., 2019)	Cds; cytb-1; cytb-2
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MH615002	(Léveillé et al., 2019)	COI
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MK214285	(Léveillé et al., 2019)	Cytb
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MK091092; MK091091	(Léveillé et al., 2019)	Cds
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Sudan	DQ111754; DQ111751; DQ111755; DQ111757; DQ111752; DQ111753;	(Oyamada et al., 2005)	18S rRNA

					DQ111759; DQ111758; DQ111756		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Cuba	MN393911; MN393913; MN393910; MN393912	(Díaz-Sánchez et al., 2021)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MK091090; MK091084; MK091089; MK091085; MK091086; MK091087; MK091088	(Léveillé et al., 2019)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	USA	MH557087	(Léveillé et al., 2020)	COI
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Malawi	LC556379	(Guo et al., 2020)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Zambia	LC331052; LC331053; LC331054; LC331055	(Qiu et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Taiwan	EU289222	(Forlano et al., 2007)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Australia	MG062866; MG062865	(Greay et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Saint Kitts and Nevis	JX112783	(Loftis et al., 2013)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Iran	KT736298	(Soltani & Dalimi, 2018)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Iran	KX880502; KX880503; KX880504; KX880505; KX880506	(Soltani & Dalimi, 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	JN584477; JN584478; JN584475; JN584476	(Pawar et al., 2012)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MG543849	(Lakshmanan et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Iran	KU360328; KU360327; KU360326	(Barati et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Nigeria	AB365071	(Sasaki et al., 2008)	18S rRNA
Hepatozoon sp. ; canis	*Canis lupus familiaris*	Mammalia	Canidae	USA; Brazil	AY864676; AY864677; AY864678; AY864679	(Paludo et al., 2005)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Germany	MN791088; MN791089	(Hodžić et al., 2020)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris; Vulpes vulpes; Haemaphysalis bispinosa; Rhipicephalus sanguineus*	Mammalia; Arachnida	Canidae; Ixodidae	Germany	MK757806; MK757798; MK757802; MK757807; MK757808; MK757809; MK757810; MK757811; MK757813; MK757801; MK757797; MK757799; MK757800; MK757814; MK757812; MK757711;	(Helm et al., 2020)	18S rRNA

					MK757768; MK757709; MK757793; MK757769; MK757757; MK757785; MK757804; MK757786; MK757791; MK757756; MK757789; MK757759; MK757790; MK757784; MK757771; MK757758; MK757776; MK757750; MK757754; MK757763; MK757766; MK757737;	MK757815; MK757777; MK757781; MK757780; MK757778; MK757792; MK757783; MK757788; MK757805; MK757774; MK757796; MK757795; MK757761; MK757752; MK757755; MK757787; MK757803; MK757751; MK757762; MK757765; MK757770; MK757738;		

					MK757767; MK757824; MK757825		
Hepatozoon canis	*Canis lupus familiaris; tick*	Mammalia; Arachnida	Canidae; Ixodidae	Brazil	KF972443; KF972442; KF972444; KF972445; KF972441	(Gonçalves et al., 2014)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Croatia	FJ497022; FJ497012; FJ497021; FJ497019; FJ497020; FJ497017; FJ497011; FJ497009; FJ497018; FJ497015; FJ497010; FJ497014; FJ497023; FJ497016; FJ497024; FJ497013;	(Vojta et al., 2009)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Cape verde	GQ395386	(Götsch et al., 2009)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Malaysia	KT267952; KT267953; KT267954; KT267955; KT267956; KT267957; KT267958; KT267959; KT267960; KT267961; KT267962; KT267963; KT267964; KT267965; KT267951	(Mohammed, 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India, Thailandia	KU096058; KU765200; KU765202; KU527125; KU527126; KU527127	(Liu et al., 2016)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	KX588232	(Bölükbaş et al., 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	KX641899; KX641900; KX641901	(Gou et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	KX377968	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	KX863669	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	KX818220	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Czech Republic	KY021177; KY021178; KY021181; KY021183; KY021184; KY021176; KY021180; KY021182	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MH922767; MH922768	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Thailand	MW402988; MW402989	(Do et al., 2021)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	South Korea	MK238383; MK238384	(Seo et al., 2020)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil; Poland	MN103412; MN103528; MN103520; MN103519	(Mierzejewska et al., 2021)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Taiwan	JF459994	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KP233215	(Oliveira et al., 2014)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MF797806	(Lakshmanan et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris; Rhipicephalus sanguineus*	Mammalia; Arachnida	Canidae; Ixodidae	Nigeria	JQ976621; JQ976620; JQ976622; JQ976623; JX027010; JX027011; JX027018; JQ976629; JX027012; JX027017; JX027019; JQ976626; JQ976628; JX027020; JX027015; JX027016; JQ976627; JX027014; JQ976624; JQ976625; JX027013	(Kamani et al., 2013)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Not available	KP182934; KP182932; KP182933; KP182930; KP182929; KP182931	(Adao et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	MG254622; MG254603; MG254593; MG254611; MG254591; MG254606; MG254576; MG254583; MG254597; MG254604; MG254605; MG254589; MG254595; MG254623;	(Orkun et al., 2018)	18S rRNA

					MG254599; MG254600; MG254609; MG254620; MG254607; MG254612; MG254621; MG254579; MG254580; MG254587; MG254594; MG254618; MG254592; MG254601; MG254602; MG254619; MG254574; MG254577; MG254585; MG254590; MG254575; MG254598; MG254608; MG254582; MG254617; MG254578; MG254613; MG254614; MG254573; MG254588; MG254615; MG254596; MG254610; MG254586; MG254584; MG254581; MG254616		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	JX118828	(Ramos et al., 2015)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KU232310; KU232308; KU232309; KU232307; KU232305; KU232304; KU232306; KU232302; KU232303	(Furtado et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Philippines	LC428208	(Galay et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Thailand	KF621082; KF621085; KF621088; KF621089; KF621091; KF621095; KF621096; KF621086; KF621087; KF621090; KF621092; KF621083; KF621093; KF621094; KF621097; KF621084	(Kongklieng et al., 2015)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Pakistan	MG209586; MG209580; MG209581; MG209582; MG209583; MG209584; MG209585; MG209587; MG209589; MG209590; MG209591; ; MG209593; MG209594; MG209592; MG209589; MG209589;	(Ahmad et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Jordan	JF827605; JF827606	(Qablan et al., 2012)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	FJ943578	(Ramos et al., 2010)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	EU571737	(Lasta et al., 2009)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris; tick*	Mammalia; Arachnida	Canidae; Ixodidae	Italy	JF827276; JF827277	(Otranto et al., 2011)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Pakistan	KU535868; KU535870; KU535869; KU535871	(Qamar et al., 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Qatar	MF142765	(Alho et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Not available	FJ743476	(Rubini et al., 2009)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Mexico	KT215362; KT215361; KT215374; KT215377; KT215375; KT215370; KT215360; KT215369; KT215373; KT215363; KT215365; KT215354; KT215355; KT215366; KT215371; KT215376; KT215353; KT215372; KT215359; KT215368; KT215364; KT215357	(Jarquín-Díaz et al., 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris;* tick	Mammalia; Arachnida	Canidae; Ixodidae	India	MK757648; MK757647	Unpublished	18S rRNA

Hepatozoon canis	*Canis lupus familiaris; tick*	Mammalia; Arachnida	Canidae; Ixodidae	Iran	MT810115; MT810118	(Zeinali et al., 2020)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KF692039; KF692040; KF692038	(Miranda et al., 2014)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Portugal	LC018209; LC018208; LC018210; LC018206; LC018207; LC018203; LC018194; LC018199; LC018196; LC018202; LC018195; LC018205; LC018200; LC018204; LC018193; LC018201; LC018197; LC018198	(Maia et al. 2015)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Not available	MW362245; MW362244	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Malta	KJ946246; KJ946247; KJ946245	(Licari et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KY026191; KY026192	(Morgado et al., 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Malaysia	MG807345; MG807346; MG807347	(Prakash et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Mauritius	MF588667; MF588668; MF588669	(Daskalaki et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Hungary	MK301147; MK301150; MK301146; MK301151;	Unpublished	18S rRNA

					MK301148; MK301152; MK301149		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	MT396731; MT396726; MT396727; MT396728 MT396734; MT396733; MT396732; MT396729; MT396735	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Thailand	MW255598; MW255601; MW255599; MW255600; MW255597;	(Do et al., 2021)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Jordan	MW092541; MW092540; MW092539	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	MT433122; MT433125; MT821184; MT433126; MT433124; MT433123; MT433121	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris; Haemaphysalis concinna*	Mammalia; Arachnida	Canidae; Ixodidae	Not available	KC509528; KC509532; KC509526; KC509527; KC509529; KC509530; KC509531	(Hornok et al., 2013)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Algeria	MK645949; MK645947; MK645967; MK645971; MK645946; MK645948;	(Medkour et al., 2020)	18S rRNA

					MK645951; MK645952; MK645953; MK645954; MK645955; MK645956; MK645957; MK645959; MK645960; MK645961; MK645962; MK645963; MK645964; MK645965; MK645967; MK645968; MK645969; MK645970; MK645950; MK645958;		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Egypt	MZ203845	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Colombia	JN217101; JN217102	(Vargas-Hernandez et al., 2011)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Malta	KX069232; KX069233; KX069236; KX069234; KX069235; KX069238; KX069241; KX069240; KX069242; KX069244; KX069237; KX069239; KX069243	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	GQ176285	(Pereira et al., 2011)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	MH891623	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	FJ943578	(Ramos et al., 2010)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	MT081050; MT081051	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	DQ060327; DQ060325; DQ060329; DQ060324; DQ060328; DQ060326;	(Karagenc et al., 2006)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Pakistan	KT955848	(Aktas et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Angola	KX082909; KX082905; KX082906; KX082907; KX082908; KX082910; KX082911; KX082912; KX082913; KX082914	(Cardoso et al., 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	DQ198378; DQ198379	(Rubini et al., 2005)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Colombia	MK910142; MK910141; MK910143; MK910144	(Thomas et al., 2020)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	MG496257; MG496273	Unpublished	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	MW570843	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	JN835188	(Miranda et al., 2014)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	KJ513193; KJ513198	(Düzlü et al., 2014)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KJ831221; KJ831219	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Cyprus	KU255116	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	MG772658	(Lopes et al., 2019)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Cape verde	KU961914; KU961916; KU961917; KU961918; KU961919; KU961921; KU961922; KU961924; KU961925; KU961926; KU961927; KU961928; KU961929; KU961930; KU961931; KU961932; KU961934; KU961935; KU961936; KU961937; KU961938; KU961939; KU961940; KU961941; KU961943; KU961945; KU961947; KU961948; KU961950; KU961951;	(Lauzi et al., 2016)	18S rRNA

