A review of *Trypanosoma* species known from Malagasy vertebrates

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Abstract

We report on the different species of trypanosomes known from Malagasy vertebrates based on published literature; this review provides baseline information for future public health research. Further, we provide data at a worldwide scale of invertebrate groups known to be *Trypanosoma* vectors and their presence or absence on Madagascar, as further insight into the potential vectors on the island. Different microscopic studies highlighted the presence of eight described species of *Trypanosoma* in Malagasy vertebrates, including five species known from reptiles: *T*. *therezieni*, *T*. *domerguei*, *T*. *haranti*, *T*. *petteri*, and *T*. *betschi*; two species in birds: *T*. *everetti* and *T*. *avium*; and one species in rodents, *T. lewisi*. In addition, other unidentified taxa have been reported in reptiles, birds, bats, rodents, and lemurs based on microscopic techniques or molecular screening.

Key words: *Trypanosoma*, reptiles, birds, bats, mammals, Madagascar

Résumé détaillé

La présente revue résume les informations disponibles sur les différentes espèces de trypanosomes infectant les vertébrés malgaches dans le but d'établir une base de recherche pour les études ultérieures sur leur implication potentielle dans la santé publique. En outre, des données sur les groupes de vecteurs connus dans le monde ont été documentées afin de déterminer si ces taxa sont présents à Madagascar et pourraient assurer la transmission de *Trypanosoma*. Si aucune information n'est disponible sur la présence de *Trypanosoma* chez les poissons malgaches, des recherches microscopiques antérieurs ont permis d'identifier huit espèces de *Trypanosoma* dont cinq espèces chez les reptiles, à savoir : *T*. *therezieni* chez *Calumma brevicorne*, *T*. *haranti* chez *Liopholidophis lateralis*, *T*. *petteri* chez *Phelsuma lineatum*, *T*. *betschi* chez *Zonosaurus madagascariensis* et *T*. *domerguei* chez *Oplurus cuvieri.* Deux espèces de trypanosomes ont été décrits chez les oiseaux : *T*. *avium* chez *Falco newtoni*, *Atelornis pittoides*, *Acridotheres tristis*, *Cyanolanius madagascarinus*, *Schetba rufa* et *Tylas eduardi* et *T*. *everetti* chez *Ploceus sakalava*. *Trypanosoma lewisi*, un parasite cosmopolite a été trouvé chez le rongeur introduit *Rattus rattus*. Par ailleurs, des taxa de *Trypanosoma* non identifiés et encore non décrits ont été également trouvés chez différent groupes de vertébrés comme les reptiles tels *Calumma nasutum*, *Furcifer willsii* et *Pelomedusa subrufa*, les oiseaux tels *Atelornis crossleyi*, *Motacilla flaviventris*, *Hypsipetes madagascariensis*, *Berniera madagascariensis*, *Xanthomixis zosterops* et *Zosterops maderaspatana*, les chauves-souris tels *Miniopterus mahafaliensis* et *M*. *brachytragos*, un rongeur endémique *Nesomys rufus* (Nesomyidae : Nesomyinae) et chez un lémurien, *Indri indri*, mais faute de données disponibles sur leur caractérisation morphologique et moléculaire, l'identité taxonomique de ces parasites restent à élucider. Une récente étude moléculaire sur *Hoplobatrachus tigerinus* a montré l'absence du genre *Trypanosoma* chez cette espèce introduite.

Mots clés : *Trypanosoma*, reptiles, oiseaux, chauves-souris, mammifères, Madagascar

Introduction

Protozoan parasites of the genus *Trypanosoma* (Kinetoplastida: Trypanosomatidae) are taxonomically diverse, geographically widespread,

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and known to infect different vertebrate groups, including fish, amphibians, reptiles, birds, and mammals (Stevens, 2008; Noyes, 1998; Barret *et al*., 2003). In humans, Trypanosomiasis has specific geographic range depending on availability of vectors (Noyes, 1998; Barret *et al*., 2003). *Trypanosoma* is transmitted by a wide range of hematophagous arthropods (Stevens *et al*., 2001; Hamilton *et al*., 2007) and based on the discovery of trypanosomes in a female sand fly (Diptera: Ceratopogonidae) from Burmese Cretaceous amber deposits, it was suggested that this group of parasites existed since at least 380 million years (Haag *et al*., 1998; Poinar & Poinar, 2004).

