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Leishmania in Marsupials—An Overview of Infection Records in the Americas and Australia

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Abstract

Marsupials have been the subjects of studies of both experimental and natural infections with different species of *Leishmania* in the Americas as well as Australia. Over a century has passed since the first description of a mammal being infected with *Leishmania* and since then several reviews have been published on the systematics of the parasites as well as their hosts. Consequently, an update of this information is needed in order to assure correct identification of the species involved in each case. A comprehensive review was undertaken and included most of the records of marsupials being infected with *Leishmania* sp. Emphasis was placed on parasitological, eco epidemiological and taxonomic information of both the parasites and mammalian hosts. The clinical profiles of the infections varied from severe, which principally occurred in experimentally infected animals, to asymptomatic, which was typical of natural infections. Marsupials must be considered one of the most important groups of mammalian hosts of *Leishmania* sp. Important factors, such as their ancient origin, wide geographical distribution and susceptibility to infections by different species of *Leishmania,* but with considerable resistance to the disease, could indicate that didelphids play a key role in the evolution of *Leishmania* in the New World.

Keywords

Leishmania, Marsupials, Wild Hosts, Americas, Australia

1. Introduction

Leishmaniasis is a vector-borne disease caused strictly by intracellular parasitic protozoa of the genus *Leishmania*. Its geographic distribution covers approximately 88 countries where almost 350 million people live. The majority of these countries are in the tropics and subtropics, and include the USA, the rain forests of Central and South America, Australia and the deserts of western Asia.

The insect vectors of *Leishmania* comprise a dozen species of sand flies belonging two genera: *Phlebotomus* in the Old World and *Lutzomyia* in the New World.

Mammalian hosts of *Leishmania* are very diverse in comparison to the vectors, with nearly 100 species from more than 10 orders. This diversity plays a key role in the maintenance of these parasites in nature, and is one of the most important factors in determining their dispersion and diversity.

Among the New World mammalian groups that serve as reservoirs of *Leishmania* spp., marsupials must be considered one of the most important. This infraclass occurs predominantly in the New World and Australasia and represents a monophyletic group derived from the last common ancestor of extant metatherians.

Marsupials are characterized by giving birth to relatively immature litters that, in most cases, complete their development in the mother's pouch. Approximately 70% of the extant species of marsupials occur in Australia, New Guinea, and adjacent islands, with the remaining diversity occurring in the New World, mainly in South America but also in Central and North America well north of Mexico [1].

Marsupials in the Americas belong to the Superorder Ameridelphia, which is composed of two families: the Didelphidae (opossums) and the Caenolestidae (shrew opossums). Marsupials in Australasia belong to the Superorder Australidelphia, which contains 17 extant families: Microbiotheriidae, Dasyuridae, Myrmecobiidae, Thylacomyidae, Peramelidae, Notoryctidae, Phascolarctidae, Vombatidae, Phalangeridae, Burramyidae, Tarsipedidae, Petauridae, Pseudocheiridae, Potoroidae, Acrobatidae, Hypsiprymnodontidae and Macropodidae [1].

The ecology of marsupials is substantially diverse, and is indicative of their remarkable diversification in Australia and the Americas. Marsupials inhabit virtually all of the same niches that placental mammals do, and occur in every major terrestrial habitat. As a group, marsupials also possess diverse diets including carnivory, herbivory and omnivory, and species capable of feeding on a wide range of food sources [2].

In spite of initially being considered only as secondary reservoir of *Leishmania* spp., marsupials have come to be accepted as playing a very important role in the epidemiology of leishmaniasis by acting as sylvatic and/or synanthropic hosts. There have been several reports describing natural and experimental infections of marsupials by different species of *Leishmania* belonging both subgenera *L.* (*Leishmania*) and *L.* (*Viannia*).

Over a century has passed since the discovery of *Leishmania* spp. and several revisions have been published on the systematics of the parasite as well as of their hosts. Therefore, periodic updates are very important for assuring correct identification of the species involved.

The aim of the present review is to provide detailed information about the species of marsupials that have documented cases of their infection, naturally or experimentally, with *Leishmania* spp. Aspects of the biology, systematics and parasites of these species are also addressed.

1.1. Marsupial Hosts of *Leishmania* in the Americas

As we are going to show, all of the studies involving infections of marsupials with *Leishmania* in the New World have been with species of the family Didelphidae. These cases included 8 out of 19 extant didelphid genera: *Didelphis*, *Marmosa*, *Metachirus*, *Caluromys*, *Phylander*, *Monodelphis*, *Marmosops* and *Gracilinanus* (Figure 1).

Figure 1. Geographical distribution of records of infection with *Leishmania* spp. in different didelphid genera in the Americas from 1962 to 2015. All data were mapped through ArchView software using geographical coordinates provided by the authors or estimated based on reference points provided in the studies and utilizing ArchView and Google Earth.

1.2. Didelphidae

The family Didelphidae is certainly one of the main groups of mammals in the life cycle of *Leishmania* because of the importance of many of its species as reservoir hosts. These species are among the best-studied mammalian hosts of *Leishmania* with a great number of records of infections. Furthermore, *Didelphis* is the only genus of New World marsupials that have already been experimentally infected with the parasite.

After *Didelphis*, the genus *Marmosa* must be considered second in importance with 18 records of infections [15 in *M.* (*Marmosa*) and 3 in *M.* (*Micoreus*)]; followed by *Metachirus*, *Gracilinanus* and *Caluromys*, with 2 records each, and *Phylander*, *Monodelphis* and *Marmosops*, with one each.

2. The Genus *Didelphis* (Opossums)

Opossums possess several important features that facilitate their role as reservoir hosts of *Leishmania* spp., including an ancient origin; a wide geographic distribution, occurring from the USA to Argentina; and inhabiting various habitats where *Leishmania* are endemic (**Figure 1**). Unlike other sylvatic mammalian hosts, species of *Didelphis* characteristically adapt easily to anthropic habitats, being able to take part in both sylvatic and peri-domestic parasite cycles, and can even serve as a link between them.

Initially the genus *Didelphis* contained three species [3]: *D. virginiana* occurring in North and Central America; *Didelphis marsupialis* living predominantly in South America, but sympatric with the former in Central America; and *D. albiventris* described from higher altitudes in South America. Subsequently, three new species were recognized, *D. aurita*, *D. pernigra and D. imperfect* [3] [4] [5], bringing the total number of species of *Didelphis* to six.

2.1. *Didelphis* and *Leishmania*

Among the six extant species of the genus *Didelphis*, infection with *Leishmania* has been previously documented for four: *D. marsupialis*, *D. albiventris*, *D. aurita and D. virginiana*. In the present study, we report for the first time the infection of *D. pernigra* in Peru. This species was previously considered as *D. albiventris*, but was recognized as a distinct species with the revision of the genus [6].

2.2. *Didelphis* in Brazil

2.2.1. *D. marsupialis* (Common Opossum)

All records of *Leishmania* spp. infection of *D. marsupialis* in Brazil are natural infections, and most were in the states of Amazonas and Para in the Amazon Region (**Table 1**).

In Amazonas, Arias and Naiff [7] [8] emphasized the importance of *D. marsupialis* as a reservoir host of the *L. guyanensis* in disturbed primary forest because of the high levels of infection they observed, varying from 20% to 71%. 4% depending on the area studied. The same studies also found considerable infection

Table 1. List of records of marsupials infected with *Leishmania* spp. in Brazil. Data provided include the states where the studies were carried out, the mammalian host species, the parasite species, the type of infection and the diagnostic methods and references.

