

## Review Article: A Review of Mosquitoes Associated with Rift Valley Fever Virus in Madagascar

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**Abstract.** Rift Valley fever (RVF) is a viral zoonotic disease occurring throughout Africa, the Arabian Peninsula, and Madagascar. The disease is caused by a *Phlebovirus* (RVF virus [RVFV]) transmitted to vertebrate hosts through the bite of infected mosquitoes. In Madagascar, the first RVFV circulation was reported in 1979 based on detection in mosquitoes but without epidemic episode. Subsequently, two outbreaks occurred: the first along the east coast and in the central highlands in 1990 and 1991 and the most recent along the northern and eastern coasts and in the central highlands in 2008 and 2009. Despite the presence of 24 mosquitoes species potentially associated with RVFV transmission in Madagascar, little associated entomological information is available. In this review, we list the RVFV vector, *Culex antennatus*, as well as other taxa as candidate vector species. We discuss risk factors from an entomological perspective for the re-emergence of RVF in Madagascar.

### INTRODUCTION

Rift Valley fever (RVF) is a disease of humans and domestic animals in several African countries.<sup>1</sup> The disease is caused by an arthropod-borne virus (RVF virus [RVFV]) belonging to the family *Bunyaviridae*, genus *Phlebovirus*, which was first isolated in 1931 during outbreak in Kenya.<sup>2</sup> RVF touches a wide range of wild and domestic vertebrate species, and the severity of the disease varies according to the age of the host.<sup>3</sup> A recent RVF outbreak that occurred in Madagascar was probably associated with infected domestic animals imported from east Africa.<sup>4,5</sup> Another study suggested that this outbreak most likely originated from an endemic cycle localized in southern Madagascar, where virus circulation may occur annually.<sup>6</sup> Although not quantified, it is possible that these two mechanisms co-occur in Madagascar, with a recurrent introduction that helps RVFV maintenance and recirculation in the endemic cycle.<sup>7</sup> The role of mosquitoes in RVF transmission on the island was considered to be associated with the first RVFV isolation and the 2008–2009 outbreak.<sup>8,9</sup>

Even given the presence of 32 mosquito species in Madagascar that are known or suspected vectors of RVFV, little information is available for these taxa from an entomological perspective. Herein, we focus on the mosquito species present in Madagascar associated with RVFV transmission based on data in the literature. Our objective here is to determine the status of each vector and review aspects of their biology, geographical distribution, and ecology that might be important for RVFV vector transmission.

### HISTORY OF RVF OCCURRENCE IN MADAGASCAR

Three RVFV circulation periods are known to have taken place in Madagascar. In 1979, the virus was isolated from mosquitoes captured in a humid forest near Andasibe-Périnet in central eastern Madagascar, but no evidence of an epizootic period was reported.<sup>8</sup> In 1990 and 1991, RVFV was isolated from humans and livestock in the lowland eastern coastal and upland central highlands, respectively.<sup>10,11</sup> Twenty years later, in 2008 and 2009, an RVF outbreak was reported in several

regions of the island with virus detection and isolation in mosquitoes, humans, and livestock.<sup>4,9</sup> As supporting evidence, anti-RVFV (immunoglobulin M [IgM] and IgG) antibodies have been detected in livestock and humans during periods between virus outbreaks.<sup>12,13</sup> These results suggest a silent but continuous circulation of the virus in livestock.

### RVF TRANSMISSION

On a global basis, the occurrence and spread of the RVF outbreaks on the African mainland and the Arabia Peninsula are variable and found in different ecoclimatic zones; vector species and vector capacity are influenced by ecological,<sup>14</sup> behavioral,<sup>15</sup> and RVFV molecular factors.<sup>16,17</sup> For example, in an arid area, such as the Arabian Peninsula, RVFV transmission by mosquitoes is related to rainfall and water runoff management, with temporary rain pools and floodplains representing favorable vector breeding sites.<sup>18–20</sup> In subhumid areas in east Africa, RVF emergence is partly caused by the vertical transmission of the virus in eggs of *Aedes* spp., especially those belonging to the *Neomelanicionion* subgenus,<sup>21</sup> that are laid in wetland habitats. In the context of El Niño–Southern Oscillation (ENSO) events, wetlands become flooded after abnormally high rainfall, which in turn, favors the hatching of infected *Aedes* eggs and the development of the immature stages. This leads to the epizootic episode after adult emergence, which is soon followed by a parallel emergence of *Culex*.<sup>22,23</sup> In west Africa, the virus circulates in the Sahelian area transmitted by *Aedes* and *Culex* mosquitoes, which develop in temporary pools where cattle and sheep concentrate during the rainy season. Dam construction and ecological modification of the environment, including the presence of rice fields, may lead to the outbreaks directly associated with vector abundance.<sup>24,25</sup>

