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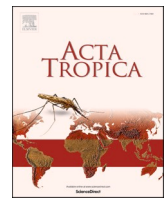
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Interaction between Old World fruit bats and humans: From large scale ecosystem services to zoonotic diseases

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ABSTRACT

The Old World tropical and subtropical frugivorous bat genus *Rousettus* (Pteropodidae) contains species with broad distributions, as well as those occurring in restricted geographical areas, particularly islands. Herein we review the role of *Rousettus* as a keystone species from a global “One Health” approach and related to ecosystem functioning, zoonotic disease and public health. *Rousettus* are efficient at dispersing seeds and pollinating flowers; their role in forest regeneration is related to their ability to fly considerable distances during nightly foraging bouts and their relatively small body size, which allows them to access fruits in forested areas with closed vegetation. *Rousettus* are also reservoirs for various groups of pathogens (viruses, bacteria, fungi, protozoa), which, by definition, are infectious agents causing disease. The study of day roosts of different species of *Rousettus* and the successful establishment of captive breeding colonies have provided important details related to the infection dynamics of their associated pathogens. Large-scale conversion of forested areas into agricultural landscapes has increased contact between humans and *Rousettus*, therefore augmenting the chances of infectious agent spillover. Many crucial scientific details are still lacking related to members of this genus, which have direct bearing on the prevention of emerging disease outbreaks, as well as the conservation of these bats. The public should be better informed on the capacity of fruit bats as keystone species for large scale forest regeneration and in spreading pathogens. Precise details on the transmission of zoonotic diseases of public health importance associated with *Rousettus* should be given high priority.

1. Introduction

Bats are classified in the order Chiroptera, including more than 1400 identified species (Fenton, 2020). They are generally nocturnal and have a variety of dietary preferences including those that are animalivores (eating insects and vertebrates), sanguivores and consumers of different plant parts (fruits, pollen, nectars and leaves). Fruit-consuming species play key roles in ecosystem functioning, such as seed dispersal and flower pollination, and insect-consuming species help to regulate arthropods that are agricultural pests and responsible for the transmission of zoonotic diseases to people (Kunz et al., 2011; Gonsalves et al., 2013; Chan et al., 2020). During the day, a period when bats are not active, they roost in different structures, including caves, crevices, trees, and human infrastructures (bridges, building attics, etc.). In different portions of the world, people and bats can occupy the same buildings. This increases exposure of domesticated animals and humans to infectious

agents associated with bats, such as coronaviruses, Ebola virus, Hendra virus, Nipah virus, lyssaviruses, *Rickettsia* spp. or *Bartonella* spp. (e.g. Wong et al., 2007; Joffrin et al., 2018; Lu et al., 2021).

Rousettus (Pteropodidae), a family restricted to the Old World, is the only tropical and subtropical fruit bat genus having a distribution including Africa, Asia, Indian Ocean islands, Australasia and subtropical Europe. In this review, we focused on *R. leschenaultii*, *R. aegyptiacus*, *R. madagascariensis* and *R. obliviosus* (Fig. 1), with the first two species distributed in different portions of Southern Asia, the Middle East, Southern Europe, and African mainland and associated islands, and the second two species being insular and found on western Indian Ocean islands (Fig. 2). These four species were chosen because they are closely related in a phylogenetic sense, and play important roles in ecosystem functioning at a large-scale in continental areas and on islands in the tropical and subtropical Old World. In addition, we compare published data on the ecology and parasitology of *R. leschenaultii* and

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R. aegyptiacus, which are among the most studied Pteropodidae, to those available for sister species, *R. madagascariensis* and *R. obliviosus*, which have been less intensively studied. These different bats have been shown to provide key ecosystem services and, on the basis of different

inferences, their historical distributions are associated with the extent of forest cover in the Middle East and African mainland (Stribna et al., 2019). Members of this genus are also subjected to anthropogenic pressures such as hunting, mostly agriculturalists protecting their fruit

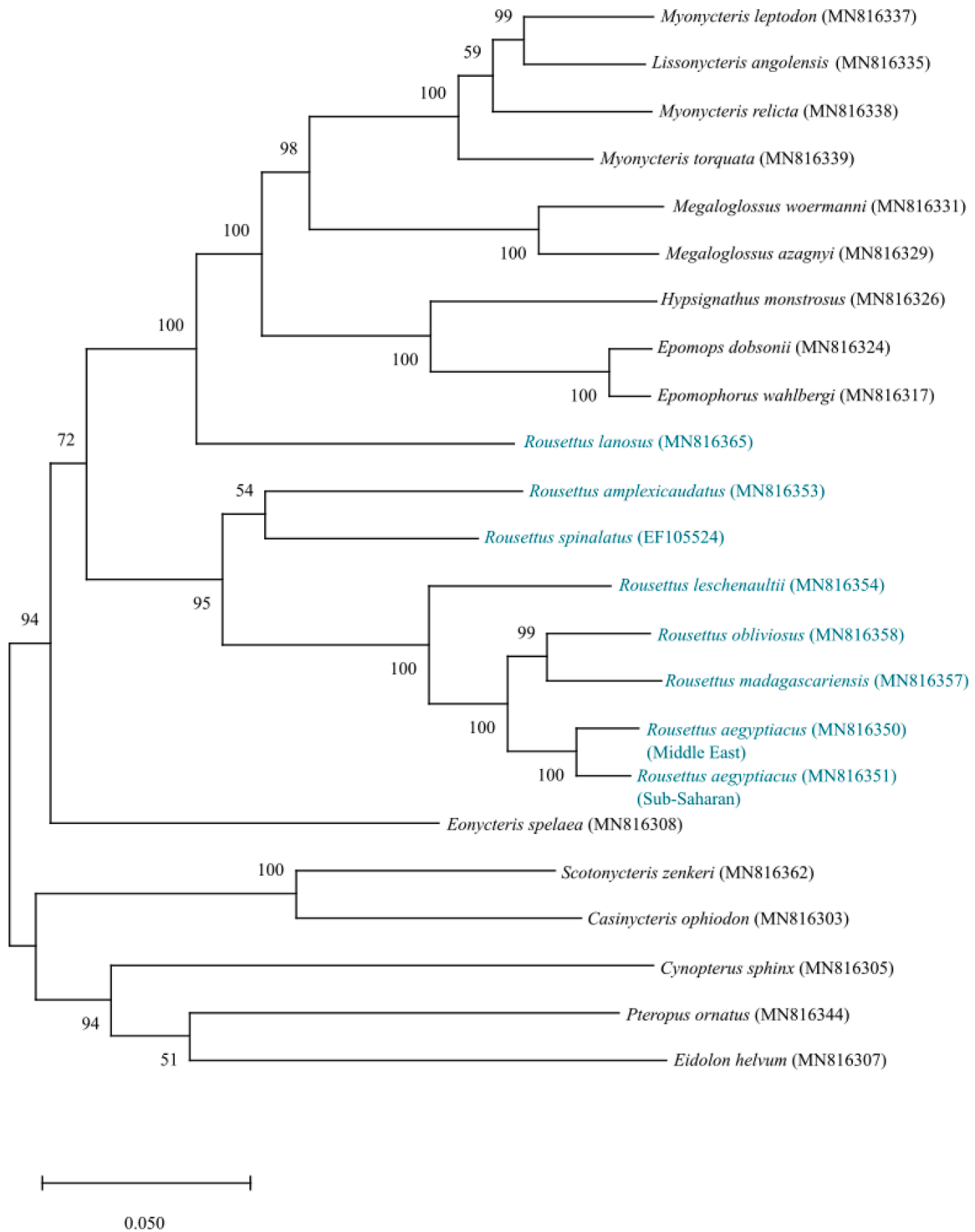


Fig. 1. Phylogenetic relationship between *Roussettus* species (in green) by Maximum Likelihood method using MEGA X. This midpoint rooted phylogenetic tree is based on the complete mitochondrial genome, with the General Time Reversible evolutionary model, and 1000 bootstrap replicates (adapted from Hassanin et al., 2020). Genbank accession numbers are in parentheses. *Roussettus amplexicaudatus* is the most basal species of the genus and *R. spinalatus* is the most closed sister species of *R. amplexicaudatus*. Almeida et al. (2016) showed that *R. spinalatus* was the first species splitting from *R. amplexicaudatus*, and this can explain the basal place of *R. spinalatus* with *R. amplexicaudatus*. Recent published information (Almeida et al., 2016; Hassanin et al., 2019; Vogeler and Tschapka, 2021) indicates that *R. lanosus* falls outside the *Roussettus* clade and best placed in another genus; and here, mitochondrial sequence data supports this proposition. There is no available sequence data for *R. celebensis* and *R. linduensis*.

crops. Although an ever increasing number of studies have described many pathogens associated with the genus *Rousettus* (Table 1), they are still hunted and consumed for food by people in some areas of Asia, Africa and western Indian Ocean islands (Jenkins and Racey, 2008; Fan et al., 2019). Such practices increase contact between people and *Rousettus* and therefore augment the risk of infectious agent transmission.