State	Marsupial species	*Leishmania* species	Type of infection-%	Method	Ref
Bahia	*Didelphis albiventris*	*L. infantum*	N-1 case	H	Sherlock *et al.* 1984
		L. infantum	N-2.4%	H, C	Sherlock *et al.* 1988
		L. braziliensis	N-1.2%	H, C	Sherlock *et al.* 1988
		L. amazonensis	N-1.2%	H, C	Sherlock *et al.* 1988
Pernambuco		*L. braziliensis*	N-13.5%	I, MB	Brandão-Filho *et al.* 2003
São Paulo		*Leishmania* spp	N-91.6%	Elisa, MB	Santiago *et al.* 2007
		L. braziliensis	N-1.6%	MB	Quintal *et al.* 2011
Minas Gerais		*L. braziliensis*	N-28.6%	C, MB	Quaresma *et al.* 2011
Pernambuco		*L. infantum*	N-6.3%	MB, K39, C	Lima *et al.* 2013
		Leishmania (*V*) spp	N-37.5%	MB, K39, C	Lima *et al.* 2013
Rio Grande do Norte		*Leishmania infantum*	N-5%	MB	Costa *et al.* 2014
Amazonas	*Didelphis marsupialis*	*L. guyanensis*	N-20-71%	X, C, H, Iso	Arias and Naiff 1981
		L. amazonensis	N-4.7-25%	X, C, H, Iso	Arias and Naiff 1981
		L. guyanensis	N-20-71%	H, C	Arias and Naiff 1981
Pará		*L. amazonensis*	N/4.7%	C, H, Iso	Lainson *et al.* 1981
		L. guyanensis	N/4.7%	C, H, Iso	Lainson *et al.* 1981
Minas Gerais	(?)	*Leishmania* spp	N/21.6%	IFA, DAT, MB	Schallig *et al.* 2007
São Paulo	*Didelphis aurita*	*Leishmania* spp	N/NP	I, C, H	Yoshida *et al.* 1979
		L. mexicana	N/NP	MB	Yoshida *et al.* 1985
		L. forattinii	N/NP	C, MA, MB	Yoshida *et al.* 1993
		Leishmania spp	N/91.6%	ELISA, MB	Santiago *et al.* 2007
Rio de Janeiro		*L. infantum*	N/16.6%	I, MB	Carreira *et al.* 2012
Mato Grosso	*Marmosa murina*	*Leishmania* spp	N/7.7%	C, H	Lainson & Shaw 1969
		Leishmania spp	N/8%	S, C, H, H	Lainson & Shaw 1970
		L. amazonensis	N/NP	H, Iso	Miles *et al.* 1980
Pará		*Leishmania* spp	N/1 case	S, H, C	Lainson & Shaw 1969
Pernambuco	*Marmosa spp*	*L. braziliensis*	N/16.7%	I, MB	Brandão-Filho *et al.* 2003
		Leishmania (*V*) spp	N/25%	MB, K39, C	Lima *et al.* 2013
Amazonas	*Marmosa demerarae*[a]	*L. amazonensis*	N/100%	X, C, H, Iso	Arias *et al.* 1981
Pará	*Metachirus nudicaudatus*	*L. amazonensis*	N/NP	C, Iso	Miles *et al.* 1980
		L.amazonensis	N/66.7%	C, H, Iso	Lainson *et al.* 1981
São Paulo	*Marmosa paraguayanus*	*L. braziliensis*	N/33.3%	MB	Quintal *et al.* 2011
		L. amazonensis	N/66.7%	MB	Quintal *et al.* 2011
Minas Gerais	*Marmosops incanus*	*L. guyanensis*	N/50%	C, MB	Quaresma *et al.* 2011
Minas Gerais	*Gracilinanus agilis*	*L. braziliensis*	N/75%	C, MB	Quaresma *et al.* 2011
Brasilia		*Leishmania* spp	N/19%	MB	Cardoso *et al.* 2015
Pernambuco	*Monodelphis domestica*	*Leishmania* (*V*) spp	N/25%	MB, K39, C	Lima *et al.* 2013
Pará	*Philander opossum*	*L. amazonensis*	N/18%	C, H, Iso	Lainson *et al.* 1981

Natural infection (N), Histology (H), Culture (C), Imprint (I), Molecular Biology (MB), Xenodiagnosis (X), Isoenzyme (Iso), Indirect Immunofluorescence Assay (IFA), Dipstick Test (K-39), Direct Agglutination Test (DAT), Smear (S), Monoclonal Antibody (MA), Enzyme-linked Immunosorbent Assay (ELISA), not presented (NP), ([a]) Originally referred to by the authors as *Micoureus demerarae*.

of *D. marsupialis* with *L. amazonensis*, ranging from 4.7% to 25%.

In the state of Para, Lainson *et al.* [9] observed a lower level of infection than reported in Amazonas, on the order of 4.7% for both parasite species.

In addition to the records of *Leishmania* infection of *D. marsupialis* in the Amazon Region, there is one report of a prevalence of 21.6% among the *D. marsupialis* in the state of Minas Gerais [10]. However, it is quite probable that the species involved was *D. aurita* and not *D. marsupialis*, because the latter does not occur in the state of Minas Gerais.

2.2.2. *D. albiventris* (White-Eared Opossum)

Didelphis albiventris must be considered the second most important reserve host species of the genus *Didelphis*, with eleven records of infection with *L. infantum*, *L. braziliensis* and *L. amazonensis*. Ten of these cases were in Brazil where this species is the most cited in the genus, including the state of Bahia with *L. infantum*, *L. braziliensis* and *L. amazonensis*; the state of Pernambuco with *L. braziliensis* and *L.* (*Viannia*); the state of Rio Grande do Norte with *L. infantum*; the state of Minas Gerais with *L. braziliensis*; the state of São Paulo with *Leishmania* spp.; and the federal district of Brasilia with *Leishmania* spp (**Table 1**).

In the state of Bahia there have been three studies. The first [11] described a case of natural infection of one opossum with *L. infantum* in the city of Jacobina. This report was highlighted as the first record for the continent of a non-canid wild animal being naturally infected with the agent of visceral leishmaniasis. The same study also demonstrated that *D. albiventris* was the most abundant wild mammal around the houses in the area and that *Lutzomyia longipalpis*, the principal vector of visceral leishmaniasis in the New World, was observed promptly feeding on the animals.

In the second study in Bahia, also in Jacobina, Sherlock *et al.* [12] investigated commensal and sylvatic reservoirs of *Leishmania* spp. *Didelphis albiventris* was the most frequently caught mammal with 44% of the total, among which were also a bat, seven different rodent species, armadillos and canids. Of the 84 individuals of *D. albiventris* studied, two (2.4%) were infected with *L. infantum*, one (1.2%) with *L. amazonensis* and one (1.2%) with *L. braziliensis*. The authors reasoned that the low rate of infection indicates that *D. albiventris* should not be considered the primary and most important reservoir of visceral leishmaniasis in Jacobina. However, it is important to point out that despite the apparent low prevalence, other important epidemiological indicators, such as predominance in domestic and peri-domestic habitats, attractiveness to the insect vector and concomitancy with human cases of the disease, could counter such low percentages of infection.

The third study in Bahia is probably related to the two previously mentioned studies. In this case, Sherlock [13] described the natural infection of *D. albiventris* with *L. infantum*, however, it is not clear which species was actually studied because it was referred to as the "black ear opossum *Didelphis albiventris*", but this species has characteristic white ears.