Within the Kinetoplastida, the family Trypanosomatidae comprises a paraphyletic group adapted to colonize a diverse range of eukaryotic hosts (Hughes & Piontkivska, 2003; Piontkivska & Hughes, 2005; Simpson *et al*., 2006). Trypanosomes are traditionally divided into two groups based on the transmission route of the insect vector: the *Salivaria* group, transmitted via the vector's proboscis, and the *Stercorcaria* group, transmitted via the vector's feces (Hoare, 1964).

Published phylogenies of *Trypanosoma* suggest that most clades are generally associated with particular vertebrate hosts (Sehgal *et al*., 2001; Noyes *et al*., 2002; Hamilton *et al*., 2007; Ferreira *et al*., 2008), with little or no apparent negative effects on infected hosts (Smith *et al*., 2005). Nevertheless, some *Trypanosoma* species are harmful to other host species following their introduction into a novel taxonomic group (Onyango *et al*., 1966; Maraghi & Molyneux, 1989; Wyatt *et al*., 2008). Trypanosomes have different complex life cycles; generally diphasic occurring between a vertebrate host, where they are represented by a trypomastigote form in the bloodstream, and undergo development within the digestive tract of the invertebrate vector (Botero *et al*., 2016).

On Madagascar, information concerning trypanosomes in wild animals is poorly documented in the literature. Nevertheless, within the highly-endemic fauna of the island, trypanosomes have been reported from different vertebrate groups, generally based on blood smear screening and in certain cases molecular analysis. The aim of this review is to compile published information on *Trypanosoma* known from non-human vertebrates on Madagascar, with the intent to provide a baseline for future research on their diversity, phylogenetic relationship, and potential implications for public health.

Occurrence of trypanosomes in Malagasy vertebrates

Trypanosoma in aquatic vertebrates

Trypanosoma are common symbionts of freshwater and marine fishes throughout the world (Kreier & Baker, 1987). The trypanosomes of aquatic hosts are transmitted by leeches, such as *Hemiclepsis marginata* (family Glossiphoniidae) and *Hirudo nipponica* (family Hirudinidae) (Molyneux, 1977; Stevens *et al*., 2001; Hayes *et al*., 2014; Fermino *et al*., 2015). Within non-terrestrial vertebrates, *Trypanosoma* are transmitted by blood-sucking leeches (Hamilton *et al*., 2005) and a variety of arthropods (Johnson *et al*., 1993; Lehane, 2005; Pinto *et al*., 2015). Within the fish fauna of Madagascar, we are unaware of any published information on *Trypanosoma* parasites.

Trypanosoma in reptiles

Based on blood smear screening, six families of reptiles are known to be infected by *Trypanosoma* (Table 1). Some taxa, such as *T*. *therezieni*, which is apparently non pathogenic in its natural host *Calumma brevicorne* (family Chamaeleonidae), are host-specific. However, during an experimental study of other chameleon species (e.g., *C*. *parsonii*, *C*. *oustaleti*, *C*. *verrucosus*, and *Furcifer lateralis*), Brygoo (1963) demonstrated that inoculation of infected blood of *T. therezieni* in these taxa was fatal.

In other hosts, *T. domerguei*, *T*. *haranti*, *T*. *petteri*, and *T*. *betschi* were found in *Oplurus cuvieri* (family Iguanidae), *Liopholidophis lateralis* (family Colubridae), *Phelsuma lineatum* (family Gekkonidae), and *Zonosaurus madagascariensis* (family Gerrhosauridae), respectively (Brygoo, 1965, 1966b). Further, three reptile species, *Calumma nasutum*, *Furcifer willsii*, and *Pelomedusa subrufa* (family Pelomedusidae) are parasitized by unidentified *Trypanosoma* (Brygoo, 1965).