Mosquitoes can become infected by feeding on an infected host that exhibits a viremia higher than 10<sup>1.3</sup> plaque-forming unit (pfu)/mL.<sup>26</sup> RVFV can be transmitted to vertebrates and mosquitoes by several mechanisms. (1) The transmission of RVFV occurs through direct contact with body fluids (blood, saliva, and/or nasal discharges) of infected animals or aborted ruminant fetuses.<sup>27,28</sup> Humans can be infected by contact with infected tissues or aerosols of infected blood generated during ruminant abortion or animal slaughter.<sup>27,29</sup> (2) Vector transmission occurs through the bite of infected mosquitoes.<sup>30</sup> The

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first evidence of vector transmission goes back to 1948, when RVFV was first isolated in a laboratory experiment and identified from field-collected mosquitoes (*Eretmapodites* spp. and *Ae.* [*Aedimorphus*] *tarsalis* group).<sup>31</sup> (3) Vertical transmission of RVFV from infected female mosquitoes to their progeny also occurs. This means of transmission was reported in the field for *Ae.* (*Neomelanicionion*) sp.<sup>21</sup> and suggested for *Ae.* (*Aedimorphus*) subgenus.<sup>18</sup>

Although RVF transmission to humans by infected mosquitoes was never been directly reported, probably more than one species of the *Ae. tarsalis* group and 78 mosquito species from eight genera have been associated with RVFV. Based on the functioning of virus–vector systems,<sup>32</sup> three criteria are necessary to show the vector status of a given mosquito species: (1) the isolation of RVFV from wild-caught mosquitoes, (2) the observation in a laboratory setting of vector competence, and (3) evidence from the field of an association between the arthropod vector and the vertebrate populations in which the infection is occurring. In this paper, we propose that mosquito vectors can be subdivided into three categories: vector, candidate vector, and potential vector. If only one criterion is validated, the mosquito species is qualified as a potential vector; in the case of two criteria, the mosquito species is qualified as a candidate vector, and for all three criteria, the mosquito species is qualified as a vector.

#### MOSQUITO VECTORS IN MADAGASCAR

Twenty-four species have been associated with RVFV infections in Madagascar, representing 11% of known culicidian species on the island.<sup>33</sup> Most of these species have zoophilic behavior (cattle, sheep, and goat), and some of them are described opportunistic anthropophilic feeders.<sup>15,34,35</sup> These taxa belong to the genera *Aedes*, *Anopheles*, *Culex*, *Eretmapodites*, and *Mansonia* following traditional morphological classifications.<sup>36,37</sup>

In Madagascar, six species of *Aedes* fall into the vector, candidate vector, and potential vector categories associated with RVFV. Most of these are known to feed on animals, and *Ae. albopictus* and *Ae. aegypti* are highly anthropophilic.<sup>12</sup> These six taxa belong to subgenera known and/or suggested (based on fieldwork) to vertically transmit RVFV on the African mainland (*Aedimorphus*, *Neomelanicionion*, and *Stegomyia*), suggesting that RVFV maintenance by vertical transmission is possible in Madagascar. Five *Anopheles* species are associated or potentially associated with RVF transmission; all are zoophilic or zooanthrophilic taxa,<sup>33</sup> and three species are reported to be infected with RVFV in continental Africa and Madagascar.<sup>9,21</sup> Ten *Culex* vector species associated with RVF infection are present in Madagascar. Nine of them are already reported in the field to be RVFV-positive in Africa and Madagascar.<sup>9,19,25,38–41</sup> One *Eretmapodites* species and two *Mansonia* species also could be potential vectors in Madagascar.