In the state of Pernambuco there have been two studies of infection of *D. albiventris*. In the first, Brandão-Filho *et al.* [14] found (5\37) 13.5% of *D. albiventris* to be infected with *L.* (*Viannia*), with 13.3% in the forest and 3.1% in plantations. They suggested that besides rodents, opossums were among the animals most likely to function as reservoirs for *L.* (*V.*) *braziliensis* in Northeastern Brazil.

The second study was carried out by Lima *et al.* [15] in the municipality of São Vicente Férrer. They found rates of infection of *D. albiventris* to be 37.5% for *L.* (*Viannia*) and 6.3% for *L. infantum*, with one animal being co-infected by both species.

In the state of Rio Grande do Norte there has been only one record of an individual *D. albiventris* being naturally infected with *L. infantum*. The study surveyed small wild mammals from a Biological Reserve located in the municipality of Natal and domestic animals from an urban area [16]. The results showed that of 20 marsupials, including 16 *Didelphis albiventris* and 4 *Monodelphis domestica*, only one *D. albiventris* (5%) tested serologically positive for *L. infantum*.

In the state of São Paulo there have been two records of infection of *D. albiventris* with *Leishmania* spp. The first was from a study carried out by Quintal *et al.* [17] in the extreme western part of the state in a remnant of Atlantic Forest. They found that 1.6% of *D. albiventris* tested positive to qPCR. The second case was from a study in the city of Bauru in the central region of the state where Santiago *et al.* [18] observed a high rate of infection among opossums (91.6%), with 112 being *D. albiventris* and 10 being *D. aurita*. However, these species are sympatric in the area and the percentage was attributed to both of them together.

The last record of infection of *D. albiventris* with *Leishmania* in Brazil occurred in an endemic area for American tegumentary leishmaniasis, located in the northern part of the state of Minas Gerais. Here Quaresma *et al.* [19] studied domestic and synanthropic wild hosts of *L. braziliensis* in an Indigenous Territory. Opossums were the second most frequent animal captured representing 19.6% of the total, 28.6% of which were infected with *L. braziliensis*. The rate of infection of the peri-domicile areas and the trails between the houses were comparable with 20% and 21.4%, respectively.

2.2.3. *D. aurita* (Black-Eared Opossum)

All the reports of *Leishmania* spp. infection of *D. aurita* occurred in the Brazilian states of São Paulo and Rio de Janeiro. The parasite species involved were *L. mexicana*, *L. forattinii* and *L. infantum* (**Table 1**).

In the state of São Paulo there have been four publications relating to the infection of *D. aurita* by *Leishmania* spp, *L. mexicana* and *L. forattinii*. The first was Yoshida *et al.* [20], who in a research note reported the first case of natural infection of a marsupial with *Leishmania* in the state. The authors considered the probable importance of marsupials as hosts of *Leishmania*, in addition to rodents. In the second paper, Yoshida *et al.* [21] characterized the *Leishmania* species that was isolated from the *D. aurita* of their previous note as *Leishmania* *mexicana*, and in the third paper, Yoshida *et al.* [22] described *Leishmania* (*L.*) *foratinii* as a new parasite species infecting opossums and rodents captured in primary Atlantic Forest. The fourth record for São Paulo was mentioned above under the account for *D. albiventris*, where Santiago *et al.* [18] observed that 91.6% of the marsupials they tested were naturally infected; however, this was attributed to the two species *D. albiventris* and *D. aurita*, combined.

In the state of Rio de Janeiro, there has been one report of infection of *D. aurita* with *Leishmania*. Carreira *et al.* [23] observed a prevalence of 16.6% among *D. aurita* in a single endemic area for visceral leishmaniasis in Atlantic Forest. Macroscopic examination revealed that one opossum exhibited symptoms compatible with spleen hypertrophy whereas three others possessed amastigotes in the spleen. In addition, one of the opossums possessed parasites in a submandibular lymph node.

2.3. *Didelphis* in Colombia

D. marsupialis

There have been six reports of *Leishmania* spp. infection of *D. marsupialis* in Colombia. One of these reports was an experimental infection with *L. infantum*, whereas the others were natural infections with the following parasite species: *L. infantum* (three), *L. braziliensis* (one) and *L.* (*Viannia*) (one) (Table 2).

Table 2. List of records of marsupials infected with *Leishmania* spp. in South America other than from Brazil. Data provided include countries where the studies were carried out, the mammalian host species, the parasite species, the type of infection, the diagnostic methods and references.

Country	Marsupial species	*Leishmania* species	Type of infection/%	Method	Ref
Colombia	*Didelphis marsupialis*	*L.infantum*	N/32%	I, C, H	Corredor *et al.* 1989
			N/22.7%	C, MB, H, Iso	Travi *et al.* 1994
			E/NP	X, C, MB	Travi *et al.* 1998
			N/9.5-14.3%	MB	Travi *et al.* 1998
		L. braziliensis	N/20%	X, MB	Alexander *et al.* 1998
		Leishmania (*Viannia*) spp.	N/33.3%	MB	Ocampo *et al.* 2012
	Marmosa demerarae	*L. braziliensis*	N/66.7%	X, MB	Alexander *et al.* 1998
Trinidad	*Marmosops fuscatus*[a]	*Leishmania* spp	N/NP	C	Tikasingh 1969
			N/11.1-33.3%	I, C, H	Tikasingh 1974
	Marmosa robinsoni[b]	*Leishmania* spp	N/NP	C	Tikasingh 1969
			N/16.7%	I, C, H	Tikasingh 1974
	Caluromys philander	*Leishmania* spp	N/4.3%	I, C, H	Tikasingh 1974
Venezuela	*Didelphis marsupialis*	*L. braziliensis*	N/2.5%	C, H	Scorza *et al.* 1984
		L.garnhami	N/2.5%	C, H	Scorza *et al.* 1984
		L. braziliensis	E/50%	X	Scorza *et al.* 1984
		L. infantum	N/7.1%	S, MB	Zulueta AM *et al.* 1999
Peru	*Didelphis pernigra*[c]	*L. peruviana*	N/2.8%	C, MB	Llanos-Cuentas *et al.* 1999

Natural infection (N), Experimental infection (E), Histology (H), Culture (C), Imprint (I), Molecular Biology (MB), Xenodiagnosis (X), Isoenzyme (Iso), Smear (S), not presented (NP), ([a]) Originally referred to by the author as *Marmosa fuscata,* ([b]) Originally referred to by the author as *Marmosa mitis,* ([c]) Originally referred to by the authors as *Didelphis albiventris.*

In the case of the experimental infection, Travi *et al*. [24] inoculated an adult female and four recently weaned young opossums with amastigotes or promastigotes. The parasite burden was estimated by culture, testing for parasite DNA in skin samples, histopathological analysis and xenodiagnoses. The authors utilized two routes of inoculation, and observed the same effectiveness when inoculated through the dermis as when inoculated with a large number of parasites directly into the blood stream. Most animals presented subclinical infection, with a discrete inflammation of the liver, lymph nodes and spleen. An exception was one animal that showed evident signs of disease, including abundant cell parasitism, general spleen necrosis and fatty degeneration in the liver. The xenodiagnoses found sand flies to become infected even after feeding on subclinically infected opossums, which reinforces their potential as reservoirs, as had previously been observed in dogs by Molina *et al*. [25].