					KU961952; KU961954; KU961955; KU961956; KU961957; KU961958; KU961959; KU961960; KU961961; KU961962; KU961963; KU961964; KU961965; KU961967; KU961968; KU961942; KU961944; KU961933; KU961966; KU961915; KU961946; KU961949; KU961920; KU961953; KU961923		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	MN174861	(Aguiar et al., 2018)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	KX236166	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Pakistan	MN900602; MN900603; MN900610; MN900692	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Colombia	MT579549	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Romania	MN540616; MN540617; MN540618; MN540619; MN540620; MN540621	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	DQ071888	(Forlano et al., 2007)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MN628317; MN628318; MN628319; MN628320; MN628321; MN628322; MN628323; MN628324; MN628325; MN628326; MN628327; MN628328; MN628329	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Italy	FJ608736	(Pietrobelli et al., 2007)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris; ticks*	Mammalia; Arachnida	Canidae; Ixodidae	Romania	KY433319; KY433320; KY433321; KY433326; KY433327	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	LC053450	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Mexico	MT672778	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Argentina	KY940658	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Italy	KU821656; KU821657; KU821658; KU821659; KU821660; KU821661; KU821662	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	China	MW281789; MW281722	Unpublished	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	MT909554	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Israel	KY741982	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris; Felis catus*	Mammalia	Canidae; Felidae	Vietnam; Thailand; Philippines	MN689651; MN689652; MN689653; MN689655; MN689656; MN689658; MN689660; MN689662; MN689664; MN689665; MN689667; MN689668; MN689669; MN689670; MN689671; MN689654; MN689659; MN689661; MN689666; MN689663; MN689657;	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Tunisia	MT588816; MT588817	(Bouattour et al., 2021)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	China	MT499354; MT499355; MT499356	(Colella et al., 2020)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Iran	MW019630; MW019631; MW019632; MW019633; MW019634; MW019635;	(Iatta et al., 2021)	18S rRNA

					MW019636; MW019637; MW019638; MW019639; MW019640; MW019641; MW019642; MW019643		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Romania	JX976545	(Andersson et al., 2013)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MN181508	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Australia	MG076961	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Not available	EF650846	(Criado-Fornelio et al., 2007)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Japan	LC012821; LC012822; LC012823; LC012824; LC012825; LC012826; LC012827; LC012828; LC012829; LC012830; LC012831; LC012832; LC012833; LC012834; LC012835; LC012836; LC012837; LC012838; LC012839	(Kubo et al., 2015)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	China	KP719091	(Xu et al., 2015)	18S rRNA

Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	China	HQ718615; HQ718616; HQ718617;	(Wong et al., 2011)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MZ318674; MZ318676; MZ318689; MZ318707; MZ323359; MZ323360; MZ323361; MZ323362; MZ323363; MZ323364; MZ411572; MZ411573; MZ411581;	Unpublished	18S rRNA
Hepatozoon canis	*Canis mesomelas; Caracal caracal*	Mammalia	Canidae; Felidae	South Africa	MK621311; MK621312; MK621313; MK621314; MK621317; MK621315; MK621318; MK621309; MK621304; MK621305; MK621319; MK621303; MK621302; MK621308; MK621306; MK621307; MK621316	(Viljoen et al., 2020)	18S rRNA
Hepatozoon canis	*Canis mesomelas*	Mammalia	Canidae	South Africa	MT774531	Unpublished	18S rRNA

Hepatozoon canis	*Cerdocyon thous*	Mammalia	Canidae	Brazil	AY461378	(Criado-Fornelio et al., 2006)	18S rRNA
Hepatozoon canis	*Chrysocyon brachyurus*	Mammalia	Canidae	Brazil	MT965691; MT965692	(Arrais et al., 2020)	18S rRNA
Hepatozoon canis	*Cuon alpinus*	Mammalia	Canidae	India	HQ829447; HQ829448	(Pawar et al., 2012)	18S rRNA
Hepatozoon canis	*Cuon alpinus*	Mammalia	Canidae	Thailand	MK144332	Unpublished	18S rRNA
Hepatozoon canis	*Didelphis albiventris*	Mammalia	Didelphidae	Brazil	KY392884; KY392885	(Silva et al., 2017)	18S rRNA
Hepatozoon canis	*Felis catus*	Mammalia	Felidae	Brazil	DQ315565; DQ315566	(Rubini et al., 2006)	18S rRNA
Hepatozoon canis	*Felis catus; Canis lupus familiaris*	Mammalia	Felidae; Canidae	Thailand	MW377924; MW402991; MW402992; MW402990; MW377923	Unpublished	18S rRNA
Hepatozoon canis	*Felis domesticus*	Mammalia	Felidae	France	EU622909; EU622910	(Criado-Fornelio et al., 2009)	18S rRNA
Hepatozoon canis	*Felis domesticus*	Mammalia	Felidae	France	FJ213775	(Criado-Fornelio et al., 2009)	18S rRNA

Hepatozoon canis	*Fox*	Mammalia	Canidae	Bosnia and Herzegovina	KP216410; KP216413; KP216414; KP216415; KP216416; KP216418; KP216420; KP216421; KP216426; KP216427; KP216430; KP216433; KP216434; KP216435; KP216436; KP216437; KP216440; KP216444; KP216446; KP216449; KP216455; KP216456; KP216458; KP216459; KP216460; KP216464; KP216466; KP216468; KP216469; KP216473; KP216477; KP216478; KP216482; KP216484; KP216485; KP216486; KP216487; KP216489; KP216490; KP216491; KP216492; KP216425; KP216454; KP216462; KP216472; KP216480; KP216456; KP216458; KP216481	(Hodžić et al., 2015)	18S rRNA
Hepatozoon canis	*Haemaphysalis bispinosa; Canis lupus familiaris*	Arachnida; Mammalia	Ixodidae; Canidae	India; Kyrgyzstan	MG018464; MG050161; MG018465; MG018466; MG919976; MG919977; MG050160; MG018467; MG917710; MG917715;	Unpublished	18S rRNA

					MG917709; MG917718; MG917713; MG917719; MG917712; MG917714; MG050163; MG050162; MG917716; MG917717; MG917711		
Hepatozoon canis	*Haemaphysalis bispinosa*	Arachnida	Ixodidae	India	MG241124;	Unpublished	18S rRNA
Hepatozoon canis	*Haemaphysalis longicornis*	Arachnida	Ixodidae	Japan	LC169075; LC169076	Unpublished	18S rRNA
Hepatozoon canis	*Haemaphysalis longicornis*	Arachnida	Ixodidae	China	MK294048	Unpublished	18S rRNA
Hepatozoon canis	*Hyalomma anatolicum*	Arachnida	Ixodidae	Pakistan	JX441117	Unpublished	18S rRNA
Hepatozoon canis	*Hydrochoerus hydrochaeri*	Mammalia	Caviidae	Brazil	KY965141; KY965142; KY965143; KY965144	Unpublished	18S rRNA
Hepatozoon canis	*Ixodes holocyclus*	Arachnida	Ixodidae	Australia	MG758124	(Greay et al., 2018)	18S rRNA
Hepatozoon canis	*Ixodes ricinus; Myodes glareolus*	Arachnida; Mammalia	Ixodidae; Cricetidae	Czech Republic	KU597242; KU597253; KU597254; KU597239; KU597240; KU597241; KU597252; KU597243; KU597244; KU597245; KU597246; KU597246;	(Hamšíková et al., 2016)	18S rRNA

					KU597248; KU597249; KU597250; KU597251; KU597235; KU597236; KU597237; KU597238		
Hepatozoon canis	*Ixodes ricinus*	Arachnida	Ixodidae	Slovakia	MG253004; MG253001; MG253002; MG253003	(Víchová et al., 2018	18S rRNA
Hepatozoon canis	*Ixodes ricinus*	Arachnida	Ixodidae	Luxembourg	GU827130	(Reye et al., 2010)	18S rRNA
Hepatozoon canis	*Lycalopex gymnocercus*	Mammalia	Canidae	Brazil	KX816958	Unpublished	18S rRNA
Hepatozoon canis	*Lycalopex gymnocercus*	Mammalia	Canidae	Brazil	KM057841	Unpublished	18S rRNA
Hepatozoon canis	*Lycalopex vetulus*	Mammalia	Canidae	Brazil	MT458173; MT458171; MT458172; MT458170;	Unpublished	18S rRNA
Hepatozoon canis	*Lycaon pictus*	Mammalia	Canidae	South Africa	MT762140; MT762141	Unpublished	18S rRNA
Hepatozoon canis	*Martes foina; Vulpes vulpes*	Mammalia	Mustelidae; Canidae	Spain	MW578992; MW578993; MW578996; MW579001; MW579002; MW578979; MW578980; MW578981; MW578982; MW578983; MW578984; MW578985; MW578986; MW578987;	Unpublished	18S rRNA

					MW578988; MW578989; MW578990; MW578991; MW578994; MW578995; MW578997; MW578998; MW578999; MW579000;		
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brasil	KU569168	(Demoner et al., 2016)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Thailand	MT354613; MT355552; MT355565	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	India	MN252045; MN252044	(Bora et al., 2019)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Ireland	LS453286; LS453287; LS453288	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Cyprus	KF724626	(Attipa et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus*	Mammalia	Canidae	India	KT246304	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Brasil	JF295088	(Bouer et al., 2017)	18S rRNA
Hepatozoon canis	*Canis lupus familiaris*	Mammalia	Canidae	Ethiopia	KF646812; KF646813	*Unpublished*	18S rRNA

Hepatozoon canis	Not available	Not available	Not available	Not available	GU386283; GU386284	Unpublished	18S rRNA
Hepatozoon canis	*Canis lupus*	Mammalia	Canidae	Trinidad and Tobago	KX249834; KX249835	(Sant et al., 2017)	18S rRNA
Hepatozoon canis	Not available	Arachnida	Ixodidae	China	MG675579	(Zheng et al., 2018)	18S rRNA
Hepatozoon canis	Not available	Arachnida	Ixodidae	Kenya	KT956192	(Campana et al., 2016)	18S rRNA
Hepatozoon canis	*Panthera leo*	Mammalia	Felidae	Zambia	MT814748; MT814761	(Squarre et al., 2020)	18S rRNA
Hepatozoon canis	*Panthera tigris*	Mammalia	Felidae	Italy	MT232062; MT232063; MT232064;	(Yamamoto et al., 2017)	18S rRNA
Hepatozoon canis	*Prionailurus bengalensis; Panthera onca; Elephas maximus*	Mammalia	Felidae; Proboscidea	Thailand	MZ151528; MZ151523; MZ151529; MZ151509; MZ151516; MZ151517; MZ151527; MZ151524; MZ151512; MZ151518; MZ151511; MZ151513; MZ151507; MZ151521; MZ151526; MZ151519; MZ151522; MZ151510;	(Do et al., 2021)	18S rRNA