Trypanosoma in amphibians

Amphibians are exposed to terrestrial and aquatic ectoparasites, such as arthropods and leeches, which can serve as hosts and vectors for trypanosomes. Recent laboratory analyses of 134 *Hoplobatrachus tigerinus* (family Dicroglossidae), a frog introduced to Madagascar, found no evidence of *Trypanosoma*

infection based on either blood smear microscopy or molecular techniques (Maeder *et al*., 2018).

Trypanosoma in birds

Based on morphological techniques, nine families of birds on Madagascar are known to be infected by *Trypanosoma*, which include the Brachypteraciidae, Bernieridae, Falconidae, Motacillidae, Ploceidae, Pycnonotidae, Sturnidae, Vangidae, and Zosteropidae (Table 1). Bennett & Blancou (1974) analyzed blood smears of 32 species of birds collected on the island between 1971 and 1973. Among those, two species, *Falco newtoni* (family Falconidae) and *Acridotheres tristis* (family Sturnidae, introduced), showed about 33% prevalence rates for *T. avium*. Subsequent work by Savage *et al.* (2009) identified *T. avium* parasites in four endemic bird species, *Atelornis pittoides* (family Brachypteraciidae), and *Cyanolanius madagascarinus*, *Schetba rufa*, and *Tylas eduardi* (family Vangidae), and *Trypanosoma everetti* in the endemic species *Ploceus sakalava* (family Ploceidae). Further, unidentified *Trypanosoma* sp.

Table 1. *Trypanosoma* identified in Malagasy vertebrates based on a literature survey. Given changes in the taxonomy of numerous hosts, we present the name used in the original *Trypanosoma* study and the current name of the same host based on taxonomical review. Names of host species in bold are those endemic to Madagascar and surrounding islands.

Order	Family	Name of host species in original study	Current name of host species	*Trypanosoma* species	References
Squamata	Chamaeleonidae	*Chamaeleo brevicornis*	***Calumma brevicorne***	*T. therezieni*	Brygoo, 1965
Squamata	Chamaeleonidae	*Chamaeleo nasutus*	***Calumma nasutum***	*Trypanosoma* sp.	Brygoo, 1965
Squamata	Chamaeleonidae	*Chamaeleo willsii*	***Furcifer willsii***	*Trypanosoma* sp.	Brygoo, 1965
Squamata	Colubridae	*Liopholidophis lateralis*	***Liopholidophis lateralis***	*T. haranti*	Brygoo, 1965
Squamata	Gekkonidae	*Phelsuma lineatum*	***Phelsuma lineatum***	*T. petteri*	Brygoo, 1966b
Squamata	Gerrhosauridae	*Zonosaurus madagascariensis*	***Zonosaurus madagascariensis***	*T. betschi*	Brygoo, 1966a
Squamata	Iguanidae	*Hoplurus sebae*	***Oplurus cuvieri***	*T. domerguei*	Brygoo, 1965
Testudines	Pelomedusidae	*Pelomedusa subrufa*	*Pelomedusa subrufa*	*Trypanosoma* sp.	Brygoo, 1965
Falconiformes	Falconidae	*Falco newtoni*	***Falco newtoni***	*T. avium*	Bennett & Blancou, 1974
Coraciiformes	Brachypteraciidae	*Atelornis crossleyi*	***Atelornis crossleyi***	*Trypanosoma* sp.	Savage *et al*., 2009
Coraciiformes	Brachypteraciidae	*Atelornis pittoides*	***Atelornis pittoides***	*T. avium*	Savage *et al*., 2009
Passeriformes	Motacillidae	*Motacilla flaviventris*	***Motacilla flaviventris***	*Trypanosoma* sp.	Raharimanga *et al*., 2002
Passeriformes	Ploceidae	*Ploceus sakalava*	***Ploceus sakalava***	*T. everetti*	Savage *et al*., 2009
Passeriformes	Pycnonotidae	*Hypsipetes madagascariensis*	*Hypsipetes madagascariensis*	*Trypanosoma* sp.	Raharimanga *et al*., 2002
Passeriformes	Sturnidae	*Acridotheres tristis*	*Acridotheres tristis*	*T. avium*	Bennett & Blancou, 1974
Passeriformes	Vangidae	*Cyanolanius madagascarinus*	***Cyanolanius madagascarinus***	*T. avium*	Savage *et al*., 2009
Passeriformes	Vangidae	*Schetba rufa*	***Schetba rufa***	*T. avium*	Savage *et al*., 2009
Passeriformes	Vangidae	*Tylas eduardi*	***Tylas eduardi***	*T. avium*	Savage *et al*., 2009
Passeriformes	Bernieridae	*Bernieria madagascariensis*	***Bernieria madagascariensis***	*Trypanosoma* sp.	Savage *et al*., 2009
Passeriformes	Bernieridae	*Phyllastrephus zosterops*	***Xanthomixis zosterops***	*Trypanosoma* sp.	Raharimanga *et al*., 2002
Passeriformes	Zosteropidae	*Zosterops maderaspatana*	***Zosterops maderaspatana***	*Trypanosoma* sp.	Raharimanga *et al*., 2002
Chiroptera	Miniopteridae	*Miniopterus manavi*	***Miniopterus mahafaliensis***	*Trypanosoma* sp.	Raharimanga *et al*., 2003
Chiroptera	Miniopteridae	*Miniopterus manavi*	***Miniopterus brachytragos***	*Trypanosoma* sp.	Raharimanga *et al*., 2003
Rodentia	Muridae	*Rattus rattus*	*Rattus rattus*	*T. lewisi*	Laakkonen *et al*., 2003b
Rodentia	Nesomyidae	*Nesomys rufus*	***Nesomys rufus***	*Trypanosoma* sp.	Laakkonen *et al*., 2003b
Primata	Indriidae	*Indri indri*	***Indri indri***	*Trypanosoma* sp.	Larsen *et al*., 2016