In conclusion, these authors highlighted the role of *D. marsupialis* as a wild reservoir host of *L. infantum* in Colombia, and explained that it was a function of several factors: 1) among all the animals trapped in an endemic area (data not shown), *D. marsupialis* was the most attractive to *Lutzomyia evansi*, the principal vector species of visceral leishmaniasis in Colombia; 2) it presented significant rates of natural infection [26] [27]; and 3) this species represented, in terms of biomass, the most abundant small mammal in a focus of visceral leishmaniasis in northern Colombia [28].

Among the three records of natural infections of *D. marsupialis* with *L. infantum* in Colombia, Corredor *et al*. [29] studied a population in El Callejon, a rural area highly endemic for *L. infantum* and where originally existed a tropical dry forest. The authors stressed the importance of *D. marsupialis* in the domestic cycle of the parasite because of the high percentage (around 32%) of infection observed.

Another study took place in the municipality of San Andreas de Sotavent in northwestern Colombia inside of an ecological zone composed of tropical dry forest. Here Travi *et al*. [27] recorded a prevalence of infection of 22.7% and they pointed out the probable role of *D. marsupialis* in both sylvatic and domestic cycles of the parasite.

In the third report, Travi *et al*. [30] studied the dynamics of *L. infantum* infection in small mammals of undisturbed and degraded tropical dry forests in northern Colombia. Among the mammals, *D. marsupialis* had one of the highest prevalences of infection with 14.3% and 9.5% in the undisturbed and degraded forests, respectively. The authors concluded that although the infection rate was similar at both sites, its significant increase in relative abundance in the degraded forest facilitated the establishment of the parasite in this habitat.

In the record describing the natural infection of *D. marsupialis* with *L. braziliensis*, Alexander *et al*. [31] utilized PCR and DNA hybridization to detect the potential presence of the parasite in tissue samples from wild mammals trapped in coffee plantations at La Guaira and Jinguales, Colombia. Among the five opossums tested, only one presented a very faint positive result with a specific probe for *L. braziliensis*.

In the last record associating *D. marsupialis* with *Leishmania* infections in Colombia, Ocampo *et al*. [32] studied environmental factors associated with American cutaneous leishmaniasis in an Andean focus and in Agua Bonita. They found 33.3% of the animals to be infected with *Leishmania* (*Viannia*), as detected by PCR-Southern blot, and the importance of opossums as a reservoir host of cutaneous leishmaniasis in disturbed habitats was reinforced.

2.4. *Didelphis* in Venezuela

D. marsupialis

There have been just two studies that have recorded the infection of *D. marsupialis* with *Leishmania* spp. The first comprised both experimental and natural infections, and described *D. marsupialis* as a primary peri-urban reservoir of *Leishmania* spp in the city of Trujillo, an endemic area of tegumentary leishmaniasis. In the experimental infections, 50% of the animals became infected after inoculation with *L. braziliensis*, and through the xenodiagnoses with *Lutzomyia townsendi*, an anthropophilic sandfly species very common in the area, the percentage of infection was 5.5% [33]. In the natural infections the parasite species observed were *L. braziliensis* and *L. garnhami*, both with the same prevalence of 2.5%.

In the second study in Venezuela, Zulueta *et al*. [34] studied aspects of the epidemiology of visceral leishmaniasis in an endemic focus in eastern Venezuela. They observed that one out 14 *D. marsupialis* was infected (7.1%) with *L. donovani* species complex based on PCR (currently *L. infantum*).

2.5. *Didelphis* in Honduras

D. marsupialis

There have been two reports describing experimental infections of *D. marsupialis* with *L. infantum* in Honduras, which represent the first work to utilize marsupials in studies of experimental infection with *Leishmania*, in the New World (**Table 3**).

In the first case, Lainson and Strangways-Dixon [35] reported that one out four (25%) of the *D. marsupialis* infected through intraperitoneal and intradermal inoculations developed visceral infection. In 1964, the same authors, in a

Table 3. List of records of marsupials infected with *Leishmania* spp. in Central America Data provided include the countries where the studies were carried out, the mammalian host species, the parasite species, the type of infection, the diagnostic methods and references.

Country	Marsupial species	*Leishmania* species	Type of infection/%	Method	Ref
Panamá	***Marmosa robinsoni***	*Leishmania* spp	N/2.8%	S, C, H	Herrer *et al.* 1971
			N/1.9%	ND	Telford *et al.* 1972
		L. mexicana	N/1.6%	I, C	Herrer *et al.* 1973
Honduras	***Didelphis marsupialis***	*L. mexicana*	E/25%	C	Lainson and Strangways-Dixon 1962
			E/25%	C	Lainson and Strangways-Dixon 1964

Natural infection (N), Experimental infection (E), Histology (H), Culture (C), Imprint (I), Smear (S), Not determined (ND).

second article [36], reported that among a dozen mammal species inoculated, detectable infections were produced only in two: *D. marsupialis* (25%) and a species of rodent, *Sigmodon hispidus* (100%). Despite the high prevalence observed also among the opossums in this study, the authors only highlighted the rodents as important hosts.

2.6. *Didelphis* in Peru

D. pernigra (Formerly *D. albiventris*)

The only supposed record of *Leishmania* infections in *D. albiventris* outside of Brazil occurred in Peru, where domestic and wild mammals were found naturally infected with *L.* (*V.*) *peruviana* in the Peruvian Andes (Table 2). Opossums exhibited the highest prevalence (2.8%) among the wild animals, even though a variety of rodent genera that have been traditionally considered as wild reservoirs, such as *Phyllotis*, *Akodon* and *Oryzomys* were included [37].

It is important to point out that although the authors described correctly the opossum species as *D. albiventris*, three years later a revision of this genus recognized the Andean White-eared Opossum, *D. pernigra*, as a new species.

2.7. *Didelphis* in the USA

2.7.1. *D. marsupialis*

There is only one report concerning *Leishmania* sp. infection of *D. marsupialis* in the USA. Hanson *et al.* [38] inoculated individuals of *D. marsupialis* intracardially with an African strain of *Leishmania donovani*, and reported that those animals developed fulminating visceral leishmaniasis and concluded that they would be useful in the study of anti-leishmanial drugs (Table 4).

2.7.2. *D. virginiana* (North American Opossum)

There are two records of experimental infections of *D. virginiana* with an *L. donovani* African strain (Khartoum) (Table 4). White *et al.* [39] compared the patterns of infection with *L. donovani* among opossums, armadillos and ferrets and concluded that the opossum was the most susceptible because of the larger number of parasites in both liver and spleen. These same authors [40] evaluated the effect of two chemotherapeutic drugs on 17 individuals of *D. virginiana* that had been previously inoculated with *L. donovani*. They concluded that factors

Table 4. List of records of marsupials infected with *Leishmania* spp. in North America. The data indicate the countries where the studies were carried out, both the host and parasite species, the type of infection, the diagnostic methods and references.

Country	Marsupial species	*Leishmania* species	Type of infection/%	Method	Ref
USA	*Didelphis marsupialis*	*L. donovani*	E/NP	I	Hanson and Chapman 1980
	Didelphis virginiana		E/NP	I	White *et al.* 1989
		L. donovani	E/NP	I, H	White *et al.* 1989
Mexico	*Marmosa mexicana*	*L. mexicana*	N/50-100%	C, MB	Van Wynsberghe *et al.* 2009

Natural infection (N), Experimental infection (E), Histology (H), Culture (C), Imprint (I), Molecular Biology (MB), not presented (NP).

related to the pattern of infection, such as rapid acute death and abnormalities of hemostasis, could limit the use of this species as an animal model for testing anti-leishmanial drugs.