					MZ151505; MZ151515; MZ151520; MZ151508; MZ151504; MZ151506; MZ151514; MZ151525		
Hepatozoon canis	*Procyon lotor*	Mammalia	Procyonidae	Spain	MG897468; MG897469; MG897470; MG897471;	(Criado-Fornelio et al., 2018)	18S rRNA
Hepatozoon canis	*Pseudalopex gymnocercus; Dusicyon thous*	Mammalia	Canidae	Brazil; Spain	AY461376; AY461375; AY471615	(Criado-Fornelio et al., 2006)	18S rRNA
Hepatozoon canis	*Rhipicephalus (Boophilus) microplus*	Arachnida	Ixodidae	Brazil	HQ605710	(Miranda et al., 2011)	18S rRNA
Hepatozoon canis	*Rhipicephalus decoloratus*	Arachnida	Ixodidae	Kenya	MN294724	(Chiuya et al., 2020)	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Serbia	MZ146329	(Banovic et al., 2021)	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Brazil	MG793450; MG793449	(Ramos, 2018)	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Turkey	KY196999; KY197000; KY197001	(Aktas & Özübek, 2017)	18S rRNA

Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Egypt	MG564214; MG564216; MG564215; MG564217;	Unpublished	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Taiwan	MH595892; MH595893; MH595894; MH595895; MH595896; MH595897; MH595898; MH595902; MH595903; MH595904; MH595905; MH595906; MH595907; MH595908; MH595909; MH595910; MH595911; MH595899; MH595900; MH595901	(Chao et al., 2019)	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Brazil	MG241229	(Santos et al., 2018)	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Palestine	KT587790; KT587789	(Azmi et al., 2016)	18S rRNA
Hepatozoon canis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Portugal	MN207197	(Coimbra-Dores et al., 2020)	18S rRNA
Hepatozoon canis	*Rhipicephalus sp*	Arachnida	Ixodidae	Spain	KJ605144; KJ605145; KJ605146; KJ605147	(Latrofa et al., 2014)	18S rRNA

Hepatozoon canis	Ticks	Arachnida	Not available	China	KX870924; KX870925	(Liu et al., 2016)	18S rRNA
Hepatozoon canis	*vulpes*	Mammalia	Cannidae	France, Portugal, Spain	AY150067	(Criado-Fornelio et al., 2003)	18S rRNA
Hepatozoon canis	*Hydrochaeris hydrochaeris*	Mammalia	Caviidae	Brazil	EF622096	(Criado-Fornelio et al., 2007)	18S rRNA
Hepatozoon canis	*Various species*	Mammalia	Canidae	China	MT107087; MT107088; MT107089; MT107090; MT107091; MT107092; MT107093; MT107094; MT107095; MT107096; MT107097; MT107098	(Guo et al., 2020)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Spain	AY731062	(Criado-Fornelio et al., 2004)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Italy	GU371446; GU371447; GU371448; GU371449; GU371450; GU371451; GU371452; GU376453; GU376454; GU376455;	(Gabrielli et al., 2010)	18S rRNA

					GU376456; GU376457; GU376458		
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Italy	MW295531	(Sgroi et al., 2021)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Austria	KM115969; KM115970; KM115971; KM115974; KM115979; KM115983; KM115984; KM115986; KM115987; KM115989; KM115991; KM115993; KM115996; KM115998; KM116001; KM116003; KM116005; KM115981; KM116002; KM116000; KM115995;	(Duscher et al., 2014)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Austria	KY693670	(Hodžić et al., 2018)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Slovakia	KX879139; KX879135; KX887324; KX879129; KX879138; KX879141; KX879134; KX887325; KX887327; KX887323; KX879136; KX879137; KX887328; KX879133; KX879131;	(Miterpáková et al., 2017)	18S rRNA

					KX879130; KX887326; KX887322; KX879132; KX879140		
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Turkey	MG077085; MG077087; MG077084; MG077086	(Orkun et al., 2018)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Italy	KP644235	Unpublished	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Italy	KP715299; KP715300; KP715301; KP715302; KP715303	Unpublished	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Croatia	HM212626; HM212625; HM212627	(Dežđek et al., 2010)	18S rRNA
Hepatozoon canis	Various species	Mammalia	Various	Turkey	MN463026; MN463025; MN463023; MN463021; MN463022; MN463029; MN463024; MN463027; MN463028	(Orkun & Emir, 2020)	18S rRNA
Hepatozoon canis	*Various species*	Mammalia; Arachnida	Canidae; Ixodidae	Germany	KC584773; KC584774; KC584775; KC584776; KC584777; KC584780; KC584778; KC584779	(Najm et al., 2014)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Serbia	MH699891; MH699889; MH699892; MH699888; MH699890; MH699885;	Unpublished	18S rRNA

					MH699887; MH699886; MH699884		
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Poland	MK872809; MK872810; MK872808	(Bajer et al., 2019)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Romania	KM096414; KM096413; KM096411; KM096412	(Imre et al., 2015)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Hungary	KC886726; KF322143; KC886723; KC886724; KC886722; KC886733; KC886721; KC886725; KF322142; KC886731; KC886732; KC886728; KC886730; KC886727; KF322144; KF322141; KF322145; KC886729; KC886720;	(Farkas et al., 2014)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	France	MK673838; MK673840; MK673816; MK673834; MK673848; MK673851; MK673852; MK673853; MK673818; MK673819; MK673820; MK673821; MK673823; MK673824; MK673825; MK673826; MK673827; MK673831;	(Medkour et al., 2020)	18S rRNA

					MK673832; MK673835; MK673836; MK673837; MK673839; MK673841; MK673842; MK673843; MK673844; MK673845; MK673846; MK673847; MK673849; MK673850; MK673854; MK673828; MK673830; MK673817; MK673833; MK673829; MK673822		
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Poland	EU165370	Unpublished	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Slovakia	KX958469	(Miterpáková et al., 2017)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Slovakia	DQ869309	(Majláthová et al., 2007)	18S rRNA
Hepatozoon canis	*Vulpes vulpes*	Mammalia	Canidae	Slovakia	MG214908	(Víchová et al., 2018)	18S rRNA

Hepatozoon canis	*Vulpes vulpes* and various dogs breeds	Mammalia	Canidae	Czech Republic	KU893125; KU893118; KU893119; KU893120; KU893123; KU893124; KU893126; KU893122; KU893127; KU893121	(Mitková et al., 2016)	18S rRNA
Hepatozoon catesbianae	*Lithobates catesbeianus*	Amphibia	Ranidae	Not available	AF040972; AF041438	(Lang-Unnasch et al., 1998)	18S rRNA
Hepatozoon catesbianae	*Lithobates clamitans*	Amphibia	Ranidae	USA and Canada	AIG55089	(Léveillé et al., 2014)	Cytochrome b; cytochrome c oxidase subunit I; cytochrome c oxidase subunit III; 18S rRNA ; large subunit ribosomal;
Hepatozoon catesbianae	Earthworms	Annelidia	Lumbricidae	USA	AF130361	(Carreno et al., 1999)	18S rRNA
Hepatozoon catesbianae	*Rana catesbeiana*	Amphibia	Ranidae	USA	HQ224954	(Barta et al., 2012)	18S rRNA

Hepatozoon catesbianae	Various species	Amphibia	Ranidae	USA	MN244528; MN245144; MN245145; MN245146;	(Léveillé et al., 2020)	18S rRNA ; ITS1; 5.8S ribosomal RNA
Hepatozoon cecilhoarei	*Philothamnus natalensis natalensis*	Reptilia	Colubridae	South Africa	MG519504	(Cook et al., 2018)	18S rRNA
Hepatozoon clamatae	Various species	Amphibia	Ranidae	Not available	DQ856584; DQ856585; DQ856586; DQ856587; DQ856588; DQ856589; DQ856590; DQ856591	(Boulianne et al., 2007)	ITS1
Hepatozoon clamatae	*Rana clamitans*	Amphibia	Ranidae	USA	HQ224962; HQ224963	(Barta et al., 2012)	18S rRNA
Hepatozoon clamatae	*Rana pipiens*	Amphibia	Ranidae	Canada	MN310689; MN310690	(Léveillé et al., 2021)	COI
Hepatozoon clamatae	Various species	Amphibia	Ranidae	USA	MN244529	(Léveillé et al., 2020)	18S rRNA ; ITS1; 5.8S ribosomal RNA
Hepatozoon colubri	Not available	Not available	Not available	Iran	MN723844	Unpublished	18S rRNA

Hepatozoon cuestensis; Hepatozoon musa	*Crotalus durissus*	Reptilia	Viperidae	Brazil	MF497769; MF497765; MF497763; MF497767; MF497770; MK757772; MF497768; MF497764; MF497766	(Úngari et al., 2018)	18S rRNA
Hepatozoon domerguei	*Madagascarophis colubrinus*	Reptilia	Lamprophiidae	Madagascar	KM234646; KM234649; KM234648; KM234650	(Maia et al., 2014)	18S rRNA
Hepatozoon erhardovae	*Ctenophthalmus agyrtes*	Insecta	Hystrichopsyllidae	Hungary	KJ634066; KJ608372	(Rigó et al., 2016)	18S rRNA
Hepatozoon erhardovae	*Myodes glareolus*	Mammalia	Cricetidae	Poland	KF418367; KF418366	(Bajer et al., 2014)	18S rRNA
Hepatozoon ewingi	*Haemaphysalis bancrofti*	Arachnida	Ixodidae	Australia	MG593275; MG593274	(Greay et al., 2018)	18S rRNA ; 18S rRNA
Hepatozoon felis	*Amblyomma testudinarium larva; Haemaphysalis longicornis nymph;* various species	Arachnida	Ixodidae	Japan	AB983403; AB983428; AB983419; AB983437; AB983387; AB983390; AB983415; AB983426; AB983389; AB983432; AB983386; AB983402; AB983388; AB983406; AB983411; AB983393; AB983394; AB983401; AB983405; AB983407; AB983408; AB983409; AB983410; AB983412; AB983414; AB983417; AB983422; AB983423; AB983429; AB983430;	(Tateno et al., 2015)	18S rRNA