The ecological importance of *Rousettus* and their interaction with humans, including anthropogenic pressure and zoonotic disease transmission, remain understudied, with the exception of *R. aegyptiacus* (e.g. Townner et al., 2009; Paweska et al., 2016). In the context of zoonotic disease emergence, studies investigating the relation between ecosystem disturbance and transmission dynamics of bat infectious agents are needed. The aim of this paper is to review current knowledge on the role of *Rousettus* with regards to ecosystem services, as well as their implication in the transmission of infectious agents. We also discuss challenges associated with reducing anthropogenic pressures on these bats, which are essential for controlling emergence of bat-associated infectious diseases, as well as advancing their conservation.

2. Review process: paper and data research

Data that were examined in this review were obtained from scientific journal papers (original research article, review, short communication, note, etc.), published reports, online digital data having a solid scientific basis, available Master and PhD thesis, and books and monographs. Grey literature, personal communications and unpublished reports were not considered. We used physical and electronic information that were available on Google, Google Scholar, PubMed, Springer Link, ScienceDirect, DBatVir web site (Chen et al., 2014; <http://www.mgc.ac.cn/DBatVir/>) and ResearchGate. Key words used for online paper research were “Africa”, “Asia”, “bacteria”, “bat fly”, “bats”, “China”,

“Comoros”, “conservation”, “economy”, “ecosystem services”, “ectoparasites”, “Egypt”, “human pathogen”, “India”, “Indian Ocean”, “Madagascar”, “Middle East”, “pathogen”, “pollination”, “protozoa”, “Pteropodidae”, “*R. aegyptiacus*”, “*R. leschenaultii*”, “*R. madagascariensis*”, “*R. obliviosus*”, “*Rousettus*”, “seed dispersal”, “sub-tropical”, “tropical”, “vector”, “virus”, “zoonotic disease”. The countries chosen as key words were those where the four studied *Rousettus* species are found and, in some cases, extensively studied.

The first criteria in the selection of a paper were based on the title and the abstract. Most of the papers reviewed were in English and French; however, papers written in other languages but having an English or French abstract were also examined. Literature that first presented a specific point or information and the most updated paper were cited as priority. Only primary references were cited. Literature searches were conducted up until February 2022.

3. Evolutionary history of *Rousettus*

The genus *Rousettus* has been proposed to have an Asiatic origin (Hassanin et al., 2020). The most basal living species is *R. amplexicaudatus* (Almeida et al., 2016, Fig. 1) from which diverged all the eight other living species (Simmons, 2005). *Rousettus leschenaultii*, which diverged from *R. amplexicaudatus*, is distributed today in southern Asia (Hassanin et al., 2020). *Rousettus aegyptiacus* diverged from *R. leschenaultii* and covers an area ranging from Southern Europe, the Middle East to South Africa (Fig. 2).

Genetic studies have shown that the species living in the Comoros (*R. obliviosus*) and on Madagascar (*R. madagascariensis*) are sister taxa and genetically closer to *R. leschenaultii* than *R. aegyptiacus* (Goodman et al., 2010; Stribna et al., 2019). The arrival of this genus on islands in the western Indian Ocean is estimated to have occurred in the Middle

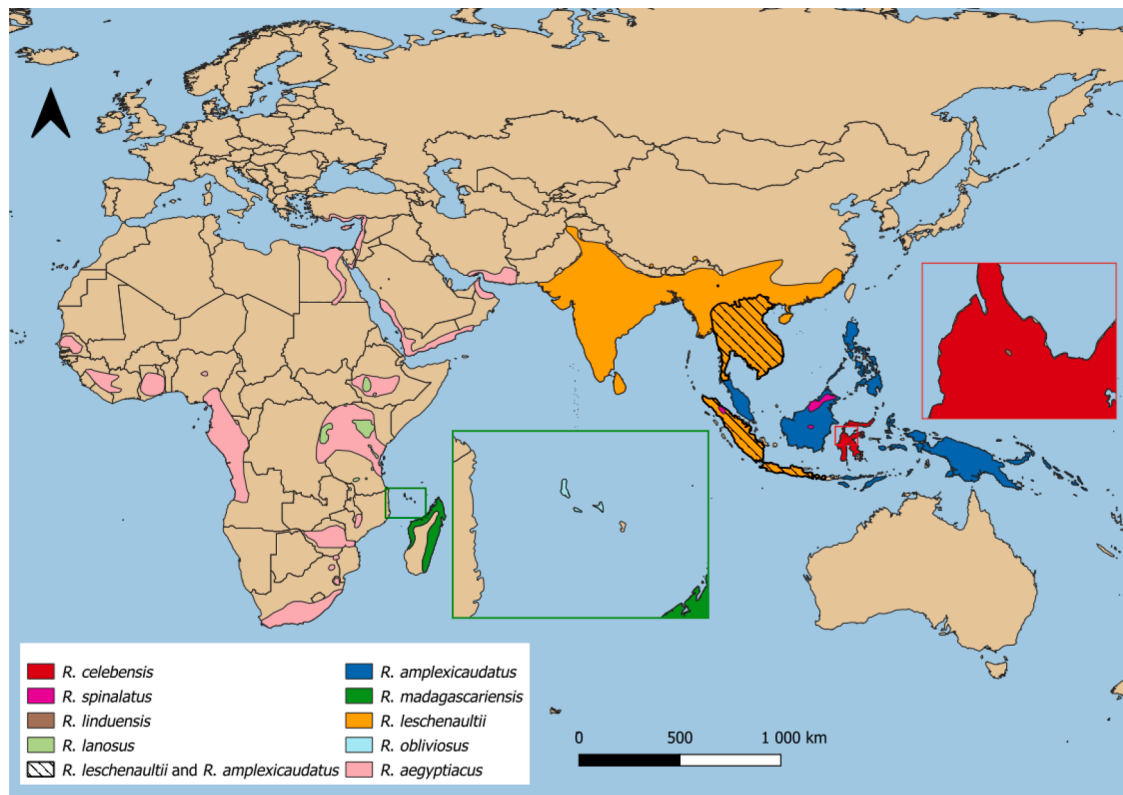


Fig. 2. Distribution of *Rousettus amplexicaudatus*, *R. spinalatus*, *R. leschenaultii*, *R. aegyptiacus*, *R. madagascariensis*, *R. obliviosus*, *R. lanosus*, *R. celebensis* and *R. linduensis* based on data from the International Union for Conservation of Nature (Bates and Helgen, 2008; Korine, 2016; Monadjem et al., 2017; Andrianai-voarivelo et al., 2019; Waldien et al., 2019; Sewall, 2020; Wiantoro et al., 2020a, b; Francis and Waldien, 2021). Within the green frame is presented the Comoro archipelago, with enlarged version on the right. The world map layer was downloaded from <http://tapiquen-sig.jimdo.com>

Table 1

Virus, bacteria and protozoa infectious agents that can impact human health identified in *Rousettus leschenaultii*, *R. aegyptiacus*, *R. madagascariensis* and *R. oblioviosus* based on serology (S) and/or molecular biology (M) methods.