3. The Genus *Marmosa* and Other Mouse Opossums

Before addressing *Leishmania* infection of mouse opossums, it is necessary to clarify that these animals comprise a great number of different taxonomic groups with numerous morphological similarities and broad concurrence in their geographical distribution (**Figure 1**).

Formerly, the term "mouse opossum" was mostly associated with the genus *Marmosa*, nevertheless this genus has been the subject of multiple revisions and several new genera have come to be considered mouse opossums as well [41].

In 1933, in one of the first revisions of the genus *Marmosa*, Tate [42] subdivided the genus into five groups, *Cinerea*, *Murina*, *Noctivaga*, *Microtarsus* and *Elegans*. Each of these groups was then subdivided into sections varying in number from two to four. For example, the *Cinerea* group contained two sections, *Marmosa Cinerea* and *M. Regina*, while the *Murina* group had four sections: *M. Murina*, *M. Mitis*, *M. Mexicana* and *M. Canesces*.

Later, Gardner and Creighton [43], re-described the groups and sections proposed by Tates, assigning the sections *Cinerea*, *Murina*, *Noctivaga* and *Elegans*, to the respective genera *Micoureus* [1] (Lesson, 1842), *Marmosa* (Gray, 1821), *Marmosops* (Matschie, 1916) and *Thylamys* (Gray, 1843). In addition, most of the species belonging the *Microtarsus* group were placed in a new genus, *Gracilinanus*.

More recently, phylogenetic research based on molecular data [44] [45] [46] determined that *Marmosa* was polyphyletic, while *Marmosops*, *Micoureus*, and *Thylamys*, as previously established by Gardner and Creighton [43], were all monophyletic. A new genus, however, was defined for "*Marmosa*" *canescens* by Voss and Jansa [47], and some new genera were later described for two clades previously suppressed by synonymy within *Gracilinanus* [48] [49]. Finally, after the last revision of genus *Marmosa*, *Micoureus*, which was previously considered a separate genus, was moved into *Marmosa* as a subgenus [50].

Currently, the term "mouse opossum" can be associated with five genera, as follows: *Marmosa* (Linnaeus's Mouse Opossum), *Marmosops* (Slender Mouse Opossums), *Thylamys* (Fat-tailed Mouse Opossums), *Tlacuatzin* (Grayish Mouse Opossum) and *Gracilinanus* (Gracile Mouse Opossum). Nonetheless, in some instances, both *Gracilinanus* and *Marmosops* have been excluded from consideration as "mouse opossums" and instead are identified as just the Gracile Opossum and the Slender Opossum.

The genus *Marmosa* specifically comprises a collection of black-masked and long-tailed pouchless marsupials. They are solitary, nocturnal and live in a wide range of tropical and subtropical habitats from Mexico to Bolivia. It has been considered the most abundant genus of the family Didelphidae, being composed by 19 currently recognized species belonging to five subgenera as follows: 1) *M. Marmosa* (Gray, 1821) represented by the species *macrotarsus*, *murina*, *tyleriana*, and *waterhousei*; 2) *M. Micoureus* (Lesson, 1842) with the species *alstoni*, *constantiae*, *demerarae*, *paraguayanus*, *phaea* and *regina*; 3) *M. Stegomarmosa* (Pine, 1972) with *andersoni* and *lepida*; 4) *M. Eomarmosa* [51] with *rubra*; and 5) *M. Exulomarmosa* [51] with the species *isthmica*, *mexicana*, *robinsoni*, *simonsi*, *xerophila*, and *zeledoni*.

3.1. *Marmosa* and *Leishmania*

Five species of *Marmosa* have already been reported to have been naturally infected by different species of *Leishmania*: 1) *M.* (*Exulomarmosa*) *robinsoni*, infected with *Leishmania* spp and *L. mexicana*; 2) *M.* (*Marmosa*) *murina*, with *Leishmania* spp and *L. amazonensis*; 3) *M.* (*Micoreus*) *demerarae*; and 4) *M.* (*Micoreus*) *paraguayanus* both infected with *L. braziliensis* and *L. amazonensis*; and 5) *M.* (*Exulomarmosa*) *mexicana* with *L. mexicana*.

3.2. *Marmosa* in Brazil

3.2.1. *Marmosa* (*M.*) *murina* (Murine Mouse Opossum)

All studies related to infections of *Marmosa murina* with *Leishmania* sp. occurred in central and northern Brazil (**Table 1**). The three papers from the central region include surveys performed in the state of Mato Grosso. Lainson and Shaw [52] found 7.7% of *M. murina* to be naturally infected with an unidentified species of cutaneous *Leishmania* sp., however, their criterion for selecting animals for testing was simply the presence of skin lesions. In a subsequent paper, the same authors re-described and expanded on the information related to their first report [53], and in a third paper, with additional coauthors, they isolated a stock of *Leishmania* from *M. murina*, that they characterized as *L. amazonensis* through enzymatic profile [54]. In the Northern Region of Brazil, there has been only one record of an individual *M. murina* being infected with an unspecified strain of *Leishmania* [52].

3.2.2. *Marmosa* (*M.*) *demerarae* (Long-Furred Woolly Mouse Opossum)

In the only record of infection of *M. demerarae* with *Leishmania* sp. in Brazil, Arias *et al.* [8] observed 100% (2/2) infection with *L. amazonensis* in an area of virgin forest, but with considerable human activities, in the state of Amazonas (**Table 1**).

3.2.3. *Marmosa* (*M.*) *paraguayanus* (Tate's Woolly Mouse Opossum)

The two records of *Leishmania* spp. infection of *M. paraguayanus* in Brazil were presented by Quintal *et al.* [17] (**Table 1**). These researchers studied six areas surrounding the Atlantic Forest in the extreme western part of the state of São Paulo, and found a prevalence of 11.6% for *Leishmania* spp by qPCR. In addition, from three tissue samples taken for parasite species identification, two were positive for *L. amazonensis* and one for *L. braziliensis*. Given the high parasitic load they found in the skin samples, these authors acknowledged the probable role of this marsupial as a potential reservoir host of *Leishmania* spp.

3.2.4. *Marmosa* spp

Concluding the accounts involving the genus *Marmosa* in Brazil, there are two more studies in which the authors did not identify the species; however, given that the studies were performed in the state of Pernambuco, and considering the geographic range of potential species, it is likely these were individuals of either *M. murina* or *M. demerarae*.

In the first paper, Brandão-Filho *et al.* [14], studied wild and synanthropic hosts in an endemic area of cutaneous leishmaniasis (**Table 1**). With the use of PCR, they observed infections with *L. braziliensis* that varied in prevalence from 16.7% to 25%, depending on the year when the samples were collected. Additionally, prevalence varied according to location of capture, with the rates being 4.1%, 1.6% and 1.2% for animals caught in forest, animal sheds and plantations, respectively.

The second record was presented by Lima *et al.* [15], who studied small mammals as hosts of *Leishmania* spp in a highly endemic area for zoonotic leishmaniasis. Twenty five percent (1/4) of *Marmosa* spp tested positive for *Leishmania* spp through PCR and none of the animals presented clinical signs suggestive of leishmaniasis such as skin lesions (**Table 1**).