has been reported from six species of birds: *Bernieria madagascariensis* and *Xanthomixis zosterops* (family Bernieridae), *Atelornis crossleyi*, *Motacilla flaviventris* (family Motacillidae), *Hypsipetes madagascariensis* (family Pycnonotidae), and *Zosterops maderaspatana* (family Zosteropidae) (Raharimanga *et al*., 2002; Savage *et al*., 2009).

The identification of *Trypanosoma* in the studies cited above were mainly based on morphological criteria, which in many cases may not provide sufficient taxonomic resolution. Molecular screening is required to better understand the systematics and evolutionary history of *Trypanosoma* occurring in birds on the island.

Trypanosoma in bats

The first report of *Trypanosoma* sp. in Malagasy bats was published by Raharimanga *et al*. (2003), based on blood smears from 14 species. They reported that three individuals of *Miniopterus manavi* (family Miniopteridae) were positive. Given the recent taxonomic changes in *Miniopterus manavi sensu* Peterson *et al.* (1995), these infected bats included two individuals of *M. mahafaliensis* (from the region of Toliara) and one individual of *M*. *brachytragos* (from Namoroka) (Goodman *et al*., 2009).

Trypanosoma in terrestrial small mammals

Different studies have been conducted to examine the presence of blood parasites in small terrestrial mammals (Laakkonen *et al*., 2003a, 2003b). These authors, using microscopic techniques, analyzed six genera of rodents from different humid forest sites and belonging to two groups, including introduced Muridae, specifically *Rattus rattus* and *Mus musculus*, and endemic members of the subfamily Nesomyinae, including *Nesomys* spp., *Eliurus* spp., *Gymnuromys roberti*, and *Brachyuromys ramirohitra*. These authors found two rodent species infected by *Trypanosoma*: *R*. *rattus* with *T*. *lewisi* at an infection rate of 28% (n = 106), and *Trypanosoma* sp. in *N. rufus*, at a rate of 5% (n = 39); this latter parasite is morphologically different from samples of *T. lewisi*.

During a three-year study of Laakkonen *et al*. (2003b) in the Ranomafana National Park, infection rates of *T*. *lewisi* in *R*. *rattus* showed some variation from 26% in 1998, 44% in 1999, and 47% in 2000. *Trypanosoma* sp. in *N*. *rufus* was observed only in 1999. The other analyzed species of nesomyines showed no evidence of trypanosomes. These authors concluded that *T*. *lewisi* was not a threat to native rodents of the park, at least in the early phase of *R*. *rattus* invasion of the largely intact forest. *Trypanosoma lewisi* have stringent host specificity for *R*. *rattus* and *R*. *norvegicus* (Desquesnes *et al*., 2002); however, this parasite is known to infect a relatively broad range of flea vectors (Hoare, 1972; Desquesnes *et al*., 2002, 2011).