Groups	Pathogen family	Pathogen	Host species	Detection methods	Location of sampling	Refs.	
Virus	Adenoviridae	Human mastadenovirus C	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)	
		Bat mastadenovirus	<i>R. aegyptiacus</i>	M	South Africa	Jansen van Vuren et al. (2018)	
	Astroviridae	Mamastrovirus spp.	<i>R. madagascariensis</i>	M	Western Madagascar	Lebarbenchon et al. (2017)	
		Mamastrovirus sp.	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)	
	Circoviridae	Cyclovirus spp.	<i>R. leschenaultii</i>	M	Southern China	Ge et al. (2011)	
	Coronaviridae	Alphacoronavirus sp.	<i>R. leschenaultii</i>	M	Southern China	Lau et al. (2012)	
		Betacoronavirus sp.	<i>R. leschenaultii</i>	M	Southern India, China	Yadav et al. (2020), Wu et al. (2021)	
			<i>R. aegyptiacus</i>	M	Kenya	Tong et al. (2009)	
			<i>R. madagascariensis</i>	M	Western Madagascar	Joffrin et al. (2020)	
	Filoviridae	Zaire ebolavirus	<i>R. aegyptiacus</i>	S	Gabon	Pourrut et al. (2009)	
			<i>R. leschenaultii</i>	S	Bangladesh	Formenty (2014)	
		Reston ebolavirus	<i>R. leschenaultii</i>	S	Bangladesh	Olival et al. (2013)	
		Lloviu(-like) virus	<i>R. leschenaultii</i>	M	Southern China	He et al. (2015)	
		Sudan Ebola(-like) virus	<i>R. leschenaultii</i>	M	Southern China	He et al. (2015)	
		Tai Forest Ebola(-like) virus	<i>R. leschenaultii</i>	M	Southern China	He et al. (2015)	
		Mengla virus	<i>R. leschenaultii</i>	M	Southern China	Yang et al. (2019)	
		Ebolavirus sp.	<i>R. madagascariensis</i>	S	Madagascar	Brook et al. (2019)	
		Marburg marburgvirus (Ravn virus)	<i>R. aegyptiacus</i>	S, M	Gabon and Republic of Congo	Towner et al. (2007)	
			Marburg marburgvirus (Marburg virus)	<i>R. aegyptiacus</i>	S	Gabon	Pourrut et al. (2009)
	Flaviviridae	Japanese encephalitis virus	<i>R. leschenaultii</i>	M	Southern China	Liu et al. (2013)	
		Uganda S virus	<i>R. aegyptiacus</i>	S	Uganda	Kading & Schountz (2016)	
		Entebbe bat virus	<i>R. aegyptiacus</i>	S	Kenya	Simpson et al. (1968)	
		Ntaya virus	<i>R. aegyptiacus</i>	S	Kenya	Simpson et al. (1968)	
		Usutu virus	<i>R. aegyptiacus</i>	S	Kenya	Simpson et al. (1968)	
		West Nile virus	<i>R. aegyptiacus</i>	S	Kenya	Simpson et al. (1968)	
		West Nile virus	<i>R. leschenaultii</i>	M	India	Paul et al. (1970), Chowdhury and Khan (2021)	
		Yellow fever virus	<i>R. aegyptiacus</i>	S	Uganda	Simpson & O'Sullivan (1968)	
		Zika virus	<i>R. aegyptiacus</i>	S	Uganda	Simpson and O'Sullivan (1968)	
	Hantaviridae	Orthohantavirus sp.	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)	
	Herpesviridae	Unclassified Herpesviridae	<i>R. aegyptiacus</i>	M	South Africa	Dietrich et al. (2018b)	
	Nairoviridae	Orthonairovirus incertae sedis (Kasokero virus)	<i>R. aegyptiacus</i>	S	Uganda	Kalunda et al. (1986)	
		Orthonairovirus incertae sedis (Yogue virus)	<i>R. aegyptiacus</i>	S, M	Senegal	Calisher et al. (2006), Walker et al. (2015)	
		Crimean-Congo hemorrhagic fever orthonairovirus	<i>R. aegyptiacus</i>	S	Gabon	Müller et al. (2016)	
	Peribunyaviridae	Bunyamwera orthobunyavirus	<i>R. aegyptiacus</i>	S	Uganda	Simpson & O'Sullivan (1968)	
		Wolkberg orthobunyavirus	<i>R. aegyptiacus</i>	M	South Africa	Jansen van Vuren et al. (2017)	
	Phenuiviridae	Rift Valley fever phlebovirus	<i>R. aegyptiacus</i>	S	Uganda	Kading et al. (2018)	
		Phlebovirus (Malsoor virus)	<i>R. leschenaultii</i>	M	Western India	Mourya et al. (2014)	
	Orthomyxoviridae	Influenza A virus	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)	
			<i>R. aegyptiacus</i>	M	Egypt	Kandeil et al. (2019)	
	Papillomaviridae	Alphapapillomavirus sp.	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)	
	Paramyxoviridae	Hendra(-like) henipavirus	<i>R. aegyptiacus</i>	S	Ghana	Amponsah-Mensah (2017)	
			<i>R. madagascariensis</i>	S	Madagascar	Brook et al. (2019)	
		Nipah(-like) henipavirus	<i>R. leschenaultii</i>	S	Southern China	Li et al. (2008)	
		Nipah henipavirus	<i>R. leschenaultii</i>	M	Western India	Gokhale et al. (2021)	
			<i>R. aegyptiacus</i>	S	Ghana	Amponsah-Mensah (2017)	
		Human Parainfluenza Virus	Cedar henipavirus	<i>R. leschenaultii</i>	S	Western India	Pavri et al. (1971)
				<i>R. aegyptiacus</i>	S	Ghana	Amponsah-Mensah (2017)
				<i>R. madagascariensis</i>	S	Madagascar	Brook et al. (2019)
			Tioman(-like) virus	<i>R. madagascariensis</i>	S	Northern Madagascar	Iehlé et al. (2007)
			Sosuga pararubulavirus	<i>R. aegyptiacus</i>	S, M	Uganda	Amman et al. (2020)
		Rubulavirus spp.	<i>R. aegyptiacus</i>	M	South Africa	Mortlock et al. (2019)	
		Sosula pararubula(-like) virus	<i>R. aegyptiacus</i>	M	South Africa	Mortlock et al. (2019)	
	Polyomaviridae	Betapolyomavirus sp.	<i>R. aegyptiacus</i>	M	Zambia	Carr et al. (2017)	
		Unclassified Polyomaviridae	<i>R. aegyptiacus</i>	M	Kenya	Tao et al. (2013)	

(continued on next page)

Table 1 (continued)