3.3. *Marmosa* in Trinidad and Tobago

Marmosa (*E.*) *robinsoni* (Robinson's Mouse Opossum)

Two manuscripts addressed natural infections of *Marmosa mitis* with *Leishmania* spp. in Trinidad and Tobago, although currently this species is considered a synonym of *M. robinsoni*, and so this last name must be considered.

The first manuscript was a preliminary report in which the authors report the isolation (through inoculation of a hamster) of a parasite morphologically corresponding to *Leishmania* from one specimen of *Marmosa mitis* [55] (**Table 2**). The second study, entitled "Enzootic rodent leishmaniasis in Trinidad, West Indies" was carried out by the same author [56] in six areas covering the northern part of the country, where they found 16.7% of *Marmosa mitis* to be naturally infected with *Leishmania* spp. Nevertheless, these results probably underestimated the real prevalence of infection because only animals that presented skin lesions were included in the study.

3.4. *Marmosa* in Panama

Marmosa robinsoni

In Panama, there have been three studies recording infections of *M. robinsoni* with *Leishmania* spp., two with *Leishmania* spp and one with *L. mexicana* (**Table 3**). In the first, Herrer *et al.* [57] described a focus of enzootic cutaneous leishmaniasis in a forest area in the eastern part of the country where they recorded a prevalence of 2.8% infection with a *Leishmania* sp., species they described as to behave like *L. mexicana* in experimentally infected hamsters. Telford *et al.* [58] studied the ecological factors relating to the mammalian hosts in the same area, but in this case trapping effort was concentrated in a secondary forest, and consequently the prevalence was 1.9% and *M. robinsoni* were considered incidental hosts. Herrer *et al*. [59] studied the reservoir hosts of cutaneous leishmaniasis in a forest habitat and observed that 1.6% of *M. robinsoni* were infected with *L. mexicana*.

3.5. *Marmosa* in Colombia

Marmosa demerarae

In Colombia there is one record where Alexander *et al*. [31] observed an infection prevalence of 66.7% (two out of three) for *L. braziliensis* among *M. demerarae* caught in coffee plantations in the western part of the country between the Andes and the coast (**Table 2**).

3.6. *Marmosa* in Mexico

***M.* (*Marmosa*) *mexicana* (Mexican Mouse Opossum)**

In Mexico, Van Wynsberghe *et al*. [60] observed that in addition to high rates of infection (50% and 100% during 1997-1998 and 2001-2004, respectively), most animals were asymptomatic in certain areas of an important focus of cutaneous leishmaniasis in the state of Campeche (**Table 4**).

4. The Genus *Marmosops* (Slender Opossums)

As originally described, the genus *Marmosops* [61] was comprised of 11 species, with *M. incanus* [62] being assigned as the type species. Later, Tate [42] treated *Marmosops* as a junior synonym of *Marmosa*, but Gardner and Creighton [43] recognized *Marmosops* as a distinct taxon, and elevated all of Tate's species groups of *Marmosa* to generic rank.

Currently, the genus *Marmosops* contains the following 14 species: *M. bishopi*, *M. cracens*, *M. dorothea*, *M. fuscatus*, *M. handleyi*, *M. impavidus*, *M. incanus*, *M. invictus*, *M. juninensis*, *M. neblina*, *M. noctivagus*, *M. parvidens*, *M. paulensis* and *M. pinheiroi*. However, some authors consider *M. creightoni* to be an additional species.

4.1. *Marmosops* and *Leishmania*

There are three records that refer to species of *Marmosops* being naturally infected with *Leishmania* spp., one in Brazil and two in Trinidad. The species involved were *M. incanus* and *M. fuscatus*, and were infected with *L. guyanensis* and *Leishmania* spp, respectively (**Figure 1**).

4.2. *Marmosops* in Brazil

***Marmosops incanus* (Grey Slender Opossum)**

Quaresma *et al*. [19] observed a prevalence of 50% (1/2) infection with *L. guyanensis* among *M. incanus* in one area in the state of Minas Gerais State where other animals, including rodents and canids, were infected with other *Leishmania* species, including *L. braziliensis* and *L. infantum* (**Table 1**).

4.3. *Marmosops* in Trinidad

In Trinidad, the opossum species cited by the authors as *Marmosa fuscata*, is now recognized as a new genus and species. Therefore *Marmosa fuscata* is currently considered as a synonym of *Marmosops fuscatus*.

***Marmosops fuscatus* (Dusky Slender Opossum)**

The first record of a *M. fuscatus* being infected with with *Leishmania* in Trinidad and Tobago was in 1969 as part of a preliminary report about natural infection with *Leishmania* sp [55] (**Table 2**). Subsequently, in 1974, the same author published a study entitled "Enzootic Rodent Leishmaniasis in Trinidad, West Indies", in which an overall infection prevalence of 11.1% was reported; although a considerably higher prevalence of infection was reported for a single area of Evergreen Seasonal Marsh Forest (33.3%), these animals were considered as only secondary hosts.

5. The Genus *Metachirus* (Brown Four-Eyed Opossum) and *Leishmania*

The genus *Metachirus* contains only a single currently recognized species, *Metachirus nudicaudatus*, which is also the largest of the pouchless didelphids found in forest habitats. In spite of the recognition of just one species, five subspecies have been identified and it has been suggested that one or more of these subspecies may in fact be genuine species [52]. There are only two records of *M. nudicaudatus* being naturally infected with *Leishmania* in Brazil (**Figure 1**).

In the first case, Miles *et al.* [54] used enzymatic characterization to identify a strain of *Leishmania* isolated from *M. nudicaudatus* as *L. amazonensis* (**Table 1**). In the second case, Lainson *et al.* [9] observed considerable prevalence (66.7%) of *L. amazonensis* infections in an area highly endemic for cutaneous leishmaniasis (**Table 1**).

6. The Genus *Caluromys* (Woolly Opossum) and *Leishmania*

Currently the genus *Caluromys* is composed of three species: *C. philander*, *C. derbianus* and *C. lanatus*. Of these, the firsts two have been reported with natural infections of *Leishmania* sp. in Trinidad and Panama (**Figure 1**).

6.1. *Caluromys philander* (Bare-Tailled Woolly Opossum) in Trinidad

In Trinidad, Tikasingh [56] observed a total prevalence of 4.3% for cutaneous leishmaniasis in six areas of a variety of different habitats in the northern part of the country (**Table 2**). This study was the first to record the presence of amastigotes in a sore on an individual of this species.

6.2. *C. derbianus* (Central American Woolly Opossums) in Panama

In Panama, Johnson and Hertig [63] studied the behavior of *Leishmania* in Panamanian sandfly species fed on naturally infected mammals.

In phlebotomines that had previously fed on one *Caluromys* (probably *C. derbianus*), they observed a number of flagellates similar to some already observed in cultures of *Leishmania* isolated from sandflies from the same area. However, it was not clear which parasite species were involved in this case because, the authors stated, trypanosomes are frequently correlated with infections in *Caluromys* (**Table 3**).

An interesting observation was of sandflies feeding on young animals that were still in the marsupium.

7. The Genus *Gracilinanus* (Gracile Mouse Opossums) and *Leishmania*

Gracilinanus was separated from the genus *Marmosa* in 1989 and currently six species are recognized: *G. aceramarcae*, *G. agilis*, *G. dryas*, *G. emiliae*, *G. marica* and *G. microtarsus*.

There are two records of species of *Gracilinanus* being infected with *Leishmania* spp., both in Brazil and both with the species *G. agilis* (Agile Gracile Mouse Opossum) (**Figure 1**).