Trypanosoma in primates

Trypanosoma in lemurs, which are endemic to Madagascar, were recently identified by Larsen *et al*. (2016), using non-targeted deep sequencing of blood transcriptomes from two species. They found the presence of *Trypanosoma* sp. in two individuals of *Indri indri* (family Indriidae) from the eastern humid forests. They also found mixed infection of trypanosomes with other pathogens including *Babesia* sp. and *Plasmodium* sp.

Trypanosoma transmission and potential vectors

No information is available on the presence of trypanosomes in Malagasy fish, although some introduced species that occur on the island (Lévêque, 1997) are known to harbor these parasites in other areas of their distribution. For example, *Cyprinus carpio* (family Cyprinidae) is the natural host of *Trypanosoma borreli* (Kruse *et al*., 1989; Carrington *et al*., 2017) and *Channa striata* (family Channidae) is infected by *T*. *striati* (Quadri, 1955). It has been reported that aquatic leeches are implicated in the transmission of some species of *Trypanosoma* (Kreier & Baker, 1987; Stevens *et al*., 2001; Hamilton *et al*., 2005; Ferreira *et al*., 2007; Lemos *et al*., 2015).

In amphibians, *Trypanosoma* are unknown, however, potential vectors such as *Culex* spp., *Aedes aegypti* (family Culicidae), *Phlebotomus* spp. (family Psychodidae) (Irwin *et al*., 2003; Depaquit *et al*., 2007) occur on Madagascar. Recently, Robert & Brokent (2014) identified for the first time on the island the presence of the family Corethrellidae (order Diptera), which elsewhere in the world is known to be a vector of *Trypanosoma* infecting frogs (Johnson *et al*., 1993).

Trypanosoma avium is known to have a nearly worldwide distribution (Sehgal *et al*., 2001). The mode of transmission of this trypanosome among Malagasy birds remains unstudied, with various blood-sucking insects as possible vectors (Molyneux, 1977; Votýpka & Svobodovà, 2004; Votýpka *et al*., 2012; Svobodová *et al*., 2017). In the Czech

and Slovak Republics, simulid flies (*Eusimulium* spp.), hippoboscid flies (*Ornithomyia avicularia*), mosquitoes (*Culex p. pipiens*), and ceratopogonid biting midges (*Culicoides* spp.) trapped while attempting to feed on raptor nestlings, were found to contain trypanosomatids in their intestine (Votýpka *et al*., 2002).

Fleas of rats are known to transmit *T*. *lewisi* and other rodent associated trypanosomes, often referred to as *T*. *lewisi*-like due to their similar morphology, and rodents are infected by either licking flea feces on their fur or ingesting infected fleas (Albright & Albright, 1991; Molyneux, 1969b). Potential vectors include *Nosopsyllus fasciatus*, *Pulex irritans*, and *Xenopsylla cheopis* (Desquesnes *et al*., 2002; Schwan *et al*., 2016) and the latter two species that have been introduced to Madagascar. Fleas are often opportunistic parasites of available mammalian hosts, including humans (Bitam *et al*., 2010). It is therefore possible that infected fleas may transmit larval stage of *Trypanosoma* to terrestrial small mammals, as well as humans. This last point needs further examination, as no information is apparently available on the occurrence of *Trypanosoma* in humans on Madagascar. In other portions of the world, bats play the role of reservoirs and vectors for trypanosomes, and can transmit trypanosomes to other mammal species via infected triatomines bugs (family Reduviidae) (Hamilton *et al*., 2012; Pinto *et al*., 2015).

Nothing is known about wild reservoirs and vectors of *Trypanosoma* occurring on Madagascar. To provide insight to this aspect, we have tabulated the documented or presumed vectors in other parts of the world and provided annotations if these vector groups are known on the island (Table 2). These comparisons provide insight into the potential vectors on Madagascar and a base for further research.