Groups	Pathogen family	Pathogen	Host species	Detection methods	Location of sampling	Refs.
	Poxviridae	Unclassified Poxviridae	<i>R. aegyptiacus</i>	M	Israel	David et al. (2020)
	Reoviridae	Rotavirus spp.	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)
	Retroviridae	Gammaretrovirus sp.	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)
	Rhabdoviridae	Lagos bat virus	<i>R. aegyptiacus</i>	M, S	Kenya, Nigeria, and Togo or Egypt	Kuzmin et al. (2008), Vora et al. (2020)
			<i>R. madagascariensis</i>	S	Madagascar	Mélade et al. (2016)
		European bat Lyssavirus	<i>R. aegyptiacus</i>	M	(Captive colonies in Denmark and Netherland)	Wellenberg et al. (2002)
		Duvenhage lyssavirus	<i>R. madagascariensis</i>	S	Madagascar	Mélade et al. (2016)
		Shimoni bat virus	<i>R. aegyptiacus</i>	S	Kenya, Nigeria	Kuzmin et al. (2011), Vora et al. (2020)
		Mokola virus	<i>R. aegyptiacus</i>	S	Nigeria	Vora et al. (2020)
		Bracorhabdovirus sp.	<i>R. leschenaultii</i>	M	Southern China	Zheng et al. (2018)
	Togaviridae	Chikungunya virus	<i>R. aegyptiacus</i>	M	No information	Calisher et al. (2006)
		Semliki Forest virus	<i>R. aegyptiacus</i>	S	Uganda	Simpson and O'Sullivan (1968)
		Alphavirus sp.	<i>R. aegyptiacus</i>	S	Uganda	Kading et al. (2018)
		O'nyong'nyong virus	<i>R. aegyptiacus</i>	S	No information	Fagre and Kading (2019)
Bacteria	Bartonellaceae	Bartonella sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
		Bartonella rouseffi	<i>R. aegyptiacus</i>	M, S	Southwestern Nigeria, Zambia	Bai et al. (2018), Qiu et al. (2020)
		Bartonella spp.	<i>R. aegyptiacus</i>	M	Kenya, South Africa	Kosoy et al. (2010), Dietrich et al. (2016)
			<i>R. leschenaultii</i>	M	Southern China	Li et al. (2021)
	Borreliaceae	Borrelia sp.	<i>R. aegyptiacus</i>	M	Zambia	Qiu et al. (2019)
	Brucellaceae	Brucella sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Corynebacteriaceae	Corynebacterium sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Enterobacteriaceae	Enterococcus sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
		Escherichia sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
			<i>R. aegyptiacus</i>	M	Republic of Congo	Nowak et al. (2017)
		Shigella sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
		Salmonella sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Mycobacteriaceae	Mycobacterium sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Mycoplasmataceae	Mycoplasma sp.	<i>R. aegyptiacus</i>	M	Northern Nigeria	Di Cataldo et al. (2020)
	Peptostreptococcaceae	Clostridium sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
		Clostridium sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Pseudomonadaeae	Pseudomonas sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Streptococcaceae	Streptococcus sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Leptospiraceae	Leptospira interrogans	<i>R. aegyptiacus</i>	M	South Africa	Dietrich et al. (2018a)
			<i>R. obliviosus</i>	M	Union of the Comoros	Lagadec et al. (2012)
		Leptospira borgpetersenii (or -like)	<i>R. aegyptiacus</i>	M	South Africa	Dietrich et al. (2018a)
		Leptospira borgpetersenii (or -like)	<i>R. madagascariensis</i>	M	Madagascar	Gomard et al. (2016)
			<i>R. obliviosus</i>	M	Union of the Comoros	Lagadec et al. (2012)
	Staphylococcaceae	Staphylococcus sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
	Yersiniaceae	Yersinia sp.	<i>R. leschenaultii</i>	M	Western India	Banskar et al. (2016)
		Yersinia pseudotuberculosis	<i>R. aegyptiacus</i>	S, M	Captive colony in New York and Japan	Childs-Sanford et al. (2009), Nakamura et al. (2013)
Protozoa	Babesiidae	Babesia sp.	<i>R. leschenaultii</i>	Microscopy	Bangladesh	Islam et al. (2020)
	Cryptosporidiidae	Cryptosporidium sp.	<i>R. leschenaultii</i>	M	Southwestern China	Wang et al. (2013)
	Eimeriidae	Eimeria rouseffi	<i>R. aegyptiacus</i>	Microscopy	Egypt	Fayed et al., (2011)
	Plasmodiidae	Hepaticystis sp.	<i>R. aegyptiacus</i>	M	North-Central Nigeria	Atama et al. (2019)
			<i>R. leschenaultii</i>	Microscopy	Bangladesh	Islam et al. (2020)
		Plasmodium rouseffi	<i>R. aegyptiacus</i>	S	Ghana	Adam (1965)
		Plasmodium voltaicum	<i>R. aegyptiacus</i>	S	Guinea, Liberia, Ivory Coast	Witsenburg (2014)
	Sarcocystidae	Neospora caninum	<i>R. leschenaultii</i>	M	Southern China	Wang et al. (2018)
		Toxoplasma gondii	<i>R. leschenaultii</i>	S, M	Northwestern, Western and South Western China	Yuan et al. (2013), Qin et al. (2014)
	Trypanosomatidae	Trypanosoma dionisii	<i>R. leschenaultii</i>	M	Southwestern China	Cai et al. (2019)
		Trypanosoma spp.	<i>R. aegyptiacus</i>	M	Gabon, South Africa	Stevens et al. (1999), Clément et al. (2020)
Fungi	Dipodascaceae	Geotrichum candidum	<i>R. leschenaultii</i>	M	South China	Li et al. (2018)
	Malasseziaceae	Malassezia sp.	<i>R. leschenaultii</i>	M	South China	Li et al. (2018)
	Pleosporaceae	Alternaria sp.	<i>R. leschenaultii</i>	M	Northern India	Misra et al. (2019)
	Saccharomycetaceae	Candida albicans	<i>R. leschenaultii</i>	M	South China	Li et al. (2018)
	Trichocomaceae	Aspergillus sp.	<i>R. leschenaultii</i>	M	Northern India	Misra et al. (2019)
		Penicillium sp.	<i>R. leschenaultii</i>	M	Northern India	Misra et al. (2019)

Pleistocene (around 2.3 to 0.9 Mya), and was associated with colonization from southern Asia, probably through an island stepping-stone process. This was followed by the divergence of *R. madagascariensis* on Madagascar, and subsequent colonization of Malagasy populations to

the Comoros, giving rise to *R. obliviosus* (Stribna et al., 2019).

Members of the genus *Rousettus* are capable of long-distance movements of 10 to 25 km from their day roost site per night for foraging (Bastian et al., 2001; Lučan et al., 2016); and gene exchange between

populations from different areas can result in low genetic interpopulation structure. In *R. leschenaultii*, analysis of mitochondrial and nuclear markers has shown no evidence of genetic structure between the populations of India and China (Chen et al., 2010), indicating a broad geographical dispersal. However, certain populations of *R. aegyptiacus* in sub-Saharan Africa show notable genetic structure (Stribna et al., 2019; Hassanin et al., 2020).

For populations of *R. madagascariensis* across Madagascar and near-shore islands, there is little genetic differentiation and the same pattern occurs in separate island populations of *R. obliviosus* in the Comoros, where islands are separated by 80 km of open water (Goodman et al., 2010). On Madagascar, this pattern is assumed to be related to long distance dispersal associated with tracking food resources, particularly for populations living in the western dry forests that show notable seasonal differences in fruit availability.

4. Ecology of *Rousettus*

4.1. Ecosystem services

The ability of *Rousettus* to echolocate (Waters and Vollrath, 2003), which is rare among pteropodid bats, their use of caves for day roosting sites and lack of dependence on trees for roosting (Chen et al., 2010), favoured the colonization of a range of habitats. This ecological breadth permitted members of the genus to expand their distribution in Asia, Middle East, Africa and Indian Ocean islands. It has been proposed that in recent geological time these bats have played an important role in the expansion of forest in tropical and subtropical regions by dispersing seeds and pollinating flowers of plants in a co-evolved bat-plant system (Stribna et al., 2019). In the eastern Mediterranean, *R. aegyptiacus* has been postulated as the driving force for the current range of tree cover, especially in semi-arid areas, by disseminating seeds of *Ficus carica* and *Morus nigra* (Moraceae), and *Arbutus andrachne* (Ericaceae) (Izhaki et al., 1995). Similarly, Tang et al. (2007) have shown in China that *R. leschenaultii* actively contributes to the seed dispersal of forest trees such as *Ficus*. In northern Madagascar, based on seeds recovered in the faeces of *R. madagascariensis*, it has been estimated that about half of the fruits it consumes are native forest plants and the balance from open areas and introduced plants (Vololona, 2020).

Dispersing the contents of fruits some distance away from the mother tree increases seed survival since plant pathogens and seed predators are more abundant within close proximity of the fruiting tree (Mahandran et al., 2018). For example, seed germinating probability of *Syzygium oblatum* (Myrtaceae) is significantly higher when dispersed by *R. leschenaultii* far from the parent tree (Tang et al., 2012). Moreover, Andrianaivoarivelo et al. (2011) demonstrated that ingested seeds of *F. rubra*, a native forest tree to Madagascar, germinate faster after passing through the digestive tube of *R. madagascariensis* than unprocessed seeds. The same pattern was also noted for larger-bodied pteropodids, such as members of the genera *Eidolon* and *Pteropus* (Bollen et al., 2004; Racey et al., 2010; Mahandran et al., 2018), which disperse seeds over a longer absolute distance than *Rousettus* (Epstein et al., 2009). However, the smaller body size of *Rousettus* and their echolocation capacity provides the means for them to access the lower portion of the forest with denser vegetation (Randrianandrianina et al., 2006), where they can feed on fruits not accessible to larger fruit bat species.