Among these mosquito species, four were found naturally infected in Madagascar: *An. coustani*, *An. squamosus*, *Cx. antennatus*, and *Ma. uniformis*.<sup>9,42</sup> Recently considered as an RVFV candidate vector,<sup>15</sup> *Cx. antennatus* also has a high vector competence.<sup>43</sup> Only this species in Madagascar meets the three criteria needed to be considered an RVFV vector. Moreover, this zooanthrophilic species is present and abundant in all five biogeographical domains of Madagascar. Recently considered as an RVFV candidate vector,<sup>15</sup> *Cx. antennatus* has high vector

competence.<sup>43</sup> Consequently, the role of this species as a major vector of RVFV is confirmed. *An. coustani* and *An. squamosus* are the most abundant *Anopheles* taxa in Madagascar, both being zoophilic with broad distributions across the island.<sup>12,15</sup> Information is currently not available on the level of vector competence, and hence, both species remain RVFV candidate vectors.<sup>15</sup>

Using this proposed system of categorization, seven other zooanthrophilic species should be included: *Cx. univittatus*, *Cx. pipiens*, *Cx. quinquefasciatus*, *Cx. poicilipes*, *Cx. tritaeniorhynchus*, *Er. quinquevittatus*, and *Ma. uniformis*. These species are also abundant and present across Madagascar.<sup>12</sup> With information on natural and experimental infection of these *Culex* and *Eretmapodites* species (Table 1) and the absence of RVFV detection in the field in Madagascar, these species are considered as candidate vectors. No experimental information is available for *Ma. uniformis* in the transmission of RVFV. However, this species is abundant, and humans are considered to be its principal host in Madagascar<sup>12</sup> and on the African mainland.<sup>35</sup> The remaining mosquito species listed in Table 1 and present in Madagascar should be considered as potential vectors.

#### RISK FACTORS ASSOCIATED WITH MOSQUITO POPULATIONS

Excluding factors associated with vertebrates (species, movement, density, susceptibility, and vaccination),<sup>69</sup> mosquito vectors are major components of RVF risk, which we refer to as the entomological risk. Classically, this entomological risk takes into account mosquito density, population dynamics, trophic behavior, longevity of each mosquito population in a given place, and vector competence of each species/population for a given virus strain, including vertical transmission. These variables are almost certainly influenced by climate (temperature and rainfall), biotic variables (breeding sites and presence of vertebrate hosts), and vector control as observed in Madagascar<sup>15,69,70</sup> and other countries.<sup>71</sup>

In Madagascar, the distributions of mosquitoes classified as RVFV vectors, potential vectors, and candidate vector are notably different and associated with biogeographical domains.<sup>12</sup> These differences might explain regional differences in RVFV prevalence and outbreaks.<sup>4,6</sup> RVF circulation and occurrences generally happen during the wet and warm season,<sup>4</sup> which correlates with the period of highest mosquito density.<sup>9,15,12</sup> This increase in mosquito vector density is caused by the creation and maintenance of different breeding sites.<sup>72</sup> Indeed, mosquitoes species already associated with RVFV in Madagascar colonize different types of larval breeding sites, with rice fields being a dominant habitat.<sup>33,69</sup>

In Madagascar, vector control is primarily targeted against mosquitoes transmitting malaria through the use of indoor residual spraying (IRS) and nets (insecticide-treated mosquito nets and long-lasting insecticidal mosquito nets).<sup>73</sup> No larvicidal measures have been undertaken on the island. The positive effect of these indoor treatments is to kill mosquitoes. Several RVFV vectors are exophilic species and probably escape these treatments. The negative effect is the appearance of more exophilic and zoophilic populations after indoor treatment, which was observed in Equatorial Guinea,<sup>74</sup> Tanzania,<sup>75</sup> Benin,<sup>76</sup> and Senegal.<sup>77</sup> For RVF infection, this negative effect is poorly documented and therefore, speculative. Consequently, vector control in Madagascar should not be a significant