					AB983435; AB983431; AB983420; AB983433; AB983436; AB983385; AB983391; AB983392; AB983396; AB983399; AB983404; AB983416; AB983421; AB983400; AB983418; AB983424; AB983427; AB983425		
Hepatozoon felis	*Caracal caracal*	Mammalia	Felidae	South Africa	MK621310	(Viljoen et al., 2020)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Spain	AY620232	(Criado-Fornelio et al., 2006)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Spain	AY628681	(Criado-Fornelio et al., 2006)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Brazil	JN123435;	(Bortoli et al., 2011)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Brazil	KM435071	(Braga, 2017)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Uruguay	MT210598; MT210593; MT210597; MT210594; MT210595; MT210596	(Bazzano et al., 2021)	18S rRNA

Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Italy	KY511259	(Otranto et al., 2017)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Austria	MK724001	(Basso et al., 2019)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Cyprus	KX808667; KX808665; KX808660; KX808661; KX808658; KX808658; KX808663; KX808662; KX808666; KX808670; KX808671; KX808668; KX808669; KX808664	(Attipa et al., 2017)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Japan	LC179796; LC179798; LC179799; LC179794; LC179797; LC179795	(Jikuya et al., 2017)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Cape verde	MK836092	(Pereira et al., 2019)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Cyprus	KY215809; KY215817; KY215807; KY215811; KY215815; KY215814; KY215808; KY215810; KY215816; KY215818; KY215813; KY215805; KY215812; KY215806	(Attipa et al., 2017)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	India	MN227271; MN227275; MN227274; MN227269; MN227268; MN227270;	(Malangmei et al., 2021)	18S rRNA

					MN227272; MN227273; MN227267; MN227276		
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Angola	MG386482; MG386483; MG386484	(Oliveira et al., 2018)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	Israel	MG722717; MG722718; MG722715; MG722716	(Kamani et al., 2018)	18S rRNA
Hepatozoon felis	*Felis catus*	Mammalia	Felidae	South Africa	MK301457; MK301458; MK301459; MK301463; MK301460; MK301461; MK301462	(Harris et al., 2019)	18S rRNA
Hepatozoon felis	*Haemaphysalis sulcata*	Arachnida	Ixodidae	Turkey	KF034779; KF034776; KF034780; KF034777; KF034775; KF034778	(Aktas, 2014)	18S rRNA
Hepatozoon felis	*Lycalopex gymnocercus*	Mammalia	Canidae	Argentina	HQ020489	(Giannitti et al., 2012)	18S rRNA
Hepatozoon felis	*Leopardus pardalis*	Mammalia	Felidae	Brazil	EU028344; EU267606	(Metzger et al., 2008)	18S rRNA
Hepatozoon felis	*Panthera leo leo*	Mammalia	Felidae	India	KX017290	(Rafiqi et al., 2018)	18S rRNA
Hepatozoon felis	*Panthera leo persica*	Mammalia	Felidae	India	HQ829440; HQ829438; HQ829439; HQ829441; HQ829442; HQ829443; HQ829444; HQ829434;	(Pawar et al., 2012)	18S rRNA

					HQ829435; HQ829436; HQ829437; HQ829430; HQ829431; HQ829433;		
Hepatozoon felis	*Panthera leo persica*	Mammalia	Felidae	Thailand	KY056823	(Bhusri et al., 2017)	18S rRNA
Hepatozoon felis	*Panthera pardus fusca*	Mammalia	Felidae	India	HQ829444	(Pawar et al., 2012)	18S rRNA
Hepatozoon felis	*Panthera tigris*	Mammalia	Felidae	Not available	MT634695	Unpublished	18S rRNA
Hepatozoon felis	*Panthera tigris*	Mammalia	Felidae	Not available	MT645336	Unpublished	18S rRNA
Hepatozoon felis	*Panthera tigris tigris*	Mammalia	Felidae	India	HQ829445; HQ829446	(Pawar et al., 2012)	18S rRNA
Hepatozoon felis	*Prionailurus bengalensis*	Mammalia	Felidae	Korea	GQ377217; GQ377218; GQ377216	(Kubo et al., 2010)	18S rRNA
Hepatozoon felis	*Prionailurus iriomotensis*	Mammalia	Felidae	Japan	AB771501; AB771502; AB771503; AB771504; AB771505; AB771506; AB771507; AB771508; AB771509; AB771510; AB771511; AB771512; AB771513; AB771514; AB771515; AB771516; AB771517; AB771518; AB771519; AB771520; AB771521;	(Tateno et al., 2013)	18S rRNA

					AB771522; AB771523; AB771524; AB771525; AB771526; AB771527; AB771528; AB771529; AB771530; AB771531; AB771532; AB771533; AB771534; AB771535; AB771536; AB771537; AB771538; AB771539; AB771540; AB771541; AB771542; AB771543; AB771544; AB771545; AB771546; AB771547; AB771548; AB771549; AB771550; AB771551; AB771552; AB771553; AB771554; AB771555; AB771556; AB771557; AB771558; AB771559;AB771560; AB771561; AB771562; AB771563; AB771564; AB771565; AB771566; AB771567; AB771568; AB771569; AB771570; AB771571; AB771572; AB771573; AB771574; AB771575; AB771576; AB771577		
Hepatozoon felis	*Prionailurus iriomotensis*	Mammalia	Felidae	Japan	AB636285; AB636286; AB636287	(Sakuma et al., 2011)	18S rRNA

Hepatozoon felis	*Rhipicephalus sanguineus; Felis catus*	Arachnida; Mammalia	Ixodidae;Felidae	Portugal	AB872948; AB872945; AB872949; AB872992; AB872944; AB872993; AB872947; AB872994; AB872995; AB896687; AB896694; AB983397; AB983395; AB983398; AB896688; AB896690; AB896691; AB896693; AB896689; AB983434; AB896686; AB896692	(Maia et al., 2014)	18S rRNA
Hepatozoon felis	*Rhipicephalus sanguineus*	Arachnida	Ixodidae	Turkey	JQ867388; JQ867390; JQ867389	(Aktas et al., 2013)	18S rRNA
Hepatozoon felis	Rhipicephalus sanguineus infested on an asiatic lion	Arachnida	Ixodidae	Thailand	KY056823	(Bhusri et al., 2017)	18S rRNA
Hepatozoon felis	*Rhipicephalus turanicus*	Arachnida	Ixodidae	Turkey	MF383513; MF383514	(Karasartova et al., 2018)	18S rRNA
Hepatozoon fitzsimonsi	*Amblyomma sparsum*	Arachnida	Ixodidae	Kenya	KT266582	(Omondi et al., 2017)	18S rRNA
Hepatozoon fitzsimonsi	*Chersina angulata*	Reptilia	Geoemydidae	South Africa	KJ702453	(Cook et al., 2014)	18S rRNA
Hepatozoon fitzsimonsi	*Kinixys belliana*	Reptilia	Testudinidae	Nigeria	MT704950	(Adetunji et al., 2020)	18S rRNA

Hepatozoon fitzsimonsi	*Kinixys zombensis*	Reptilia	Testudinidae	South Africa	KR069084	(Cook et al., 2015)	18S rRNA
Hepatozoon fitzsimonsi	*Kinixys zombensis*	Reptilia	Testudinidae	South Africa	KR069084	(Conradie et al., 2017)	18S rRNA
Hepatozoon fitzsimonsi	Not available	Reptilia	Not available	South Africa	MW494679; MW494678; MW494680; MW494681	*Unpublished*	18S rRNA
Hepatozoon griseisciuri	*Sciurus carolinensis*	Mammalia	Sciuridae	USA	MK452388	(Léveillé et al., 2020)	Mitochondrion
Hepatozoon griseisciuri	*Sciurus carolinensis*	Mammalia	Sciuridae	USA	MK452252; MK452253	(Léveillé et al., 2020)	18S rRNA
Hepatozoon ingwe	*Panthera pardus pardu*	Mammalia	Felidae	South Africa	MN793000; MN793001	(As et al., 2020)	18S rRNA
Hepatozoon involucrum	*Hyperolius marmoratus*	Amphibia	Hyperoliidae	South Africa	MG041594; MG041591; MG041592; MG041593	(Netherlands et al., 2018)	18S rRNA
Hepatozoon ixoxo	*Amietophrynus gutturalis*	Amphibia	Bufonidae	Not available	KP119771; KP119772; KP119773; KP119770	(Netherlands et al., 2014)	18S rRNA
Hepatozoon ixoxo	*Sclerophrys maculata*	Amphibia	Bufonidae	South Africa	KX512803; KX512804	(Conradie et al., 2017)	18S rRNA
Hepatozoon ixoxo	*Sclerophrys pusilla*	Amphibia	Bufonidae	South Africa	MG041604	(Netherlands et al., 2018)	18S rRNA
Hepatozoon luiperdjie	*Panthera pardus pardus*	Mammalia	Felidae	South Africa	MN793004; MN793002; MN793003	(As et al., 2021)	18S rRNA

Hepatozoon martis	*Martes martes; Martes foina*	Mammalia	Mustelidae	Bosnia and Herzegovina; Croatia	MG136687; MG136688; MG136687	(Hodžić et al., 2018)	18S rRNA
Hepatozoon musa	*Philodryas nattereri*	Reptilia	Colubridae	Brazil	KX880079	(Borges-Nojosa et al., 2017)	18S rRNA
Hepatozoon ophisauri	Not available	Not available	Not available	Iran	MN723845	Unpublished	18S rRNA
Hepatozoon ophisauri	*Rhombomys opimu*	Mammalia	Muridae	China	MW256822; MW342705	Unpublished	18S rRNA
Hepatozoon procyonis	*Nasua nasua*	Mammalia	Procyonidae	Brazil	MF685403; MF685387; MF685405; MF685408; MF685406; MF685409; MF685397; MF685398; MF685407; MF685410; MF685404; MF685390; MF685391; MF685393; MF685399; MF685396; MF685389; MF685392; MF685394; MF685388; MF685386; MF685402; MW862003; MW862006; MF685395; MW862005;	(Silva et al., 2018)	18S rRNA

					MF685401; MW862004; MK277318; MK277319; MK277320; MK277321; MK277322; MK277323; MK277324;		
Hepatozoon procyonis	*Nasua nasua*	Mammalia	Procyonidae	Brazil	MT102405	(Perles et al., 2020)	18S rRNA
Hepatozoon sciuri	*Sciurus vulgaris*	Mammalia	Sciuridae	Czech Republic	MN104640; MN104639; MN104638; MN104637; MN104636	(Modrý et al., 2021)	18S rRNA
Hepatozoon seychellensis	*Grandisonia alternans*	Amphibia	Indotyphlidae	Seychelles	KF246565; KF246566	(Harris et al., 2014)	18S rRNA
Hepatozoon silvestris	*Felis catus*	Mammalia	Felidae	Switzerland	MH078194	(Kegler et al 2018)	18S rRNA
Hepatozoon silvestris	*Felis catus*	Mammalia	Felidae	Italy	KY649445; KY649446; KY649442; KY649443; KY649444;	(Giannelli et al., 2017)	18S rRNA
Hepatozoon silvestris	*Felis silvestris silvestris*	Mammalia	Felidae	Bosnia and Herzegovina	KX757032; KX757031; KX757033;	(Hodžić et al., 2017)	18S rRNA
Hepatozoon silvestris	*Felis silvestris silvestris*	Mammalia	Felidae	Bosnia and Herzegovina	MF614155; MF614156; MF614157;	(Hodžić et al., 2018)	18S rRNA