Rousettus supplement their diet by feeding on nectar and pollen (Vololona et al., 2020) and play an important role by transferring pollen for the maintenance of genetic diversity in a plant population (Kunz et al., 2011). Their role in pollination also has economic importance especially for plants that are commercially grown or exploited, for example, *R. leschenaultii* pollinates plants of the genera *Ceiba* (Malvaceae), *Ficus*, *Musa* (Musaceae) and *Careya* (Lecythidaceae) (Raghuram et al., 2011). Seed dispersal and pollination by fruit bats have been estimated to generate annually an economy of billions of dollars (US) worldwide (Boyles et al., 2011), over and above any calculations of

ecosystem well-being that influences the survival of other plant and animal species.

4.2. Feeding ecology of *Rousettus* and adaptation to food resource scarcity

During periods of low food availability, *Rousettus* can switch their diets to food types other than fruit and pollen, most notably folivory (Marshall, 1985; Lučan et al., 2016), which can supplement low levels of dietary protein (Ruby et al., 2000). Insectivory has also been documented for *R. aegyptiacus* and *R. madagascariensis*; the former has been observed actively consuming *Pachnoda sinuata* (Scarabaeidae) that fed on ripe fruits and flowers (Barclay et al., 2006) and the latter ingesting its bat fly ectoparasites *Eucampsipoda madagascariensis* (Nycteribiidae) and *Megastrebla wenzeli* (Streblidae). During the mating period, it has been estimated that a day roost colony of approximately 1500 *R. madagascariensis* can consume more than 57 000 hematophagous bat flies per day, i.e. on average about 37 bat flies per individual bat (Ramanantsalama et al., 2018), which might significantly augment protein and fat in their diet. Further, such behaviour presumably reduces ectoparasite populations on *Rousettus*. The consumption of ectoparasites might on the other hand contribute to the transmission of infectious agents between bats, although details on such a transmission route remains poorly understood.

In *R. leschenaultii* and *R. aegyptiacus*, seasonal decrease in available wild food sources appears correlated with broader dispersal distances and extension of foraging times and distances, which in certain cases brings them in closer proximity to humans and domestic animals (Lučan et al., 2016). A similar behaviour occurs in *R. madagascariensis*, which were observed spending more time outside the cave at night when fruits are scarce (Ramanantsalama and Goodman, 2020). At least in western Madagascar, with extensive areas of exposed sedimentary rock and often with numerous local caves and rock shelters, day roosting sites do not seem to be a limiting factor for this species. Further, as many caves are found outside forested areas, this species is not forest dependent in a strict sense. Given high rates of deforestation and agriculture expansion across the Old World distribution of *Rousettus*, including the cultivation of a range of fruits, it is possible that the previous limiting factor was food availability in the low-fruited season; and population expansion can be explained by increased availability of agriculture fruits (Lučan et al., 2016).

4.3. Roosting ecology of *Rousettus*

As previously mentioned, with their echolocation capacity, members of the genus *Rousettus* often occupy cave day roost sites, which provide a stable environment temperature and in turn reduces expenditures for thermoregulation and the risk of predation. They can share the same day roost site with other bat species and other mammals, including rodents such as *Rattus* spp. (Muridae). In cave systems, *Rousettus* generally roost in different portions of the cave as compared to other species of cave-roosting bats. *Rousettus leschenaultii* and *R. aegyptiacus* in different portions of their geographical range use sites in close proximity to humans such as mosques, wells, abandoned houses, underground mining quarries and monuments of which several are regularly visited by people (Qumsiyeh, 1985; Kumar et al., 2015; Lučan et al., 2016).

5. Infectious agents of *Rousettus*: diversity and zoonotic risks

5.1. Viruses

During the last decades, various studies conducted on Asian and African populations of *Rousettus* have investigated viral diversity and transmission dynamics. Most of these studies focused on *R. aegyptiacus*, in western and central Africa, as compared to the other members of the genus (Fig. 3b). The majority of identified virus strains associated with *Rousettus* are from the family *Coronaviridae*, followed by

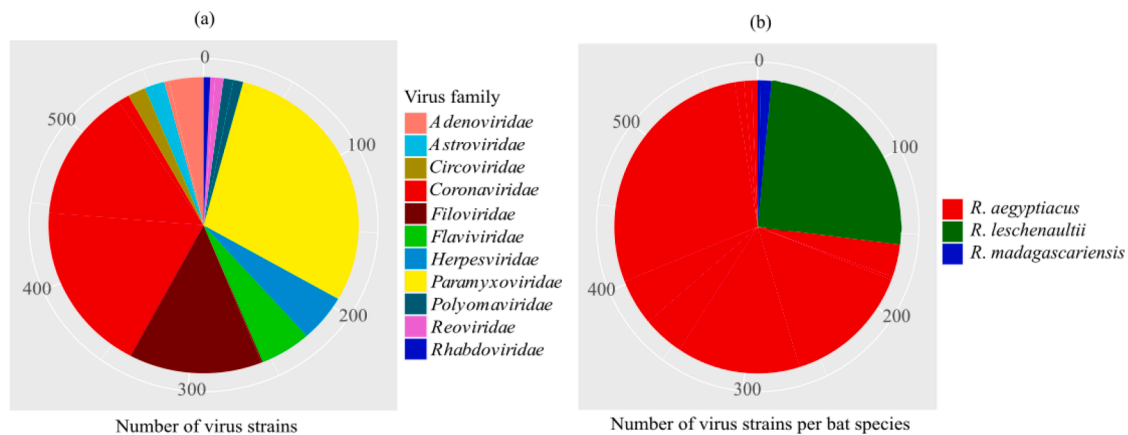


Fig. 3. Virus genetic diversity identified in *Roussettus aegyptiacus*, *R. leschenaultii* and *R. madagascariensis*, (a) per virus family and (b) per species of *Roussettus*, based on DBatVir free database (<http://www.mgc.ac.cn/DBatVir/>). There are no published data on viruses associated with *R. obliviosus*.

Paramyxoviridae and *Filoviridae* (Fig. 3a). It is important to mention that viruses isolated from *Roussettus* were largely the result of research focusing on pathogens of public health importance. More global studies in *Roussettus* parasitology have identified a diverse range of other viral families that can also cause diseases in humans, such as the families *Adenoviridae*, *Astroviridae*, *Circoviridae*, *Flaviviridae*, *Hantaviridae*, *Herpesviridae*, *Nairoviridae*, *Orthomyxoviridae*, *Papillomaviridae*, *Peribunyaviridae*, *Phenuiviridae*, *Polyomaviridae*, *Poxviridae*, *Reoviridae*, *Retroviridae*, *Rhabdoviridae* and *Togaviridae* (Table 1).

Genetic and serologic data have demonstrated *Filoviridae* (Ebola and Marburg viruses) circulation in *R. leschenaultii* and *R. aegyptiacus* (Towner et al., 2009; Olival et al., 2013; Yang et al., 2017). The latter species is the known reservoir of Marburg virus which has caused sporadic outbreaks of a severe form of haemorrhagic disease in sub-Saharan Africa, especially in Angola, Democratic Republic of the Congo, Kenya, South Africa, Uganda and Zimbabwe (Brauburger et al., 2012). Further, transmission of Marburg viruses to humans via faeces and urine of *R. aegyptiacus* was reported in tourists visiting *R. aegyptiacus* day-roost caves in Uganda (Amman et al., 2012). Actually, filovirus prevalence in pteropodid bats is higher among bats occupying cave roost sites as compared to tree roosts because of aerosol exposure associated with bat excretion (Pourrut et al., 2009; Igreja, 2011). Antibodies against filoviruses have also been reported in *R. madagascariensis* (Brook et al., 2019). However, transmission to humans has not yet been reported for filoviruses associated with *R. leschenaultii* and *R. madagascariensis*.

Human-induced forest fragmentation in tropical Africa has led to increase contact between fruit bats and people, facilitating filovirus outbreaks, most notably in Gabon, Republic of Congo and Democratic Republic of Congo (Rulli et al., 2017). There is serological evidence showing the implication of *Roussettus* in Ebola virus shedding in these areas (Olivero et al., 2020). This may be favoured by increased production of agriculturally grown fruit trees, particularly in areas with seasonal variation in native fruits or reduction in available fruits associated with deforestation. The probability of filovirus transmission to humans may be increasingly important during *Roussettus* reproductive periods when these bats, particularly females, forage with a greater frequency on agriculture fruits (Barclay and Jacobs, 2011).