TABLE 1  
Mosquito species associated with RVF transmission around the world

Genus and species*	Natural infection		Infection		Transmission		References		
	Country	Periods	ID	Rate (%)	ID	Rate (%)	NT	ID + IR	ID + TR
<i>Aedes</i>									
<i>Stegomyia</i>									
<i>  africanus</i>	Uganda	1956					44		
<i>Aedimorphus</i>									
<i>  argenteopunctatus</i> †					6.8, 7.8 log <sub>10</sub> CPD <sub>50</sub> pfu/mL	14, 80			45
<i>  cumminsii</i>	Senegal	1983					21		
<i>  dalzielii</i> †	Senegal	1983					46		
<i>  dentatus</i>	South Africa	1969			6.8, 9.8 log <sub>10</sub> CPD <sub>50</sub> pfu/mL	32, 50		45	
<i>  tarsalis</i>	Uganda‡	1948					31		
<i>  vexans</i>	Saudi Arabia	2000			10 <sup>8.5</sup> pfu/mL, 10 <sup>10.1,10.2</sup> pfu/mL	23, 25	19	29, 48	48
<i>  ochraceus</i>	Senegal, Kenya	1993, 2006			10 <sup>1.3,1.6</sup> pfu/mL, > 10 <sup>6.4</sup> pfu/mL	43	41, 49	26	26
<i>Finlaya</i>									
<i>  notoscriptus</i>					10 <sup>7</sup> pfu/mL			50	
<i>  japonicus</i>					≥ 10 <sup>8.5</sup> pfu/mL			51	
<i>Neomelaniconion</i>									
<i>  circumluteolus</i> †	Uganda, South Africa	1955			≥ 10 <sup>8</sup> pfu/mL	21	44	52	52
<i>  mcintoshi</i>	Zimbabwe, South Africa	1969, 1974, 1978			10 <sup>8</sup> pfu/mL	14	53	52	52
<i>  palpalis</i>	Central African Republic	1969			≥ 10 <sup>8</sup> pfu/mL	55	54	52	52
<i>  unidensatus</i>					6.8, 7.8 log <sub>10</sub> CPD <sub>50</sub> pfu/mL	58		45	45
<i>Stegomyia</i>									
<i>  africanus</i>	Uganda	1956					44		
<i>  dendrophilus</i>	Uganda	1948					31		
<i>  albopictus</i> †					4.3, 5.9 log <sub>10</sub> pfu/mL	4, 12		55	55
<i>  aegypti</i> †	Sudan	2007			5.8 log <sub>10</sub> pfu/mL, ≥ 10 <sup>8.0</sup> pfu/mL	7, 14	56	52, 57	52, 57
<i>  calceatus</i>					≥ 10 <sup>8</sup> pfu/mL	< 2		52	52
<i>Ochlerotatus</i>									
<i>  atlanticus</i>					10 <sup>8.3</sup> , > 10 <sup>9.5</sup> pfu/mL	9, 40		58	58
<i>  canadensis</i>					10 <sup>6.2,7.2</sup> pfu/mL	10, 54		59	59
<i>  cantator</i>					10 <sup>6.7</sup> pfu/mL	3		59	59
<i>  caspius</i>					≥ 10 <sup>5.3</sup> pfu/mL	20		30	30
<i>  communis</i>					10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	NT		60	60
<i>  detritus</i>					10 <sup>8.5</sup> pfu/mL			61	61
<i>  dorsalis</i>					10 <sup>7.3,8.8</sup> , 10 <sup>7.9,9.4</sup> pfu/mL	0		60, 62	60, 62
<i>  exrucians</i>					10 <sup>6.2,7.2</sup> pfu/mL	11		59	59
<i>  fitchii</i>					10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	0		60	60
<i>  implicatus</i>					10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	0		60	60
<i>  infirmatus</i>					> 10 <sup>7.6</sup> , > 10 <sup>7.5</sup> pfu/mL	< 1, 4		58	58
<i>  juppi</i>	South Africa	1980			3.6, 8 log <sub>10</sub> pfu/mL	25	57	63, 57	57
<i>  solliticans</i>					10 <sup>6.2,7.2</sup> pfu/mL	17		59	59
<i>  sticticus</i>					10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	8		60	60
<i>  stimulans</i>					10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	0		60	60
<i>  taeniorhynchus</i>					10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	0		60	60
<i>  caballus</i>					10 <sup>6.2,7.2</sup> pfu/mL	12		48, 59	48, 59
<i>  vigilax</i>	South Africa	1953			3.6, 7.8 log <sub>10</sub> pfu/mL	0	64	57	57
<i>Protomacleania</i>					10 <sup>7</sup> pfu/mL			50	
<i>  triseriatus</i>					10 <sup>6.2,7.2</sup> pfu/mL	36		59	59