Hepatozoon sipedon	*Nerodia sipedon sipedon*	Reptilia	Colubridae	Canada	JN181157	(Barta et al., 2012)	18S rRNA
Hepatozoon sipedon	*Nerodia sipedon sipedon*	Reptilia	Colubridae	USA	JN181157	(Barta et al., 2012)	18S rRNA
Hepatozoon sipedon	Not available	Not available	Not available	Canada	AF110243; AF110244; AF110245; AF110246; AF110247; AF110248; AF110249; AF110241; AF110242;	(Smith et al., 1999)	18S rRNA
Hepatozoon sp.	*Acomys russatus*	Mammalia	Muridae	Egypt	KT337469; KT337470; KT337472; KT337467; KT337468; KT337471	(Alsarraf et al., 2016)	18S rRNA
Hepatozoon sp.	*Ailuropoda melanoleuca*	Mammalia	Ursidae	China	MK645858;	(Yu et al., 2019)	18S rRNA
Hepatozoon sp.	*Amblyomma americanum*	Arachnida	Ixodidae	USA	KC162911; KC162910; KC162913	(Shock et al., 2014)	18S rRNA
Hepatozoon sp.	*Amblyomma americanum*	Arachnida	Ixodidae	USA	MT259335	(Thompson et al., 2020)	18S rRNA
Hepatozoon sp.	*Amblyomma dissimile*	Arachnida	Ixodidae	Brazil	MG437271	Unpublished	18S rRNA
Hepatozoon sp.	*Amblyomma fuscum*	Arachnida	Ixodidae	Brazil	KU955319	(Blanco et al., 2017)	18S rRNA

Hepatozoon sp.	*Amblyomma rotundatum; Pogona vitticeps*	Arachnida; reptilia	Ixodidae; Sauropsida	Brazil	MT733844; MT733845; MT733847; MT733846; MT733848	(Mendoza-Roldan et al., 2021)	18S rRNA
Hepatozoon sp.	*Ameiva ameiva Linnaeus*	Reptilia	Lacertidae	Amazonia	MN833642; MN833641; MN833640; MN833639	(Picelli et al., 2020)	18S rRNA
Hepatozoon sp.	*Apodemus mystacinus*	Mammalia	Muridae	Turkey	MH523103; MH523101; MH523102; MH523100	(Usluca et al., 2019)	18S rRNA
Hepatozoon sp.	*Apodemus uralensis*	Mammalia	Muridae	Turkey	MH523098; MH523099	(Usluca et al., 2019)	18S rRNA
Hepatozoon sp.	*Aponomma varanense*	Arachnida	Ixodidae	Thailand	JQ670908; JQ670909; JQ670910	(Sumrandee et al., 2015)	18S rRNA
Hepatozoon sp.	*Aponomma varanense; Pithon reticulatus;* various species	Arachnida; Reptilia	Ixodidae; Pythonidae	Thailand	KF301647; KF301648; KF301649; KF301650; KF524356; KF524357; KF524358; KF524359; KF524360; KF524361; KF524362; KF524363	Unpublished	18S rRNA
Hepatozoon sp.	*Artibeus planirostris; Artibeus litoratus*	Mammalia	Phyllostomidae	Brazil	MN399957; MN399959; MN399960; MN399958; MN399956	Unpublished	18S rRNA

Hepatozoon sp.	*Bandicota indica*	Mammalia	Muridae	Thailand	AB181504	(Dantrakool et al., 2004)	18S rRNA
Hepatozoon sp.	*Boiga irregularis*	Reptilia	Colubridae	Australia	AF297085	Unpublished	18S rRNA
Hepatozoon sp.	*Caiman crocodilus yacare*	Reptilia	Alligatoridae	Brazil	KJ413132; KJ413113; KJ413133; KJ413127; KJ413115; KJ413112; KJ413122; KJ413121; KJ413123; KJ413114; KJ413117; KJ413129; KJ413131; KJ413138; KJ413124; KJ413116; KJ413128; KJ413119; KJ413134; KJ413130; KJ413135; KJ413126; KJ413118; KJ413125; KJ413120; KJ413136; KT881534; KT881531; KJ413137; KT881536; KX453648; KT881539; KX453641; KT881540; KT881537; KT881538; KX453645	(Maia et al., 2016)	18S rRNA
Hepatozoon sp.	*Calomys callosus*	Mammalia	Cricetidae	Brazil	KP757838	(Wolf et al., 2016)	18S rRNA
Hepatozoon sp.	*Calomys sp; Akodon sp*	Mammalia	Cricetidae	Brazil	MH111420; MH111419; MH111408; MH111410; MH111407; MH111417;	(Perles et al., 2018)	18S rRNA

					MH111405; MH111409; MH111411; MH111423; MH111415; MH111406; MH111422; MH111412; MH111416; MH111413; MH111418; MH111414; MH111421; MH111404		
Hepatozoon sp.	*Various species*	Mammalia	Canidae	Algeria	KJ499495; KJ499505; KJ499513; KJ499490; KJ499503; KJ499514; KJ499515; KJ499502; KJ499492; KJ499506; KJ499491; KJ499521; KJ499534; KJ499489; KJ499533; KJ499522; KJ499531; KJ499519; KJ499528; KJ499529; KJ499536; KJ499526; KJ499527; KJ659858; KJ499479; KJ499523; KJ499535; KJ499537; KJ499484; KJ499499; KJ499525; KJ499493; KJ499494; KJ499517; KJ499524; KJ659861; KJ499482; KJ499496; KJ499497; KJ499510; KJ499501; KJ499507; KJ499508; KJ499509; KJ499516;	(Maia et al., 2014)	18S rRNA

					KJ499530; KJ499483; KJ499485; KJ499487; KJ499512; KJ499520; KJ499488; KJ499504; KJ499481; KJ499498; KJ499511; KJ499486; KJ499518; KJ659862; KJ659859; KJ499480; KJ499532; KJ659860		
Hepatozoon sp.	*Various species*	Mammalia	Canidae; Cricetidae	USA	JF491230; JF491228; JF491231; JF491233; JF491226; JF491236; JF491229; JF491232; JF491237; JF491238; JF491239; JF491240; JF491241; JF491242; JF491234; JF491235; JF491243; JF491244; JF491245; JF491246; JF491227; JF491225	(Allen et al., 2011)	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	KX641902	(Guo et al., 2016)	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	MZ297965; MZ297964; MZ297962; MZ298096; MZ298095; MZ297963; MZ298097; MZ297966; MZ297303	Unpublished	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KP642760; KP642759	(Oliveira, 2015)	18S rRNA

Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	MW350131; MW350129; MW350130; MW350127; MW350128	Unpublished	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Turkey	KF439864; KF439865; KF439866; KF439867	(Aydin et al., 2015)	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Sudan	AF418558	(Inokuma et al., 2002)	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Brazil	KT323937	(Malheiros et al., 2016)	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Bosnia and Herzegovina	MK107808; MK107810; MK107811; MK107812; MK107813; MK107807; MK107809	Unpublished	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Zambia	KF270654; KF270651; KF270658; KF270644; KF270646; KF270673; KF270663; KF270668; KF270643; KF270660; KF270667; KF270665; KF270642; KF270669; KF270666; KF270659; KF270664	(Williams et al., 2014)	18S rRNA
Hepatozoon sp.	*Canis lupus familiaris*	Mammalia	Canidae	Thailand	MK830998	(Buddhachat et al., 2020)	18S rRNA

Hepatozoon sp.	*Canis lupus familiaris; Thylamys macrurus; Cerdocyon thous; leopardus pardalis; various species*	Mammalia	Canidae; Didelphidae	Brazil	KX776310; KX776318; KX776315; KX776317; KX776311; KX776313; KX776322; KX776325; KX776319; KX776297; KX776308; KX776301; KX776293; KX776329; KX776298; KX776326; KX776328; KX776291; KX776312; KX776294; KX776330; KX776323; KX776307; KX776300; KX776302; KX776303; KX776321; KX776304; KX776314; KX776296; KX7763207; KX776295; KX776331; KX776299; KX776286; KX776292; KX776289; KX776316; KX776290; KX776324; KX776354; KX776364; KX776391; KX776374; KX776363; KX776387; KX776390; KX776373; KX776335; KX776365; KX776359; KX776366; KX776337; KX776384; KX776306; KX776375; KX776378; KX776361; KX776392; KX776348; KX776393; KY197002; KX776357; KX776377; KX776386;	(Sousa et al., 2017)	18S rRNA

					KX776287; KX776394; KX776309; KX776367; KX776399; KX776376; KX776400; KX776362; KX776358; KX776381; KX776389; KX776347; KX776353; KX776344; KX776369; KX776305; KX776288; KX776368; KX776372; KX776379; KX776339; KX776352; KX776342; KX776360; KX776405; KX776403; KX776333; KX776341; KX776402; KX776406; KX776401; KX776338; KX776334; KX776398; KX776407; KX776349; KX776340; KX776404; KX776343; KX776371; KX776380; KX776408; KX776370; KX776345; KX776345; KX776351; KX776355; KX776356; KX776382; KX776385; KX776396; KX776346; KX776350		
Hepatozoon sp.	*Canis mesomelas*	Mammalia	Canidae	South Africa	MG919977; MG919980; MG919981; MG919986; MG919982; MG919987; MG919984; MG919985;	(Matjila et al., 2008)	18S rRNA

					MG919983; MG919973; MG919975; MG919974; MG919978; MG919979;		
Hepatozoon sp.	*Carollia perspicillata*	Mammalia	Phyllostomidae	Brazil	MN369545; MN369548; MN369549; MN369547; MN369546	(Santos et al., 2020)	18S rRNA
Hepatozoon sp.	*Cathartes aura*	Aves	Cathartidae	USA	GU344682	Unpublished	16s rna
Hepatozoon sp.	*Cerastes cerastes cerastes*	Reptilia	Viperidae	Egypt	KJ574012	Unpublished	18S rRNA
Hepatozoon sp.	*Cerastes cerastes; various species*	Reptilia	Viperidae; colubridae	Mauritania; turkey	KJ408511; KJ408514; KJ408515; KJ408520; KJ408521; KJ408523; KJ408525; KJ408526; KJ408512; KJ408516; KJ408517; KJ408528; KJ408529; KJ408531; KJ408510; KJ408524; KJ408522; KJ408530; KJ408518; KJ408519; KJ408532; KJ408527; KJ408513	(Tomé et al., 2014)	18S rRNA
Hepatozoon sp.	*Cerdocyon thous*	Mammalia	Canidae	Brazil	AY600625	(Criado-Fornelio et al., 2006)	18S rRNA