Atypical infection on *Trypanosoma* of rodents to human: Implications for public health

Spillover of pathogens can occur across different pathways between wild or domestic animals and humans, leading to a variety of effects (Daszak *et al*., 2000; Cleaveland *et al*., 2001; Wolf *et al*., 2007; Truc *et al*., 2013; Pumhom *et al*., 2015). Introduced rodent species, such as *Mus musculus*, *Rattus rattus*, and *R*. *norvegicus* are known to have negative impacts even at the level of ecosystems (Goodman, 1995; Pitt, 2014; Shiels & Pitt, 2014; Riofrío-Lazo & Páez-Rosas, 2015). *Trypanosoma lewisi* is a cosmopolitan species originally found in *Rattus* spp. (Desquesnes *et al*., 2002). However, the high infection rates of *T*. *lewisi* in *Rattus* may lead to contact of this parasite with humans via arthropod vector feces and atypical cases of *T*. *lewisi* or *T*. *lewisi*-like infections have been recorded outside Madagascar (Sarataphan *et al*., 2007; Shah *et al*., 2011; Verma *et al*., 2011; Truc *et al*., 2013), which are sometimes fatal (Howie *et al*., 2006; Doke & Kar, 2011; Verma *et al*., 2011).

Based on the above case examples, the presence of *T*. *lewisi* in populations of introduced *Rattus* on Madagascar should be considered as a potential human health risk. Based on evidence from elsewhere in the world, human infants may be more susceptible (Verma *et al*., 2011). Exploitation of different habitat types by *R*. *rattus* provides the means for *T*. *lewisi* to be dispersed across a considerable portion of the island. Fleas are the potential vector of *T*. *lewisi* and other rodent-borne trypanosomes (Nuttall, 1908; Minchin & Thomson, 1910; Minchin & Thomson, 1915; Schwan *et al*., 2016). As stercorcarian trypanosomes, these parasites undergo development and differentiation within the gut of the arthropod vector (Molyneux, 1969a, 1969b), and are transmitted to their mammalian hosts by contamination through ingestion of infected rat fleasor feces (Strickland, 1911; Maraghi *et al*., 1995).

Trypanosoma lewisi was reported to infect other host species. For example, in Brazil, it was recently recorded in captive monkeys, also as opportunist infections (Maia da Silva *et al*., 2010).*Trypanosoma lewisi* have variable virulence when they encounter a new or naïve host species (Maraghi & Molyneux, 1989; Wyatt *et al*., 2008). In addition, this species has been shown via experiments to increase infection of *Toxoplasma gondii* in lab rats (Guerrero *et al*., 1997; Chinchilla *et al*., 2004). This aspect suggests that the presence of *Trypanosoma lewisi* may be favorable for other pathogens.

On Madagascar, different *Trypanosoma* species have been documented to occur, however, few data are available on their pathogenicity. Further, molecular genotyping of the named *Trypanosoma* and those only identified as *Trypanosoma* sp. needs to be conducted. It is important to mention that to date no case of human infection of *Trypanosoma* has been reported from the island; this is probably associated with a lack of investigation and large scale screening is needed from different ecological settings.

Human infection of *T*. *lewisi* is rare and the route of transmission to humans is unclear (Verma *et al*., 2011). Nonetheless, the presence of fleas, such as

Table 2. Vertebrate hosts and vectors of *Trypanosoma* across the worldwide and information on their occurrence on Madagascar. Distributional limits under the worldwide column are presented in some cases at the level of continents, countries, regions, republics, states, and cities.