The first report was in the state of Minas Gerais in southeastern Brazil where Quaresma *et al*. [19] studied wild, synanthropic and domestic hosts in an endemic area of cutaneous leishmaniasis (**Table 1**). Of the total animals caught, *G. agilis* represented 4.1%, of which 75% (3/4) were infected with *L. braziliensis*. It has been suggested that the presence of a significant number of rodents and marsupials infected with *L.* (*V.*) *braziliensis* could be related to a high rate of transmission and that these animals could be important in the maintenance of the parasite in the area.

The second record was in the federal district of Brasilia during a study in two areas, the Brasília National Park (BNP) and the Contagem Biological Reserve (CBR), which are federal conservation units of different types of habitats including grasslands, cerrado and gallery forests [64] (**Table 1**). For the two study areas, 19% (3 out 16) of the *G. agilis* tested positive for *Leishmania* spp through PCR and sequencing. Although the authors concluded that there were no significant differences in infection rates among the mammal species surveyed, the study highlighted the role of *G. agilis*, in addition to two rodent species, as hosts of *Leishmania* spp [64].

8. The Genus *Monodelphis* (Short-Tailed Opossums) and *Leishmania*

Currently the genus *Monodelphis* is comprised of 20 species: *M. adusta*, *M. americana*, *M. brevicaudata*, *M. dimidiata*, *M. domestica*, *M. emiliae*, *M. glirina*, *M. iheringi*, *M. kunsi*, *M. maraxina*, *M. osgoodi*, *M. palliolata*, *M. rubida*. *M. scalops*, *M. sorex*, *M. theresa*, *M. umbristriata*, *M. unistriata*, *M. reigi* and *M. ronaldi* [65] [66] [67] [68] [69].

Until now there has been only one record of an interaction between a species of *Monodelphis* and *Leishmania* sp., which was a natural infection of a *M. do-*

mestica (Gray Short-tailed Opossum) in Brazil (**Figure 1**). In the study, Lima *et al*. [15] found the natural infection prevalence for *M. domestica* to be 25% (1/4) with *Leishmania* (*Viannia*) spp., in a highly endemic area for zoonotic leishmaniasis in the state of Pernambuco in northeastern Brazil (**Table 1**).

9. The Genus *Philander* (Four-Eyed Opossums) and *Leishmania*

Originally, the genus *Philander* was assumed to contain only a single species, *P. opossum*, with the following seven subspecies: *P. opossum andersoni*, *P. o. azaricus*, *P. o. canus*, *P. o. grisescens*, *P. o. melanurus*, *P. o. opossum*, and *P. o. quica* until *P. mcilhennyi*. Currently seven species, commonly known as Four-eyed Opossums, are recognized for the genus: *P. andersoni*, *P. deltae*, *P. frenatus*, *P. mcilhennyi*, *P. mondolfii*, *P. olrogi* and *P. opossum* [67] [70].

There is only one record of infection of a species of *Philander* with *Leishmania* sp., which involved *P. opossum* in Brazil (**Figure 1**).

Philander opossum (Gray Four-Eyed Opossum) in Brazil

In the only study to have recorded an infection of *P. opossum* with *Leishmania*, Lainson *et al*. [9] observed a prevalence of natural infection of 18% (2/11) with *L. amazonensis*, in an area highly endemic for cutaneous leishmaniasis in the state of Para. In both infected individuals, the parasite was isolated from the skin (**Table 1**).

10. Marsupial Hosts of *Leishmania* in Australia

Although traditionally Australia has been considered to be free of *Leishmania*, in 2004 the first cases of natural infection were diagnosed in captive *Macropus rufus*. The first studies involving experimental infection of marsupials with *Leishmania* occurred in Australia just after World War II in 1945 and 1948.

There have been four studies referencing the infection of marsupials with *Leishmania* in Australia; two were experimentally infected animals and two were natural infections (**Figure 2**). Together these studies included three marsupial families: Phalangeridae, Pseudocheiridae and Macropodidae, represented by the genera, *Trichosurus*, *Pseudocheirus* and *Macropus*, respectively.

11. The Genus *Macropus*

The genus *Macropus* has 13 extant species which are placed into 3 subgenera: *Notamacropus*, *Osphranter and Macropus*. These taxa include several types of terrestrial wallabies, wallaroos and kangaroos, as follows:

Subgenus *Notamacropus*: *Macropus agilis* (Agile Wallaby), *Macropus dorsalis* (Black-striped Wallaby), *Macropus eugenii* (Tammar Wallaby), *Macropus irma* (Western Brush Wallaby), *Macropus parma* (Parma Wallaby), *Macropus parryi* (Whiptail Wallaby), *Macropus rufogriseus* (Red-necked Wallaby).

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Figure 2. Geographical distribution of records of infection with *Leishmania* spp. in *Trichosurus, Pseudocheirus* and *Macropus* in Australia. All data were mapped through ArchView software using geographical coordinates provided by the authors or estimated based on reference points provided in the studies and utilizing ArchView and Google earth. For experimental infections, the location indicated where the animals were necropsied.

Subgenus *Osphranter*: *Macropus antilopinus* (Antilopine Kangaroo), *Macropus bernardus* (Black Wallaroo), *Macropus robustus* (Common Wallaroo), *Macropus rufus* (Red Kangaroo).

Subgenus *Macropus*: *Macropus fuliginosus* (Western Grey Kangaroo), *Macropus giganteus* (Eastern Grey Kangaroo).

Concerning records of *Leishmania* spp. infection in Australian marsupials, the genus *Macropus* is the most important with four species that have already been found naturally infected: *M.* (*O.*) *rufus*, *M.* (*O.*) *robustus*, *M.* (*O.*) *bernardus* and *M.* (*N.*) *agilis* (Figure 2). In all cases the species of parasite was not identified.

11.1. *Macropus rufus* (Red Kangaroo) and *Leishmania*

Macropus rufus was the first mammal species to be documented as naturally infected with *Leishmania* spp. in Australia by Rose *et al.* [71]. The authors observed that 11 kangaroos from Northern Territory had chronic, sometimes self-resolving, skin lesions and in 6 out of those 11 the parasites were isolated and characterized as *Leishmania* spp.

These findings raised speculation of the possibility of the local occurrence of unrecognized human cases of cutaneous leishmaniasis caused by an imported parasite that could become endemic in Australia (Table 5).

11.2. *Macropus robustus* (Northern Wallaroo) and *Leishmania*

Dougall *et al.* [72] observed that seven out of eight individuals of *M. robustus* that presented skin lesions suggestive of cutaneous leishmaniasis were seropositive to *Leishmania* in ELISA and the parasite was also isolated in culture (Table 5). In addition, PCR results demonstrated that the parasite corresponded to the same one observed in *M. rufus* by Rose *et al.* [71].

11.3. *Macropus bernardus* (Black Wallaroo) and *Leishmania*

Dougall *et al.* [72] reported one individual of *M. bernardus* to be PCR positive to *Leishmania* spp. This individual exhibited ear lesions similar to those observed in *M. robustus*, but also small nodular lesions around the eyes, indicating possible mucosal involvement (Table 5).

11.4. *Macropus agilis* (Agile Wallaby) and *Leishmania*

Dougal *et al.* [72] observed that samples collected from sections of the ears from

Table 5. List of records of marsupials infected with *Leishmania* spp. in Australia.