The emergence of pathogenic bat-paramyxoviruses, such as Nipah virus (NiV) and Hendra virus (HeV), is a recurrent phenomenon in human populations. In 2012, a wildlife biologist was infected by a recently named paramyxovirus, *Sosuga pararubulavirus* (*Paramyxoviridae*), following fieldwork on rodents and bats in South Sudan and Uganda (Albariño et al., 2014). The person in question developed severe symptoms with maculopapular rash and fever, but no epidemic transmission via individuals in contact with the patient was noted. This

virus has been demonstrated to be transmitted by *R. aegyptiacus* (Amman et al., 2020).

Other paramyxoviruses of public health importance are suspected to be harboured by *Roussettus*. For example, serological data suggest possible NiV-like infection of *R. leschenaultii* in China and Vietnam (Li et al., 2008; Hasebe et al., 2012). More recently, NiV RNA has been found in liver, throat and rectal swabs of *R. leschenaultii* in India, and anti-NiV IgG antibodies have also been detected (Gokhale et al., 2021), indicating that this species is exposed to NiV or a closely related virus. The presence of NiV RNA in throat swabs of *R. leschenaultii* suggests a possible transmission mode to humans if individuals of this bat forage on cultivated fruit that are consumed by people without washing. However, although a trait-based modelling approach used by Plowright et al. (2019) identified a high likelihood for *R. aegyptiacus* to be exposed to NiV-like, experimental infection with NiV, did not find any viral replication or seroconversion, suggesting that NiV or NiV-like may not efficiently replicate in *R. aegyptiacus* (Seifert et al., 2020), in contrast to *R. leschenaultii*.

Emerging human coronaviruses belong to the subgenera *Buldecovirus*, *Duvinacovirus*, *Embecovirus*, *Merbecovirus*, *Sarbecovirus*, *Setracovirus* and *Tegacovirus* (Corman et al., 2018; Wong et al., 2019; Lednicky et al., 2021; Vlasova et al., 2022). Among these five coronavirus subgenera, only *Merbecovirus* has been identified in *Roussettus* (Wu et al., 2021); the other were α - and β -coronavirus within the subgenera *Decacovirus* and *Nobecovirus*, respectively (Lau et al., 2012; Joffrin et al., 2020). In Chinese populations of *R. leschenaultii*, α -coronavirus has been documented to be transmitted to the insectivorous bat *Hipposideros pomona* (Hippodidae) (Lau et al., 2012). Such information on cross-species transmission possibility is important since the human coronavirus subgenus *Merbecovirus* was also detected in *R. leschenaultii* (Wu et al., 2021), and a risk of coronavirus spillover from bat to human should not be minimized. *Sarbecovirus* could also be transmitted between different bat species (Woo et al., 2009; Wong et al., 2019), with a potential risk of transfer to humans when bat roosting colonies are in or close to synanthropic settings.

The family *Rhabdoviridae* also includes potential human pathogens; and for *Roussettus*, *Rhabdoviridae* strains include *Lyssavirus*, particularly *Lagos bat virus* (Kuzmin et al., 2011), found in *R. aegyptiacus* (Table 1). Vora et al. (2020) have shown a *Lagos bat virus* seroprevalence of 50% in a colony of *R. aegyptiacus* in Nigeria and at a site where a biannual cultural festival is conducted and when people enter a cave to catch these bats. However, to date no festival participant was noted to be infected by *Lagos bat virus*.

Influenza viruses were also noted to infect *Roussettus*. These viruses are known for their flexibility in terms of interspecific transmission and to adapt and circulate in new bird and mammal hosts. In Egypt, H9N2

virus has circulated in poultry since the early 21st century (Abolnik et al., 2010). Bats were not considered as potential reservoirs of influenza viruses (Tong et al., 2012) until recently when a genetically distinct H9N2 virus was found in Egyptian populations of *R. aegyptiacus* (Zheng et al., 2018). The hemagglutinin and neuraminidase encoding segments of this virus in *R. aegyptiacus* were closely related to the avian H9N2-viruses. This likely indicates a recent spillover from birds to *R. aegyptiacus*. Although emergence of avian-origin H9N2 virus in humans occurred repeatedly in recent years (Song and Qin, 2020), particular molecular features of the *R. aegyptiacus* H9N2 virus suggest a low risk for zoonotic transmission (Ciminski et al., 2020).

5.2. Bacteria

With the popularity of microbiome studies, bacterial infectious agents in bats have received increased attention, and several bacterial metagenomic studies have been published for *Rousettus* bats. For example, two studies have described the bacterial microbiota of *R. leschenaultii* and *R. aegyptiacus*, from guano collected in caves in Western India and northern South Africa, respectively (Banskar et al., 2016; Dietrich and Markotter, 2019). In addition, using multiple types of individual samples (saliva, urine, faeces, skin, rectal swabs, fur), other studies have analysed the bacterial microbiota of *R. aegyptiacus* (Hatta et al., 2016; Dietrich et al., 2018b). *Rousettus* mainly harbours bacteria belonging to the families Bartonellaceae, Brucellaceae, Corynebacteraceae, Enterobacteraceae, Leptospiraceae, Mycobacteriaceae, Peptostreptococcaceae, Pseudomonadaeae, Staphylococcaceae and Streptococcaceae (Table 1).

Bartonella (Bartonellaceae) has been identified in *R. aegyptiacus* (Dietrich et al., 2016) and more recently also in *R. leschenaultii* (Li et al., 2021). Dietrich et al. (2016) have shown that *Bartonella* from *R. aegyptiacus* are genetically distant from all other known *Bartonella* genotypes reported from other African bats except *Eidolon helvum*, and suggest some level of evolutionary co-divergence of *Bartonella* isolated from the sympatric bats *R. aegyptiacus* and *E. helvum* (Kosoy et al., 2010; Hayman et al., 2015; Urushadze et al., 2017). *Bartonella* of *R. aegyptiacus* are also similar to those found in *Eucampsidoda* (Nycteriibidae), which are dipteran hematophagous ectoparasite flies of this bat (Dietrich et al., 2016; Bai et al., 2018). These results indicate a possible vector-borne transmission of *Bartonella* among bats, as for bat colonies in West Africa and Malagasy region (Kamani et al., 2014; Wilkinson et al., 2016), which is coherent with the fact that *Bartonella* are generally known to be spread to people by hematophagous bat mites, ticks, lice, flies and fleas (Billetter et al., 2008; Sándor et al., 2018). Some *Bartonella* can cause pathogenicity in humans, resulting in high fever, skin lesion and muscle pain, and may induce endocarditis, lymphadenitis and meningitis. However, only one study has shown the possibility of *Rousettus*-borne *Bartonella* transmission to humans (Bai et al., 2018). This study found antibodies in people participating in a biannual event in Nigeria, during which bats were captured and consumed; people can be infected after handling bats, and being bitten, scratched, or exposed to body fluids (urine, faeces, etc.).

A growing number of studies have highlighted bats as a reservoir for *Leptospira* (Leptospiraceae) bacteria and pointing to their potential role in the epidemiology of leptospirosis, which is the most widespread zoonotic disease in the world (Dietrich et al., 2015). *Leptospira* bacteria have been documented in *R. aegyptiacus*, *R. obliviosus* and *R. madagascariensis* (Gomard et al., 2016; Dietrich et al., 2018a), where individual bats can be co-infected by *L. interrogans* and *L. borgpetersenii*-like lineages, both considered as potentially pathogenic for people. Interestingly, *L. interrogans* of *R. aegyptiacus* in South Africa and *R. obliviosus* from the Comoros are genetically close to those found in locally occurring small mammals, such as *Crocidura* sp. (Soricidae), and *Mastomys* spp. and *Rattus rattus* (Muridae). This indicates possible transmission between terrestrial small mammals and bats (Dietrich et al., 2018a). In contrast, the *L. borgpetersenii*-like lineages found in *R. aegyptiacus* and

R. madagascariensis were novel *Leptospira* lineages and probably evolved in geographic isolation with their hosts (Dietrich et al., 2018a). To date, no case of *Rousettus*-to-human transmission of *Leptospira* has been reported, and this is also the case for other bat-borne *Leptospira*.