Hepatozoon sp.	*Cerdocyon thous*	Mammalia	Canidae	Brazil	AY461377	(Criado-Fornelio et al., 2006)	18S rRNA
Hepatozoon sp.	*Cerdocyon thous*	Mammalia	Canidae	Brazil	KC127679; KC127680	(Almeida et al., 2013)	18S rRNA
Hepatozoon sp.	*Cerdocyon thous*	Mammalia	Canidae	Brazil	KT881501; KT881521; KT881528; KT881512; KT881502; KT881524; KT881515; KT881530; KT881504; KT881514; KT881518; KT881529; KT881508; KT881500; KT881509; KT881505; KT881519; KT881519; KT881535; KT881511; KT881525; KT881532; KT881510; KT881506; KT881516; KT881507; KT881522; KT881526; KT881533; KT881517; KT881513; KT881520; KT881527; KT881523	(Sousa et al., 2017)	18S rRNA
Hepatozoon sp	*Cerdocyon thous*	Mammalia	Canidae	Brazil	KT873277; KT873268; KT873269; KT873280; KT873272; KT873275; KT873271; KT873270; KT873273; KT873274; KT873278; KT873279; KT873282; KT873283; KT873263;	(Sousa et al., 2017)	18S rRNA

					KT873262; KT873284; KT873260; KT873265; KT873267; KT873276; KT873266;KT873264; KT873285;		
Hepatozoon sp.	*Chrysocyon brachyurus*	Mammalia	Canidae	Brazil	MK424119	(Perles et al., 2019)	18S rRNA
Hepatozoon sp.	*Chrysocyon brachyurus*	Mammalia	Canidae	Brazil	KU507416	(Yamamoto et al., 2017)	18S rRNA
Hepatozoon sp.	*Clethrionomys glareolus*	Mammalia	Cricetidae	Slovakia	KJ649313	(Hamšíková et al. 2016)	18S rRNA
Hepatozoon sp.	*Crocuta crocuta*	Mammalia	Canidae	Tanzania	EF188809	(East et al. 2006)	18S rRNA
Hepatozoon sp.	*Crotalus durissus terrificus*	Reptilia	Viperidae	Brazil	KC342522; KC342523; KC342524; KC342525; KC342526; KC342527; KC342528;	(O'Dwyer et al., 2013)	18S rRNA
Hepatozoon sp.	*Crotalus molossus*	Reptilia	Viperidae	Mexico	MT385834; MT385835	Unpublished	18S rRNA
Hepatozoon sp.	*Dendroaspis polylepis; various species; Morelia viridis*	Reptilia	Elapidae; Pythonidae	Indonesia; Swaziland	KC866367; KC866368; KC866369; KC866370	(Haklová et al., 2013)	18S rRNA

Hepatozoon sp.	*Dermacentor atrosignatus*	Arachnida	Ixodidae	Thailand	JQ751276	(Sumrandee et al., 2015)	18S rRNA
Hepatozoon sp.	*Dermacentor auratus*	Arachnida	Ixodidae	Thailand	KF318170; KF318171; KF318169	(Sumrandee et al., 2015)	18S rRNA
Hepatozoon sp.	*Didelphis marsupialis*	Mammalia	Didelphidae	Brazil	MK257775	(Cole et al., 2019)	18S rRNA
Hepatozoon sp.	*Dipsas mikanii*	Reptilia	Dipsadidae	Brazil	MW591599; MW591556	(Úngari et al., 2021)	18S rRNA
Hepatozoon sp.	*Dromiciops gliroides; Abrothrix olivaceus*	Mammalia	Microbiotheriidae	Chile	FJ719818; FJ719815; FJ719817; FJ719813; FJ719816; FJ719819; FJ719814;	(Merino et al., 2009)	18S rRNA
Hepatozoon sp.	*Echis coloratus*	Reptilia	Viperidae	Saudi Arabia	MN497412	(Abdel-Baki et al., 2020)	18S rRNA
Hepatozoon sp.	*Felis catus*	Mammalia	Felidae	Brazil	KP410283	(André et al., 2015)	18S rRNA
Hepatozoon sp.	Various species	Reptilia	Lacertidae	Brazil	KM234615; KM234614; KM234617; KM234618; KM234613; KM234612; KM234616	(Harris et al., 2015)	18S rRNA
Hepatozoon sp.	*Gerbilliscus leucogaster*	Mammalia	Muridae	South Africa	KU955995; KU955996; KU955997	(Harris et al., 2016)	18S rRNA

Hepatozoon sp.	*Haemaphysalis hystricis*	Arachnida	Ixodidae	Japan	LC169077	(Masatani et al., 2017)	18S rRNA
Hepatozoon sp.	*Haemaphysalis sulcata*	Arachnida	Ixodidae	Turkey	MK918613; MK918614	(Orkun et al., 2020)	18S rRNA
Hepatozoon sp.	*Helicops angulatus*	Amphibia	Colubridae	Brazil	MT561455	Unpublished	18S rRNA
Hepatozoon sp.	*Hipposideros cervinus*	Mammalia	Hipposideridae	Malaysia	KC848055; KC848056; KC848057	(Pinto et al., 2013)	18S rRNA
Hepatozoon sp.	*Isoodon macrourus*	Mammalia	Peramelidae	Australia	KX361174; KX361175; KX361177; KX361176;	(Barbosa et al., 2017)	18S rRNA
Hepatozoon sp.	*Isoodon obesulus*	Mammalia	Peramelidae	Australia	EF152221; EF152222; EF152223; EF152224; EF152230; EF152229; EF152228; EF152220; EF152225; EF152219; EF152226; EF152227; EF152218	(Wicks et al., 2006)	18S rRNA
Hepatozoon sp.	*Ixodes hexagonus*	Arachnida	Ixodidae	Germany	JX679178	(Najm et al., 2014)	18S rRNA
Hepatozoon sp.	*Ixodes persulcatus*	Arachnida	Ixodidae	China	KX016028; KX016029	(Wei et al., 2016)	18S rRNA
Hepatozoon sp.	*Ixodes tasmani from*	Arachnida	Ixodidae	Australia	EU430238; EU430237; EU430236; EU430234; EU430231; EU430232;	(Vilcins et al., 2009)	18S rRNA

	Sarcophilus harrisii				EU430240; EU430235; EU430233; EU430239		
Hepatozoon sp.	*Kinosternon scorpioides*	Reptilia	Testudinidae	Brazil	KY684006; KY684007; KY684004; KY684005	(Yamamoto et al., 2017)	18S rRNA
Hepatozoon sp.	*Leopardus tigrinus*	Mammalia	Felidae	Brazil	FJ876446; FJ876448; FJ876445; FJ876444; FJ876447	(André et al., 2010)	18S rRNA
Hepatozoon sp.	*Leptodactylus*	Amphibia	Leptodactylidae	Brazil	JX987775	(Leal et al., 2015)	18S rRNA
Hepatozoon sp.	*Leptodactylus latrans*	Amphibia	Leptodactylidae	Brazil	MW584362; MW584361; MW584356; MW584365	(Ungari et al., 2021)	18S rRNA
Hepatozoon sp.	*Liasis fuscus*	Reptilia	Pythonidae	Australia	AY252105; AY252104; AY252106; AY252109; AY252107; AY252108; AY252111; AY252110; AY252103	(Ujvari et al., 2004)	18S rRNA
Hepatozoon sp.	*Lithobates vaillanti*	Amphibia	Ranidae	Mexico	MN816297	(Isaak-Delgado et al., 2020)	18S rRNA
Hepatozoon sp.	*Lycalopex culpaeus*	Mammalia	Canidae	Chile	MW633713; MW633712; MW633710; MW633709; MW633711	Unpublished	18S rRNA
Hepatozoon sp.	*Lycalopex griseus*	Mammalia	Canidae	Argentina	MK049948; MK049949; MK049950; MK049951	(Millán et al., 2019)	18S rRNA
Hepatozoon sp.	*Lycaon pictus*	Mammalia	Canidae	South Africa	MW676058; MW676059; MW676060; MW676061;	(Netherlands et al., 2021)	18S rRNA

					MW676065; MW676118; MW676111; MW676097; MW676100; MW676078; MW676085; MW676095; MW676083; MW676089; MW676110; MW676062; MW676091; MW676112; MW676079; MW676094; MW676093; MW676077; MW676096; MW676090; MW676070; MW676074;	MW676082; MW676113; MW676114; MW676086; MW676103; MW676088; MW676087; MW676092; MW676084; MW676099; MW676115; MW676068; MW676098; MW676102; MW676104; MW676067; MW676063; MW676117; MW676109; MW676064; MW676075; MW676071;		

					MW676101; MW676066; MW676072; MW676119; MW676108; MW676069; MW676069; MW676073; MW676116; MW676107; MW676120; MW676076; MW676081; MW676106; MW676080; MW676105; MW676121;		
Hepatozoon sp.	*Mabuya wrightii*	Reptilia	Scincidae	Seychelles	HQ292771; HQ292772; HQ292773; HQ292774; HQ292775	(Harris et al., 2011)	18S rRNA
Hepatozoon sp.	*Macrovipera lebetina obtusa*	Reptilia	Viperidae	Iran	MZ208822; MZ208821; MZ208827	Unpublished	18S rRNA
Hepatozoon sp.	*Madagascarophis colubrinus*	Reptilia	Lamprophiidae	Madagascar	KM234647	(Maia et al., 2014)	18S rRNA
Hepatozoon sp.	*Malpolon monspessulanus*	Reptilia	Colubridae	Morocco	JX244266; JX244267; JX244268; JX244269;	(Tomé et al., 2012)	18S rRNA
Hepatozoon sp.	*Martes martes*	Mammalia	Mustelidae	Spain	EF222257; EF222256;	(Criado-Fornelio et al., 2009)	18S rRNA