(continued)

TABLE 1  
Continued

Genus and species*	Natural infection			Infection		Transmission		References	
	Country	Periods	ID	Rate (%)	ID	Rate (%)	NT	ID + IR	ID + TR
<i>Skusea pambaensis</i>	Kenya	2006					41		
<i>Anopheles tenebrosus</i> §	Zimbabwe, Madagascar	1969, 2008	NT	NT	NT	NT	9, 47	30	30
<i>cousantii</i> †	Madagascar	1979					8		
<i>coustani + fuscicolor</i> †			10 <sup>7.6</sup> > 10 <sup>9.5</sup> pfu/mL	48, 100	10 <sup>7.6</sup> pfu/mL, 10 <sup>9.5</sup> pfu/mL	< 1		58	58
<i>crucians</i>			> 10 <sup>8.8</sup> pfu/mL	64	> 10 <sup>8.8</sup> pfu/mL	< 1		62	62
<i>quadrinaculatus</i> †									
<i>Cellia squamosus</i> †	Kenya, Madagascar	2006–2007, 2008					9, 41		43
<i>pharoensis</i> †	Kenya	1985	≥ 10 <sup>6.0</sup> pfu/mL	100	9.5 log <sub>10</sub> SMICLD <sub>50</sub> /mL	4†	21	30	
<i>arabensis</i> †	Sudan	2007		2			56	29	
<i>multicolor</i>			9.5 log <sub>10</sub> SMICLD <sub>50</sub> /mL	90	9.5 log <sub>10</sub> SMICLD <sub>50</sub> /mL	13		43	43
<i>stephensi</i> ¶			NT	NT	NT	NT		65	65
<i>paultani + squamosus</i> †	Madagascar	1979					8		
<i>Myzomyia cinereus</i>	South Africa	1974–1975					57		
<i>Coquillettidia fuscopennata</i>	Uganda	1960					66		58, 60
<i>perturbans</i>									
<i>grandidieri + Ma. uniformis</i> †	Madagascar	1979	10 <sup>6.6</sup> , > 10 <sup>9.5</sup> pfu/mL	47, 100	10 <sup>6.6</sup> , 10 <sup>9.5</sup> pfu/mL	17, 71		58	
<i>Culex antennatus</i> †	Madagascar	2008	10 <sup>5.5,6</sup> pfu/mL	60, 100	> 10 <sup>7</sup> pfu/mL, ≥ 10 <sup>8</sup> pfu/mL	7, 84	9	30, 52	30, 52
<i>amultirostris</i>			10 <sup>7</sup> pfu/mL	55				50	
<i>erythrothorax</i>			10 <sup>8.8</sup> pfu/mL	70	≥ 10 <sup>8.8</sup> pfu/mL	7		62	62
<i>pipiens</i> †	Egypt, Kenya	1977, 1987, 1991	10 <sup>6.5</sup> MICLD <sub>50</sub> /mL, ≥ 10 <sup>8</sup> pfu/mL	40, 91	> 10 <sup>7</sup> pfu/mL, ≥ 10 <sup>8</sup> pfu/mL	7, 100	39, 67	52, 68	30, 52
<i>univittatus</i> †	Kenya	2006	5.1, 6.5 log <sub>10</sub> pfu/mL	20, 87	5.1, 6.5 log <sub>10</sub> pfu/mL	33	41	57	57
<i>quinquefasciatus</i> †	Kenya	2006	4.6 log <sub>10</sub> pfu/mL, 10 <sup>7</sup> pfu/mL	25, 30	≥ 10 <sup>8</sup> pfu/mL to 4.6 log <sub>10</sub> pfu/mL	5, 44	41	50, 57	52, 57
<i>bitaeniorhynchms</i> †	Kenya	2006					41		
<i>tritaeniorhynchms</i> †	Saudi Arabia	2000							
<i>tarsalis</i>			6.9 log <sub>10</sub> pfu/mL	73			19	19	
<i>zombaensis</i>	South Africa, Kenya	1981, 1989	10 <sup>7.9</sup> ≥ 10 <sup>8.8</sup> pfu/mL	88, 93	10 <sup>7.9</sup> , ≥ 10 <sup>8.8</sup> pfu/mL	6, 31		60, 62	60, 62
<i>simpsoni + vansomeri</i>	Madagascar	1979	5.2, 8 log <sub>10</sub> pfu/mL	35, 92			40, 67	40	
<i>+ univittatus</i> †							8		
<i>antennatus + simpsoni</i>	Madagascar	1979					8		
<i>+ vansomeri</i> †									
<i>simpsoni + vansomeri</i>	Madagascar	1979					8		
<i>+ annulioris</i> †									
<i>neaveri</i> †	South Africa	1981	6.6, 8.5 log <sub>10</sub> pfu/mL	14	10 <sup>6.2,7.2</sup> pfu/mL	1, 51, 11, 11	40	63	59
<i>salinarius</i>			10 <sup>6.2,7.2</sup> pfu/mL	51, 88		13, 70		59, 48	59
<i>theileri</i> †	South Africa	1971	5.3, 8 log <sub>10</sub> pfu/mL	68, 99	5.3, 6.4 log <sub>10</sub> pfu/mL	4	47	57	57
<i>nigripalpus</i>			≥ 10 <sup>8.8</sup> pfu/mL	49	≥ 10 <sup>8.8</sup> pfu/mL	11		62	62
<i>perexiguus</i>			10 <sup>5.3, ≥ 7</sup> pfu/mL	30, > 75	> 10 <sup>7</sup> pfu/mL	40		30	30
<i>restuans</i>			10 <sup>1.3</sup> pfu/mL	100	10 <sup>1.3</sup> pfu/mosquitoes	40		60, 62	60