Other bacteria that probably can spread from *Rousettus* to humans have been reported and include the genera *Borrelia* (Borreliaceae), *Mycoplasma* (Mycoplasmataceae) and *Yersinia* (Yersiniaceae) (Table 1). Strains of *Borrelia* isolated from a febrile patient in Zambia clustered with those of *R. aegyptiacus* (Qiu et al., 2019) and transmission from bat ectoparasites has been suspected and is explained in the section below. In Nigeria, individuals of *R. aegyptiacus* that roost in vicinity of human settlements were positive for *Mycoplasma*; and although *Mycoplasma* of *Rousettus* have no similarity with those found in humans, there are some strains that were closed to those of insectivorous bats (Di Cataldo et al., 2020). There has been limited work demonstrating the effect of infectious agents on bat health and Evans et al. (2009), Mühlendorfer (2012) and Bleher et al. (2014) have shown that bacteria are generally more susceptible to affect bat health than other endogenous pathogens. Information on this aspect are more important for pathogens that can cause diseases in both human and bats, like *Yersinia pseudotuberculosis*, which killed numerous captive individuals of *R. aegyptiacus* at the Rosamond Gifford Zoo in Syracuse, New York, and a zoological park in Kanto region, Japan (Childs-Sanford et al., 2009; Nakamura et al., 2013). In western India, *Y. pestis* was detected in guano of *R. leschenaultii* but was not seen to affect bat health (Banskar et al., 2016). Data related to infection dynamics of *Yersinia* spp. are essential as they can spread to other mammals; and in zoological parks, the risk of transmission to staff members and visitors should not be underestimated.

Campylobacter jejuni bacteria have also been identified in *R. amplexicaudatus* of the Philippines using both next generation sequencing and standard PCR methods (Hatta et al., 2016). The possible presence of this pathogen in the four studied *Rousettus* species reviewed herein should not be excluded as *Campylobacter* is the second most dominant bacteria genus in the rectal microbiome of *R. amplexicaudatus* (Hatta et al., 2016); and this pathogen has been isolated in faeces of insectivorous bats (Adesiyun et al., 2009; Hazeleger et al., 2018). The disease campylobacteriosis can cause serious diarrhoea in humans; the most often implicated species is *C. jejuni* (Hatta et al., 2016).

5.3. Protozoa and fungi

Although no bat has yet been known implicated in the transmission of malaria and trypanosomiasis to humans, protozoa genera causing these diseases (*Plasmodium* for malaria and *Trypanosoma* for trypanosomiasis) have already been noted in *Rousettus* (Table 1). The genera *Hepaticystis* and *Plasmodium* (Plasmodiidae) have been isolated in *R. aegyptiacus*; and *Trypanosoma* (Trypanosomatidae) in *R. leschenaultii* and *R. aegyptiacus* (Adam, 1965; Atama et al., 2019; Cai et al., 2019; Clément et al., 2020). These protozoa have not yet been documented in *R. madagascariensis* or *R. obliviosus*, although *Trypanosoma* was already noted in Malagasy insectivorous bats (Rasoanoro et al., 2019).

Recent research has demonstrated that bats might be the basal ancestral host of non-human primate and human haemosporidians (Schaer et al., 2013; Lutz et al., 2016; Clément et al., 2020). However, details on multiple host switching of haemosporidian across mammals are still limited. Knowledge on the family Plasmodiidae mostly concerns their relation with dipteran vectors; and information related to the interaction of bats and Plasmodiidae remains scarce although a subject of important further investigations. For example, *Rousettus* host dipteran hematophagous flies of the families Nycteriibidae and Streblidae that may have the ability to transmit haemosporidian parasites (Obame-Ngoghe et al., 2016; Feng et al., 2017). To our knowledge, no protozoa isolated from *Rousettus* has been identified in humans. Studies examining the effect of protozoa infection on the health of bats are lacking in the literature.

Pathogenic fungi, related to those known in humans, occur in

R. leschenaultii (Li et al., 2018; Misra et al., 2019) and belong to the families Dipodascaceae, Malasseziaceae, Pleosporaceae, Saccharomycetaceae and Trichocomaceae (Table 1). Fungal communities in the faeces of pteropodid bats have been shown to be more abundant and diversified compared to insectivorous bats (Li et al., 2018). This might be linked to the development of the olfactory system in Pteropodidae (Kshitish Acharya et al., 1998) and related to the types of fruits consumed. Tang et al. (2007) and Korine et al. (2011) studied *R. leschenaultii* and *R. aegyptiacus*, respectively, and found that these bats detect fresh fruits by their fermented odour, which is mainly produced by overripe fruits. Even if *Rousettus* seems to prefer ripe and fresh fruits, the proximity of overripe fruits to those they consume, might be the source of fungi and explain their co-evolution with gut fungi (Li et al., 2018).

5.4. Ectoparasites and vector-borne transmission

Bats host many hematophagous ectoparasite arthropods known from mammals, including those on their skin and fur such as Acari (Acariformes: Pyemotidae; Astigmatina: Carpoglyphidae, Macronyssidae; Ixodida: Ixodidae; Mesostigmata: Spinturnicidae; Parasitiformes: Argasidae; Sarcoptiformes: Acaridae), Diptera (Nycteribiidae, Streblidae), Hemiptera (Cimicidae) and Siphonaptera (Ceratophyllidae, Ischnosyllidae) (Table 2). Nycteribiids known from *Rousettus* are generally of four different genera: *Brachytarsina*, *Cyclopodia*, *Eucampsipoda* and *Nycteribia*, all of which are known to carry viruses, bacteria and protozoa (Table 2). Jansen van Vuren et al. (2017) and Ramasindrazana et al. (2018) showed that the transmission of viruses and protozoa of the families *Peribunyaviridae* and *Plasmoviridae*, respectively, is possible between bats and their dipteran ectoparasites.

Nycteribiidae and Streblidae bat flies identified on *Rousettus* are mostly monoxenous i.e. parasitizing only one host species (Marshall, 1982; Ramasindrazana et al., 2017). This host specificity has been demonstrated for nycteribiids and streblids of *R. leschenaultii* in Sri Lanka (Seneviratne et al., 2009), as well as in nycteribiids of *R. madagascariensis* and *R. obliviosus* (Ramasindrazana et al., 2017). As during the adult stage, Streblidae are capable of flying and hence dispersing, it might be assumed for this family to demonstrate less host-specificity than non-volant Nycteribiidae; however, this does not appear to be the case and both families generally show similar levels of host specificity (Amarga et al., 2017). Ectoparasite host specificity is largely related to the combination of different factors including host physical isolation, predation of ectoparasites by the bat host, competition between ectoparasites, physiological, behavioural and morphological adaptations of ectoparasites, and the most important factor being their reproduction efficiency (Dick and Patterson, 2006).

Previous research has shown inter-individual variation of bat fly parasitic loads for *Rousettus*. For example, nycteribiids of *R. madagascariensis* prefer to parasitize adult males with denser fur that presumably provide some level of protection against host grooming activity (Rajemison et al., 2017). In addition, adult male *Rousettus* have a vascularized area on the throat characterized by a darker pelage coloration, where specialized sebaceous glands produce an oily secretion responsible of emitting specific adult male odours that presumably have some pheromonal properties (Mainoya and Howell, 1979; Rajemison et al., 2017). Gravid female bat flies prefer to feed on these individuals to obtain a blood meal, which is important for intra-uterine larval development (Fritz, 1983).