Hepatozoon sp.	*Martes martes*	Mammalia	Mustelidae	Scotland	EU686690	(Simpson et al., 2005)	18S rRNA
Hepatozoon sp.	*Martes melampus melampus*	Mammalia	Mustelidae	Japan	FJ595127; FJ595128; FJ595129; FJ595130; FJ595131; FJ595132; FJ595133; FJ595134	(Kubo et al., 2009)	18S rRNA
Hepatozoon sp.	*Mauremys leprosa*	Reptilia	Geoemydidae	Spain	KJ740753; KJ740754	Unpublished	18S rRNA
Hepatozoon sp.	*Meles meles*	Mammalia	Mustelidae	Spain	KU198330	(Barandika et al., 2016)	18S rRNA
Hepatozoon sp.	*Microtus sp*	Mammalia	Cricetidae	Turkey	MN340278; MN340276; MN340277; MN340279; MN340284; MN340280; MN340281; MN340282; MN340283; MN340277; MN340275; MN340274	Unpublished	18S rRNA
Hepatozoon sp.	*Myodes glareolus*	Mammalia	Cricetidae	Hungary	JX644997; JX644998; JX644996	Unpublished	18S rRNA
Hepatozoon sp.	*Myodes glareolus*	Mammalia	Cricetidae	Netherlands; Croatia	MH656731; MH656732; MH656729; MH656730; MH656728; MH656727	Unpublished	18S rRNA
Hepatozoon sp.	*Myodes glareolus*	Mammalia	Cricetidae	Slovakia	MH784529; MH784530; MH784531; MH784532	Unpublished	18S rRNA

Hepatozoon sp.	*Myodes glareolus*	Arachnida	Ixodidae	Germany	JQ886023	(Silaghi et al., 2012)	18S rRNA
Hepatozoon sp.	*Myodes rutilus*	Mammalia	Muridae	Japan	LC189478; LC189479	(Moustafa et al., 2017)	18S rRNA
Hepatozoon sp.	*Nasua nasua*	Mammalia	Procyonidae	Brazil	KF516510	Unpublished	18S rRNA
Hepatozoon sp.	*Neophron percnopterus*	Aves	Accipitridae	Israel	MF541372; MF541371; MF541370	Unpublished	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	China	KF939620; KF939621; KF939622; KF939623; KF939624; KF939625; KF939626; KF939627; KF939628	Unpublished	18S rRNA
Hepatozoon sp.	Not available	Arthropoda	Not available	Not available	MT114683	Unpublished	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	Not available	KU667309; MN512148KU667308	(Demoner et al., 2016)	18S rRNA
Hepatozoon sp.	Not available	Reptilia	Alligatoridae	Brazil	KJ425235	(Bouer et al., 2017)	18S rRNA
Hepatozoon sp.	Various species	Not available	Not available	Brazil	MG925078; MG925091; MG925086; MG925079; MG925080; MG925081; MG925082; MG925085; MG925083; MG925092; MG925090; MG925088;	(Perles et al., 2019)	18S rRNA

					MG925089; MG925093; MG925094; MG925084; MG925087		
Hepatozoon sp.	Not available	Not available	Not available	Not available	MW810626; MW810627; MW810628; MW810629; MW810630; MW810631	Unpublished	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	Yemen	MW076443; MW076444; MW076449; MW076446; MW076448; MW076445; MW076447	(Tomé et al., 2021)	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	Zimbabwe	KJ598887; KJ598886	(Kelly et al., 2014)	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	South Africa	MH924605; MH924606; MH924607; MH924608; MH924609; MH924610; MH924611; MH924612; MH924613; MH924614; MH924604	(Harris et al., 2018)	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	Poland	EU908289	Unpublished	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	USA	KR262503; KR262504; KR262499; KR262502; KR262500	(Campana et al., 2016)	18S rRNA

Hepatozoon sp.	Not available	Mammalia	Muridae	USA	EF620026; EF620027	(Johnson et al., 2007)	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	Brazil	LC417346; LC417342; LC417343; LC417344; LC417345; LC417341	(Calil et al., 2019)	18S rRNA
Hepatozoon sp.	Not available	Not available	Not available	Equador	JQ080304; JQ080302; JQ080303	(Bataille et al., 2012)	18S rRNA
Hepatozoon sp.	Not available	Mammalia	Muridae	Sweden	MK071735	(Gondard et al., 2020)	18S rRNA
Hepatozoon sp.	*Oceanodroma melani*	Aves	Hydrobatidae	Mexico	KF022102	(Merino et al., 2014)	18S rRNA
Hepatozoon sp.	*Oecomys mamorae*	Mammalia	Cricetidae	Brazil	KX776332; KX776327; KX776336; KX776388; KX776383	(Sousa et al., 2016)	18S rRNA
Hepatozoon sp.	*Oligoryzomys longicaudatus; Abrothrix olivaceus;*	Mammalia	Cricetidae	Chile	MH594207; MH594206; MH594205; MH594204; MH594208	Unpublished	18S rRNA
Hepatozoon sp.	*Oligoryzomys longicaudatus*	Mammalia	Cricetidae	Chile	MW881033; MW881032; MW881034; MW881035	Unpublished	18S rRNA
Hepatozoon sp.	*Ornithodoros atacamensis*	Arachnida	Argasidae	Chile	MH174343; MH174344; MH174345	(Muñoz-Leal et al., 2019)	18S rRNA

Hepatozoon sp.	*Ornithodoros rietcorreai*	Arachnida	Argasidae	Brazil	MF383348; MF383349; MF383350	Unpublished	18S rRNA
Hepatozoon sp.	*Panthera pardus pardus*	Mammalia	Felidae	South Africa	MN792996; MN792997; MN792998; MN792999	(As et al., 2019)	18S rRNA
Hepatozoon sp.	*Pelophylax perezi*	Amphibia	Ranidae	Portugal	KF733812	(Harris et al., 2013)	18S rRNA
Hepatozoon sp.	*Peromyscus gossypinus;* various species	Mammalia	Muridae	USA	MN012924; MN012925; MN012931; MN012928; MN012929; MN012930; MN012926; MN012927	(Yamamoto et al., 2017)	18S rRNA
Hepatozoon sp.	*Peromyscus leucopus*	Mammalia	Cricetidae	USA	KM225833	(Harris et al., 2015)	18S rRNA
Hepatozoon sp.	*Philodryas patagoniensis*	Reptilia	Colubridae	Uruguay	MN003368; MN003357; MN003356; MN003367; MN003369; MN003370; MN003360; MN003359; MN003364; MN003361; MN003363; MN003365; MN003366; MN003358; MN003362	(Bazzano et al., 2020)	18S rRNA

Hepatozoon sp.	*Philothamnus semivariegatus; Mehelya capensis*	Reptilia	Colubridae; Lamprophiidae	Africa; Asia; USA	KC800702; KC800704; KC800706; KC800703	(Haklová et al., 2014)	18S rRNA
Hepatozoon sp.	*Phymaturus calcogaster*	Reptilia	Liolaemidae	Not available	KX387860; KX387861	Unpublished	18S rRNA
Hepatozoon sp.	*Podarcis;* various species	Reptilia	Lacertidae	Portugal	KJ189389; KJ189390; KJ189391; KJ189392; KJ189393; KJ189394; KJ189395; KJ189396; KJ189398; KJ189399; KJ189402; KJ189404; KJ189405; KJ189406; KJ189407; KJ189408; KJ189409; KJ189414; KJ189416; KJ189419; KJ189420; KJ189423; KJ189426; KJ189427; KJ189428; KJ189429; KJ189430; KJ189431; KJ189432; KJ189433; KJ189421; KJ189411; KJ189417; KJ189397; KJ189401; KJ189412; KJ189413; KJ189387; KJ189388; KJ189400; KJ189425; KJ189418; KJ189410; KJ189422; KJ189403; KJ189415; KJ189424; KJ499500;	(Harris, et al., 2014)	18S rRNA

					KJ189435; KJ189438; KJ189439; KJ189444; KJ189445; KJ189446; KJ189447; KJ189448; KJ189450; KJ189455; KJ189456; KJ189459; KJ189460; KJ189437; KJ189453; KJ189454; KJ189461; KJ189443; KJ189434; KJ189449; KJ189463; KJ189440; KJ189441; KJ189451; KJ189442; KJ189452; KJ189436		
Hepatozoon sp.	*Podarcis bocagei; Podarcis hispânica;* Various species	Reptilia	Lacertidae	Portugal; Spain	JX531921; JX531907; JX531908; JX531909; JX531910; JX531911; JX531912; JX531913; JX531914; JX531915; JX531916; JX531917; JX531918; JX531919; JX531920; JX531924; JX531925; JX531926; JX531927; JX531928; JX531930; JX531931; JX531932; JX531933; JX531935; JX531936; JX531937; JX531938; JX531939; JX531942; JX531943; JX531944; JX531945; JX531946; JX531949;JX531950; JX531951; JX531952; JX531934;	(Tomé et al., 2018)	18S rRNA

					JX531922; JX531923; JX531941; JX531954; JX531948; JX531929; JX531940; JX531953; JX531955; JX531956; JX531958; JX531960; JX531961; JX531963; JX531964; JX531965; JX531966; JX531969; JX531970; JX531971; JX531972; JX531968; JX531962; JX531967; JX531957; JX531959		
Hepatozoon sp.	*Podarcis hispânica*	Reptilia	Lacertidae	Spain	JQ762308; JQ762309; JQ762310; JQ762311	(Harris et al., 2012)	18S rRNA
Hepatozoon sp.	*Podarcis muralis*	Reptilia	Lacertidae	Italy	KU529653	(Panelli et al., 2016)	18S rRNA
Hepatozoon sp.	*Podocnemis unifilis*	Reptilia	Podocnemididae	Colombia	MW246123	(Gutiérrez-Liberato et al., 2021)	18S rRNA
Hepatozoon sp.	*Prionailurus bengalensis*	Mammalia	Felidae	Thailand	GQ926902; GQ926901	(Salakij et al., 2008)	18S rRNA
Hepatozoon sp.	*Psammophis schokari;* various species	Reptilia	Lamprophiidae	Algeria	KC696565; KC696569; KC696567; KC696568; KC696566; KC696564	(Tomé et al., 2013)	18S rRNA

Hepatozoon sp.	*Psammophis schokari*	Reptilia	Colubridae	Not available	JQ746622	(Abdel-Baki et al., 2014)	18S rRNA
Hepatozoon sp.	*Ptyas mucosa*	Reptilia	Colubridae	India	MG249965	Unpublished	18S rRNA
Hepatozoon sp.	*Python sebae*	Reptilia	Viperidae	Mauritania	KR653312; KR653313	(Rosado et al., 2015)	18S rRNA
Hepatozoon sp.	*Rana forreri*	Amphibia	Ranidae	Not available	MN255489	(Léveillé et al., 2021)	COIII
Hepatozoon sp.	*Rattus exulan*	Mammalia	Muridae	French	MT932305; MT932306; MT932307; MT932308	(Hrazdilova et al., 2020)	Cytb
Hepatozoon sp.	*Rattus exulans*	Mammalia	Muridae	France	MT932268; MT932267; MT932265; MT932266	(Hrazdilova et al., 2021)	COI
Hepatozoon sp.	*Rattus norvegicus*	Mammalia	Muridae	Chile	MH216198; MH216196; MH216199; MH216195; MH216197	Unpublished	18S rRNA
Hepatozoon sp.	*Rattus norvegicus; mus musculus; Vulpes vulpes;* various species	Mammalia	Muridae; Canidae	Chile	MK454898; MK454892; MK454900; MK454897; MK757741; MK757743; MK757745; MK757782; MK757747; MK757753; MK757764; MK757742; MK757746; MK757773; MK757779; MK757794;	Unpublished	18S rRNA