(continued)

TABLE 1  
Continued

Genus and species*	Natural infection		Infection		Transmission		References	
	Country	Periods	ID	Rate (%)	ID	Rate (%)	NT	ID + IR
<i>Eumaloneyia rubinotus</i> †			6.9 log <sub>10</sub> pfu/mL	32	6.9 log <sub>10</sub> pfu/mL	0		57
<i>Melanoconion erratiati</i>			10 <sup>7.3</sup> , 10 <sup>10.1</sup> , 10 <sup>10.2</sup> pfu/mL	9, 79	10 <sup>10.1</sup> , 10 <sup>10.2</sup> pfu/mL	33		48, 62
<i>Neoculex territan</i>			10 <sup>6.2</sup> , 7.2 pfu/mL	74	10 <sup>6.2</sup> , 7.2 pfu/mL	25		59
<i>Oculeomyia poecilipes</i> †	Senegal, Mauritania, Kenya	1998, 1998–1999, 2006	7.8 log <sub>10</sub> CPD <sub>50</sub> pfu/mL	90	6.8, 9.8 log <sub>10</sub> CPD <sub>50</sub> /mL	15, 80	25, 41	45
<i>Culiseta inornata</i>			10 <sup>7.9</sup> , 10 <sup>9.4</sup> pfu/mL	100	10 <sup>7.3</sup> , 9.4 pfu/mL	NT		60
<i>minnesotae</i>			10 <sup>1.3</sup> pfu/mL	67	10 <sup>1.3</sup> pfu/mosquitoes	0		60
<i>Eremapodites</i> sp.	Uganda	1948					31	
<i>quinquevittatus</i> †	South Africa	1971	8.2, 7.2 log <sub>10</sub> pfu/mL	74, 81	8.2 log <sub>10</sub>	> 30	47	57
<i>Mansonia mansonioides</i>								
<i>africana</i> †	Uganda, Kenya	1959, 2007					41, 66	
<i>dyari</i>								
<i>uniformis</i> †	Madagascar, Kenya	1979, 2006	10 <sup>5.7</sup> , 10 <sup>7.6</sup> pfu/mL	33, 62	10 <sup>5.7</sup> , 10 <sup>7.7</sup> pfu/mL	< 1, 9	8, 41	58
<i>Psorophora ferox</i>			10 <sup>8.3</sup> , > 10 <sup>9.5</sup> pfu/mL	90, 100	10 <sup>8.3</sup> , > 10 <sup>9.5</sup> pfu/mL	16, 40		58

CPD<sub>50</sub> = cytopathic dose 50; ID = infection dose (the dose of virus to which the mosquito was exposed); IR = infection rate; NT = the oral experiment was not tested (i.e., mosquitoes were inoculated intrathoracically with RVFV); MICLD<sub>50</sub> = median mouse intracerebral lethal doses; SMICLD<sub>50</sub> = suckling mouse intracerebral 50% lethal doses; TR = percentage of refeeding mosquitoes that transmitted virus by bite.