Australia regions	Marsupial species	*Leishmania* species	Type of infection/%	Method	Ref
New South Wales	***Trichosorus vulpecula***	*L. donovani*	E/1 case	C, S	Armytage and Bolliger, 1945
			E/92%	C, S	Bolliger and Backhouse, 1948
	Pseudocheirus laniginosus[a]	*L. donovani*	E/1 case	C, S	Bolliger and Backhouse, 1948
Northern	***Macropus rufus***	*Leishmania* spp	N/54.5%	C, MB, EM, H	Rose *et al.* 2004
	Macropus robustus	*Leishmania* spp	N/87.5%	I, H, C, ELISA, MB	Dougall *et al.* 2009
	Macropus bernardus	*Leishmania* spp	N/1 case	I, H, C, ELISA, MB	Dougall *et al.* 2009
	Macropus agilis	*Leishmania* spp	N/2 cases	I, H, C, ELISA, MB	Dougall *et al.* 2009

Natural infection (N), Experimental infection (E), Histology (H), Culture (C), Imprint (I), Molecular Biology (MB), Smear (S), Enzyme-linked Immunosorbent assay (ELISA), Electron microscopy (EM), ([a]) Originally referred to by the authors as *Pseudocheirus peregrinus.*

two individuals of *M. agilis* tested positive for *Leishmania* spp by PCR test (Table 5).

Conversely, it was reported that *M. agilis* showed less severe symptoms than both *M. robustus* and *M. bernardus*. Moreover the lesions observed in *M. agilis* healed significantly faster, indicating a probable inherent immunity, as was suggested by the authors.

12. The Genus *Trichosurus* (Brushtail Possum)

There remains controversy over whether the number of species in the genus *Trichosurus* is five or three.

Those who recognize five species include the following: *T. vulpecula* (Common Brushtail Possum), *T. arnhemensis* (Northern Brushtail Possum), *T. caninus* (Short-eared Possum), *T. cunninghami* (Mountain Brushtail Possum) and *T. johnstonii* (Coppery Brushtail Possum) [73]. However, some consider *Trichosurus arnhemensis* and *T. johnstonii* to be subspecies of *T. vulpecula*, and thus only three species in the genus [74].

Until now there have been only two records of *Leishmania* involving this genus, with both being *Trichosurus vulpecula* inoculated with *L. donovani* (Figure 2).

Trichosurus vulpecula (Common Brushtail Possum) and *Leishmania*

The first study of experimental infection involving a marsupial host was in 1945 when Armytage and Bollinger [75] inoculated a pouch young *Trichosurus vulpecula* of about two and a half years old, still in the pouch, with, as described by the authors, 1 ml of the broth washings of a tube culture of *L. donovani*. After ten weeks, the animal was necropsied and in a smear of the spleen, liver and bone marrow revealed numerous amastigotes mainly inside of macrophages. The parasite was also isolated in cultures made from spleen, liver, bone marrow and blood (Table 5).

The second report of infection of *T. vulpecula* with *L. donovani* was presented in the study of Bollinger and Backhouse in 1948 [76]. The authors demonstrated that 92% (22/25) of the animals became infected after different schedules of intracardiac and intraperitoneal inoculations, including saline suspension from cultures, fresh blood from injected animals and material from sternal puncture. The number of parasites inoculated was not provided (Table 5).

In general, the pattern of infection was characterized by parasitism disseminated in several tissues including spleen, liver, kidney, brain, eyes, pituitary, adrenal, ovary, testis, prostate gland, lung, alimentary canal, para-cloacal glands and pancreas. The most frequently infected organs were the spleen, liver and kidney, which exhibited parasitism in most animals. These organs were followed by brain, eyes, pituitary and adrenal glands, with other organs being less frequently parasitized. The authors concluded that the Common Brushtail Possum is highly susceptible to experimental *L. donovani* infections and under suitable conditions those animals could become reservoir hosts of *Leishmania* sp.

13. The Genus *Pseudocheirus* (Ringtail Possum)

The genus *Pseudocheirus* contains five species: *P. peregrinus* (Common Ringtail Possum), *P. occidentalis* (Western Ringtail Possum), *P. canescens* (Lowland Ringtail), *P. forbesi* (Painted Ringtail) and *P. mayeri* (Pygmy Ringtail).

There is one record of infection of a species of *Pseudocheirus* with *Leishmania* sp., were the authors experimentally infected the species *Pseudocheirus laniginosus* with *L. donovani* (**Figure 2**). However, *P. laniginosus* is no longer recognized and is currently considered a synonym of *P. peregrinus*.

Pseudocheirus peregrinus (Common Ringtail Possum) and *Leishmania*

The only information concerning infection of *P. peregrinus* with Leishmania comes from Bollinger and Backhouse [76], who inoculated one animal with *L. donovani*. The parasites used were probably cultured forms obtained from blood of a previously infected *T. vulpecula* (**Table 5**). The infected *P. peregrinus* exhibited a disease pattern similar to that observed in *T. vulpecula*, with diffuse parasitism but with a smaller number of organs affected, such as spleen, liver, kidney, brain, eyes, pituitary and para-cloacal glands.

Histopathology found that in the central nervous system, and particularly in the choroid plexus, many endothelial cells were parasitized. In the eye, parasites were observed in both macrophage and endothelial cells of both the ciliary body and the choroid coat. The authors inferred that the Common Ringtail Possum could be a potential reservoir host of *Leishmania* sp. in Australia.

14. Conclusions

Presently, all records about the infection of marsupials with *Leishmania* are restricted to the New World and Australia, with Brazil being the country where the majority of the studies were performed.

In the Americas, the first studies occurred in the 1960s and all of them dealt with the family Didelphidae, which contains a great number of species that are sympatric with various species of *Leishmania*.

The situation in Australia is different. Although the first studies occurred earlier than in the New World (1940s) with experimental infections, it has only been relatively recently (2000s) that cases of natural infections have been reported, and all involving the family Macropodidae.

In general, and primarily in the New World, marsupials show a certain equilibrium in their relationship with *Leishmania*, with high rates of infection but few or no symptoms and a tendency to exhibit self-resolving skin lesions, suggesting an ancient parasite-host coevolution.

In conclusion, marsupials must be considered one of the most important mammal groups to serve as wild hosts of *Leishmania* spp. in the World.

In the future, in the New World considering the sylvatic cycles, most marsupial species cited they must maintain its importance as reservoir and probably new others will be described. On the other hand, because of not only the tendency of urbanization principally of the visceral leishmaniasis but also the cutaneous disease, in the peri-urban and urban habitats the didelphis probably will prevail because of its ease adaptability to degraded habitats.

Distinctively in the United States, the occurrence of more recent cases of canine and human leishmaniasis shows a tendency of the disease spreading northward. Likewise, the *Didelphis* also has been presenting a northward dispersion and it could have some roles on the maintenance of the parasite in some of those places.

In respect to Australia, because of the last cases describing autochthonous infections in Kangaroos, several questions must be solved, such as the role of mammal hosts, origin of the infections, the identification of vector species and verifying of the probable role of ceratopogonids in the transmission. It will be very important of the description of the eco-epidemiological picture in the endemic areas, pointing toward prophylactic measures to avoid the occurrence of human infections.

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Competing Interests

Authors declare they have no conflicts of interest.

Author's Contributions

Carreira JCA-conception, design, drafting and revising of the manuscript. Magalhães MAFM-analysis and interpretation of data of the maps. Brazil RP-revising of the manuscript. Silva AVM-drafting the manuscript.

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