					MK757758; MK757787; MK757760; MK454894; MK757744; MK454893; MK454896; MK454899; MK757748; MK454901; MK454903; MK757775; MK757749; MK454902; MK454895		
Hepatozoon sp.	*Rattus norvegicus; Cricetomys ganbiamus*	Mammalia	Muridae	Nigeria	MG786593; MG786594; MG786595; MG786596	(Kamani et al., 2018)	18S rRNA
Hepatozoon sp.	*Rattus rattus; Rattus exulans; Ratus norvegicus*	Mammalia	Muridae	France	MT919388; MT919387; MT919389	(Hrazdilova et al., 2021)	18S rRNA
Hepatozoon sp.	*Rhinella diptycha; Leptodactylus latrans*	Amphibia	Bufonidae; Leptodactylidae	Brazil	MK503647; MK503646; MK503648; MK503645; MK503643	(Ferreira et al., 2020)	18S rRNA

Hepatozoon sp.	*Rhinella diptycha; Leptodactylus latrans*	Amphibia	Bufonidae; Leptodactylidae	Brazil	MK508987; MK508989; MK508985; MK508984; MK508986; MK508988	(Ferreira et al., 2020)	18S rRNA
Hepatozoon sp.	*Rhinoclemmys melanosterna*	Arachnida	Ixodidae	Colombia	MT754271; MT754266	(Gutiérrez-Liberato et al., 2021)	18S rRNA
Hepatozoon sp.	Various species.	Reptilia	Iguanidae	Mexico	MG456822; MG456821; MG456824; MG456823; MG456818; MG456819; MG456817; MG456820	Unpublished	18S rRNA
Hepatozoon sp.	*Scelarcis perspicillata; Tarentola mauritanica;* various species	Reptilia	Lacertida; Phyllodactylidae; Sphaerodactylidae; various	Morocco	HQ734791; HQ734792; HQ734787; HQ734788; HQ734789; HQ734790; HQ734806; HQ734807; HQ734809; HQ734808; HQ734793; HQ734794; HQ734795; HQ734796; HQ734797; HQ734798; HQ734799; HQ734800; HQ734801; HQ734802;	(Maia et al., 2011)	18S rRNA

					HQ734803; HQ734804; HQ734805		
Hepatozoon sp.	*Sciurus vulgaris*	Mammalia	Sciuridae	Spain	EF222259	(Criado-Fornelio et al., 2009)	18S rRNA
Hepatozoon sp.	*Sclerophrys arábica; Asaccus platyrhynchus;* various species	Amphibia; Reptilia	Bufonidae; Phyllodactylidae; various	Oman	KX453564; KX453569; KX453571; KX453573; KX453574; KX453575; KX453576; KX453578; KX453581; KX453582; KX453584; KX453585; KX453588; KX453589; KX453592; KX453594; KX453596; KX453599; KX453601; KX453602; KX453603; KX453605; KX453606; KX453611; KX453612; KX453614; KX453615; KX453616; KX453617; KX453618; KX453619; KX453621; KX453622; KX453623; KX453624; KX453628; KX453636; KX453638; KX453561; KX453563; KX453568; KX453577; KX453579; KX453583; KX453593; KX453598; KX453604; KX453607; KX453609; KX453620; KX453625;	(Maia et al., 2016)	18S rRNA

					KX453626; KX453629; KX453631; KX453640; KX453644; KX453565; KX453572; KX453580; KX453586; KX453591; KX453610; KX453570; KX453627; KX453558; KX453559; KX453560; KX453562; KX453566; KX453567; KX453633; KX453637; KX453642; KX453587; KX453597; KX453635; KX453639; KX453643; KX453630; KX453632; KX453646; KX453613; KX453608; KX453634; KX453540; KX453541; KX453542; KX453544; KX453545; KX453546; KX453547; KX453548; KX453549; KX453550; KX453551; KX453552; KX453553; KX453554; KX453555; KX453556; KX453557; KX453558; KX453562; KX453543;		
Hepatozoon sp.	*Sclerophrys arabica*	Amphibia	Bufonidae	Oman	KY091311	(Maia et al., 2016)	18S rRNA
Hepatozoon sp.	*Snake*	Reptilia	Not available	India	MH107332	Unpublished	18S rRNA

Hepatozoon sp.	*Sus scrofa leucomystax*	Mammalia	Suidae	Japan	LC505379; LC505380; LC505381; LC505382; LC505383; LC505384; LC505385; LC505386; LC505387	(Sugita-Konishi et al., 2019)	18S rRNA
Hepatozoon sp.	*Sus scrofa leucomystax*	Mammalia	Suidae	Japan	LC062147	Unpublished	18S rRNA
Hepatozoon sp.	*Sylvilagus floridanus*	Mammalia	Leporidae	USA	FJ895406; FJ895407;	(Johnson et al., 2009)	18S rRNA
Hepatozoon sp.	*Tarentola boehmei; Tarentola deserti ;* various species	Reptilia	Phyllodactylidae	Morocco	KU680458; KU680456; KU680466; KU680457; KU680465; KU680464; KU680462; KU680463; KU680461; KU680460; KU680459; KU680455; KU680443; KU680446; KU680451; KU680425; KU680426; KU680428; KU680429; KU680430; KU680431; KU680432; KU680433; KU680440; KU680442; KU680444; KU680448; KU680449; KU680450; KU680424; KU680434; KU680422; KU680427; KU680421; KU680435; KU680436; KU680437; KU680438; KU680439; KU680423; KU680453; KU680447;	(Tomé et al., 2008)	18S rRNA

					KU680445; KU680454; KU680452; KU680441		
Hepatozoon sp.	*Tarentola delalandii; Gallotia atlantica; Gallotia galloti; Gallotia stehlini; Gallotia caesaris; Chalcides viridanus; Psammodromus algirus*	Reptilia	Phyllodactylidae; Lacertidae; Scincidae	Spain; Morocco	MG787251; MG787243; MG787244; MG787245; MG787246; MG787248; MG787247; MG787249; MG787250; MG787252; MG787253	(Tomé et al., 2018)	18S rRNA
Hepatozoon sp.	*Teira dugesii*	Reptilia	Lacertidae	Portugal	MH201399; MH201397; MH201398; MH201396	Unpublished	18S rRNA
Hepatozoon sp.	*Ticks*	Arachnida	Ixodidae	China	KX890094	(Liu et al., 2016)	18S rRNA
Hepatozoon sp.	*Trogonophis wiegmanni*	Reptilia	Trogonophidae	Morocco	MN512148	(Harris et al., 2020)	18S rRNA
Hepatozoon sp.	*Varanus salvator*	Reptilia	Varanidae	Thailand	HM585203; HM585204; HM585205; HM585206; HM585207; HM585208;	(Salakij et al., 2014)	18S rRNA

	salvator; various species				HM585209; HM585210; HM585211; HM585212; HQ317909; HQ317910; HQ317911		
Hepatozoon sp.	Various species	Amphibia; Reptilia	Ranidae; Colubridae	USA	HQ224960	(Barta et al., 2012)	18S rRNA
Hepatozoon sp.	Various species	Mammalia	Various	Spain	AY600626	(Criado-Fornelio et al., 2006)	18S rRNA
Hepatozoon sp.	*Rana pipiens*	Amphibia	Ranidae	Canada	MN244530	(Léveillé et al., 2020)	18S rRNA ; ITS1; 5.8S ribosomal RNA
Hepatozoon sp.	*Vulpes vulpes*	Mammalia	Canidae	USA	KF989489	(Kistler et al., 2014)	18S rRNA
Hepatozoon tenuis	*Afrixalus fornasini;* various species	Amphibia	Hyperoliidae	South Africa	MG041596; MG041597; MG041595; MG041598; MG041599; MG041591; MG041592; MG041593; MG041594	(Netherlands et al., 2018)	18S rRNA
Hepatozoon theileri	*Amietia delalandii*	Amphibia	Pyxicephalidae	South Africa	MG041605	(Netherlands et al., 2018)	18S rRNA

Hepatozoon theileri	*Amietia quecketti*	Amphibia	Ranidae	South Africa	KJ599676	(Netherlands et al., 2014)	18S rRNA
Hepatozoon thori	*Hyperolius marmoratus*	Amphibia	Hyperoliidae	South Africa	MG041602; MG041600; MG041601; MG041603; MG041604	(Netherlands et al., 2018)	18S rRNA
Hepatozoon tuatarae	*Sphenodon*	available Reptilia	Sphenodontidae	New Zealand	GU385470; GU385471; GU385472; GU385473;	(Herbert et al., 2010)	18S rRNA
Hepatozoon ursi	*Melursus ursinus*	Mammalia	Ursidae	India	HQ829437	(Pawar et al., 2011)	18S rRNA
Hepatozoon ursi	*Melursus ursinus*	Mammalia	Ursidae	India	HQ829429; HQ829432	(Pawar et al., 2011)	18S rRNA
Hepatozoon ursi	*Ursus arctos; various species*	Mammalia	Ursidae; Felidae	Turkey	MN150504; MN150506; MN150505; MN905023; MN905025; MN905024	(Orkun et al., 2020)	18S rRNA
Hepatozoon ursi	*Ursus arctos*	Mammalia	Ursidae	Turkey	KT274180	(Orkun & Emir, 2020)	18S rRNA
Hepatozoon ursi	*Ursus thibetanus japonicus*	Mammalia	Ursidae	Japan	EU041717; EU041718;	(Kubo et al., 2008)	18S rRNA
Hepatozoon ursi	*Ursus thibetanus japonicus*	Mammalia	Ursidae	Japan	EU041718	(Kubo et al., 2008)	18S rRNA

Hepatozoon ursi	*Ursus thibetanus japonicus*	Mammalia	Ursidae	Japan	LC431853; LC431855; LC431854	(Moustafa et al., 2020)	18S rRNA
Hepatozoon ursi	*Ursus thibetanus japonicus*	Mammalia	Ursidae	Japan	AB586028	(Ikawa et al., 2011)	18S rRNA