\* Nomenclature from the Walter Reed Biostatistics Unit at the Smithsonian Institution (wrbusi.edu).

† Vector, candidate vector, and potential vector in Madagascar.

‡ The species found to be naturally RVFV-positive by Smithburn and others<sup>31</sup> was not specified, and it consisted of the *Ae. tarsalis* group.

§ Transmission obtained after inoculation of the virus in adult and/or larval stage.<sup>30,65</sup>

¶ Transmission obtained after inoculation of the virus in adult and/or larval stage.<sup>30,65</sup> Infection rate and transmission rate are obtained at 26 °C as mentioned in all studies.

component of variation of transmission risk of RVF. However, the appearance of more exophilic and zoophilic populations cannot be removed from the RVFV transmission risk factors list, because transmission involves mainly exophilic and zoophilic species.<sup>33</sup>

Vector competence of Malagasy mosquitoes, including their ability to transmit RVFV to their progeny, is very poorly known. Vertical transmission has been observed in Africa in the *Neomelanicion* subgenera of the *Aedes* genus, which is also present in Madagascar, and hence, it may occur on the island.<sup>12</sup> Because of the lack of evidence in Madagascar of natural populations of *Aedes* spp. being infected with RVF, the role of vertical transmission in maintenance of the disease remains hypothetical. However, the majority of involved *Aedes* subgenera is present in Madagascar.<sup>9,12,78</sup> Additional detection of RVF is needed (especially in the western domain, where high RVFV prevalence has been reported, and the southwestern domain, where endemic foci areas have been suggested to occur<sup>6</sup>), particularly in the context of viral maintenance through a possible vertical transmission. Field studies on vector biology and RVF entomological surveys need to be further advanced to determine if endemic cycles occur.

#### IS IT POSSIBLE TO IDENTIFY RVF RISK AREAS IN MADAGASCAR?

Recent history of RVFV circulation in Madagascar showed 13 administrative regions of the island, specifically the northern, eastern, and central domains, where RVF epidemics/epizootics occurred.<sup>4</sup> The highest RVFV prevalence rates were observed in livestock in the western and northern domains.<sup>6</sup> The suggested RVFV candidate vectors (*An. squamosus* and *An. coustani*) and major vector (*Cx. antennatus*) reproduce in areas with large areas of water.<sup>33</sup> Consequently, remote sensing technology can be relevant to predict RVF outbreaks by identifying the environmental factors, such as breeding sites and rainfall, associated with the abundance of RVF vectors that have been observed on mainland Africa.<sup>1,79,80</sup> In Madagascar, this technique was used on a local scale of one domain during a malaria study<sup>81</sup> and could provide interesting insights associated with RVF entomological surveys, particularly in the southwestern domain, where RVF is considered to be endemic.<sup>6</sup> Variation in monthly and annual precipitations (<http://iridl.ldeo.columbia.edu/>) and patterns of variation in larval development are important factors that vary between biogeographical domains<sup>69</sup>; hence, this technology should be used for the identification RVF risk areas. It could be very useful to estimate the relationship between abundance of breeding sites and density of adult vectors for additional vector surveillance and control.

#### GENERAL CONCLUSIONS

In Madagascar, there are 23 mosquito species considered as vectors or potential vectors of RVFV. Only one species, *Cx. antennatus*, meets the three criteria for classification as an RVFV vector and should be considered as an important vector of this disease. Several other species, such as *An. squamosus*, *An. coustani*, *Cx. univittatus*, *Cx. pipiens*, and *Ma. uniformis*, should be classified as candidate vector species. To date, contrary to what has been observed in different parts of Africa, no Malagasy *Aedes* species has been involved in the

transmission of this fever. However, several species, including endemics, belonging to the *Aedes* subgenera involved in transmission and maintenance of RVFV in Africa, specifically *Neomelanicion* and *Aedimorphus*, occur in Madagascar. Finally, a considerable amount of information and data is lacking for understanding of RVF transmission on the island, and the vector component is one of the key factors for deciphering past outbreaks and if possible, predicting future events.

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