Vector family	Vector	Known vertebrate hosts	Worldwide	Madagascar	References
DIPTERA					
Ceratopogonidae	*Culicoides* spp.	Birds	Austria, Tunisia	Present	Molyneux, 1977; Irwin *et al*., 2003
Corethrellidae	*Corethrella* spp.	Amphibia	Brazil, Florida, Mexico, Panama	Present	Johnson *et al*., 1993; Ferreira *et al*., 2008; Robert & Brokent, 2014
Culicidae	*Aedes aegypti* *Culex* spp.	Amphibia, birds	Australia, Brazil, Europe, Egypt, Florida, Prague, Moravia, Czech Republic	Present	Bailey, 1962; Molyneux, 1977; Irwin *et al*., 2003
Glossinidae	*Glossina* spp.	Reptilia, primates	Africa	Unknown	Molyneux, 1977; Leak, 1999; Votýpka *et al*., 2012
Hippoboscidae	*Ornithomya avicularia*	Birds	Canada, England, Finland, Germany	Present	Molyneux, 1977; Irwin *et al*., 2003; Rahola *et al*., 2011
Psychodidae	*Phlebotomus* spp.	Amphibia, Reptilia	Australia, Algeria, Europe, Ghana, Pakistan	Present	Molyneux, 1977; Depaquit *et al*., 2007; Kato *et al*., 2010; Nzelu *et al*., 2014
Simuliidae	*Eusimulium* spp.	Birds	Brazil, India, Malaysia, Prague,	Present	Molyneux, 1977; Pilaka & Elouard, 1999; Irwin *et al*., 2003; Votýpka & Svobodovà, 2004
	Prosimulium decemarticulatum *Simulium* spp.		Thailand, Venezuela		
Tabanidae	*Haematopota* spp. *Tabanus* spp.	Primates	Columbia, China, Europe, Guyana, Japan, Thailand, Vietnam	Present	Raymond, 1990; Otte & Abuabara, 1991; Zeegers, 2014
HEMIPTERA					
Cimicidae	*Cimex lectularius*	Bats	Africa, Asia, Europe, Oceania	Present	Paterson &Woo, 1984; Gardner & Molyneux, 1988; Salazar *et al*., 2015
Reduviidae	*Triatoma* spp. *Rhodnius* spp. *Panstrongylus megistus*	Rodents, bats, primates	Australia, Ceylon, China, Hawaii, India, Malaya, Mexico, New Guinea, Sydney, Texas, Vietnam	Present	Eads *et al*., 1963; Monteith, 1974; Brenière *et al*., 2007;Ramsey *et al*., 2012; Dujardin *et al*., 2015; Pinto *et al*., 2015
MESOSTIGMATA					
Dermanyssidae	*Dermanyssus gallinae*	Birds	London, Germany	Unknown	Macfie & Thomson, 1929; Molyneux, 1977
SIPHONAPTERA					
Ceratophyllidae	*Nosopsillus fasciatus*	Rodents	Africa, Australia, Europe, India	Unknown	Molyneux, 1970
Pulicidae	*Xenopsylla cheopis*	Rodents	Africa, Egypt, Europe, India, Mali	Present	Molyneux, 1970; Schwan *et al*., 2016
ARHYNCHOBDELLIDA					
Erpobdellidae	*Erpobdella* spp.	Amphibia	Asia, Germany	Unknown	Molyneux, 1977
Hirudinidae	*Hirudo nipponica*	Fish	Africa, Asia, Europe, Japan	Present	Molyneux, 1977; Phillips & Siddall, 2009
RHYNCHOBDELLIDA					
Glossiphoniidae	*Hemiclepsis marginata*	Fish,	Australia, Asia, Canada, Europe	Unknown	Molyneux, 1977; Lewis & Ball, 1980; Jones & Woo, 1992
	Actinobdella spp.	Amphibia,	Ghana, India, Pakistan		
	Batrachobdella picta *Glossiphonia* spp. *Helobdella algira* *Placobdella* spp.	Reptilia			

Pulex irritans and *Xenopsylla cheopis*, which can be found close to or within human settings, may lead to the transmission of trypanosome in humans. Nevertheless, human infection requires an infestation of fleas or flea feces, with people living in housing situations with potential exposure to these sources of infestation.

Conclusion

To better understand host-vector-parasite relationship of trypanosomes on Madagascar, it is important to identify the infected hosts and the vectors responsible for transmission. A detailed study using morphological and molecular techniques should provide the means to describe the diversity of *Trypanosoma* in Malagasy vertebrates. This step is important before developing studies on the life cycle and ecology of these parasites, including geographical distribution and epidemiology, as well as their possible impacts on public health. Regarding the potential vectors, future studies should examined the potential capacity of different invertebrate groups to transmit *Trypanosoma* to wild animals and humans.

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