Some genera of bat ticks, including *Argas* spp., *Ixodes* spp. and *Ornithodoros* spp., can shift host groups and even feed on humans (Estrada-Peña and Jongejan, 1999; Piksa et al., 2013; Péter et al., 2021). Gill et al. (2004) identified human blood in the bat tick *Carios kelleyi* (Argasidae) in Iowa. In the Lopburi Province of Thailand, miners who had no direct physical body contact with bats were infected by the *Kaeng Khoi orthobunyavirus* (*Peribunyaviridae*), probably after being bitten by cimicid bat ectoparasites, which are known to be reservoirs for the virus

(Williams et al., 1976). *Kaeng Khoi orthobunyavirus* was also detected in the nycteribid *Eucampsipoda sundaica*, an ectoparasite fly of *R. leschenaultii* (Feng et al., 2017). Furthermore, a person bitten by a *R. aegyptiacus* tick, probably *Ornithodoros faini*, after visiting a cave in Zambia, was infected by *Borrelia*; and on the basis of molecular studies, the *Borrelia* strain in this patient formed a monophyletic lineage with those isolated from *O. faini* and *R. aegyptiacus* (Qiu et al., 2019). No case of *Borrelia* transmission between humans has been documented; however, this finding indicates that spread of bat infectious diseases by vector arthropods should not be neglected.

At Meya-Nzouari in the Republic of the Congo, Adam (1965) found that *Anopheles hamoni* (Culicidae) feeds on the blood of *R. aegyptiacus*. This mosquito sometimes harbours *Plasmodium voltaicum*, an endogenous hematoparasite that has also been identified in *R. aegyptiacus* (Adam and Landau, 1970). Old World bat flies can harbor hematoparasite parasites; this was demonstrated by Szentivanyi et al., (2020) who studied *Polychromophilus* and *Trypanosoma* in *Miniopterus* spp. of Africa and Europe. The only haemoparasite found in *Rousettus* bat flies were *P. dionisi* (Obame-Ngoghe et al., 2016) albeit limited research has been performed on sporozoan parasites of bat flies.

Furthermore, in central Thailand, *Culex quinquefasciatus* (Culicidae) also takes blood meals from *R. leschenaultii* (Tiawsirisup et al., 2012); and *Japanese encephalitis virus* (*Flaviviridae*) was identified in both *C. quinquefasciatus* and *R. leschenaultii* (Nitattattana et al., 2005; Liu et al., 2013). *Flaviviridae* are among infectious agents that might be common in bats and their dipteran ectoparasites. These viruses need to be surveyed, particularly in areas where mosquitoes are known to be infected, as previous studies indicate a positive correlation between mosquito population size and the prevalence of dengue virus (*Flaviviridae*) in the vampire bat *Desmodus rotundus* (Phyllostomidae) and their bat flies (Streblidae) (Abundes-Gallegos et al., 2018). Hence, the possibility exists for hematophagous dipteran arthropods that are not bat parasites to transmit bat pathogens although we found no indication in the literature of this form of transfer to people.

6. *Rousettus* as a model for studying infection dynamics in bats

6.1. Longitudinal field-based studies

With the recurrent emergence of bat-related pathogens in humans, understanding details on infection dynamics in wild bat populations is crucial. As highlighted by Becker et al. (2019), deeper spatiotemporal field studies are required for bat pathogen surveillance, although such research can present logistic challenges. For example, it can be difficult to capture in the wild individuals of bat species considered as potential reservoirs of infectious agents. However, in the case of *Rousettus*, the same cave is generally used over the course of years for day roosting and often easily accessible. This makes the repeated capture of marked individuals relatively straightforward and provides the means to investigate bat population dynamics superimposed on different life-history traits and the mechanisms that drive the circulation of bat infectious agents. For example, seroprevalence of *Ebolavirus*-related (*Filoviridae*) in *R. aegyptiacus* and *R. madagascariensis* was shown to be correlated with their reproductive cycles (Pourrut et al., 2009; Brook et al., 2019); higher seroprevalence was noted during gestation and beginning of lactating periods in these two bat species.

Further, Mortlock et al. (2019) demonstrated a positive correlation between *Rubulavirus* prevalence and *Rousettus* reproduction in South Africa, using direct genetic detection of viral material in *R. aegyptiacus* urine. During the birthing period of *R. aegyptiacus*, a lower virus shedding prevalence was observed in neonates and young juveniles, as compared to adults. This may be related to the presence of maternal antibodies in neonates and young juveniles during their first months of life (Dietrich et al., 2018b). Changes in virus shedding prevalence is also synchronized with a modification of the oral microbiota composition, which is different in *R. aegyptiacus* between pregnant and non-pregnant

Table 2

Ectoparasites hosted by *Rousettus leschenaultii*, *R. aegyptiacus*, *R. madagascariensis* and *R. obliviosus*, and their associated virus, bacteria, protozoa and fungi.

Groups	Ectoparasite family	Ectoparasites	Host species	References	Ectoparasite pathogen group	Ectoparasite pathogen	Refs.
Acarine	Acaridae	<i>Acarus</i> sp.	<i>R. aegyptiacus</i>	Nartey (2015)			
	Argasidae	<i>Argas</i> spp.	<i>R. leschenaultii</i>	Seneviratne et al. (2009), Ullah et al. (2019)	<i>Rickettsiaceae</i>	<i>Rickettsia</i> sp.	Ullah et al. (2019)
		<i>Argas vespertilionis</i>	<i>R. aegyptiacus</i>	Benda et al. (2010)			
		<i>Carios batuensis</i>	<i>R. leschenaultii</i>	Klompfen et al. (1995)			
		<i>Carios papuensis</i>	<i>R. leschenaultii</i>	Klompfen et al. (1995)			
		<i>Carios multisetosus</i>	<i>R. leschenaultii</i>	Klompfen et al. (1995)			
		<i>Carios salahi</i>	<i>R. madagascariensis</i>	Klompfen & Apanaskevich (In press)			
		<i>Ornithodoros camicasi</i>	<i>R. aegyptiacus</i>	Sylla et al. (1997)			
		<i>Ornithodoros faini</i>	<i>R. aegyptiacus</i>	Schuh et al., (2017b)			
		<i>Ornithodoros</i> sp.	<i>R. leschenaultii</i>	Seneviratne et al. (2009)			
		<i>Ornithodoros salahi</i>	<i>R. aegyptiacus</i>	Hoogstraal (1953)			
	Carpoglyphidae	<i>Carpoglyphus</i> sp.	<i>R. aegyptiacus</i>	Nartey (2015)			
	Chirodiscidae	<i>Alabidocarpus roussetti</i>	<i>R. aegyptiacus</i>	Fain (1982)			
	Ixodidae	<i>Ixodes</i> sp.	<i>R. aegyptiacus</i>	Nartey (2015)			
	Macronyssidae	<i>Steatonyssus evansi</i>	<i>R. leschenaultii</i>	Ullah et al. (2019)			
		<i>Steatonyssus allredi</i>	<i>R. leschenaultii</i>	Advani and Vazirani (1981)			
		<i>Steatonyssus longipes</i>	<i>R. aegyptiacus</i>	Nartey (2015)			
	Myobiidae	<i>Binuncus roussetti</i>	<i>R. aegyptiacus</i>	Fain (1972)			
		<i>Foliomyobia jamesoni</i>	<i>R. leschenaultii</i>	Advani and Vazirani (1981)			
	Pyemotidae	<i>Pyemotis</i> sp.	<i>R. aegyptiacus</i>	Nartey (2015)			
	Sarcoptidae	<i>Chirobia</i> sp.	<i>R. madagascariensis</i>	O'Connor (1998)			
		<i>Teinocoptes</i> sp.	<i>R. madagascariensis</i>	O'Connor (1998)			
	Spinturnicidae	<i>Meristaspis kenyaensis</i>	<i>R. aegyptiacus</i>	Nartey (2015)			
		<i>Meristaspis lateralis</i>	<i>R. aegyptiacus</i>	Malek-Hosseini et al. (2016)			
			<i>R. leschenaultii</i>	Seneviratne et al. (2009)			
		<i>Meristaspis mindanaoensis</i>	<i>R. leschenaultii</i>	Uchikawa and Kobayashi (1978)			
		<i>Meristaspis</i> sp.	<i>R. madagascariensis</i>	Reeves et al. (2006)			
		<i>Ancystropus aequatorialis</i>	<i>R. aegyptiacus</i>	Estrada-Peña, Ballesta and Ibañez (1992)			
		<i>Ancystropus eonycteris</i>	<i>R. leschenaultii</i>	Uchikawa (1990)			
		<i>Ancystropus kanheri</i>	<i>R. leschenaultii</i>	Advani and Vazirani (1981)			
		<i>Ancystropus leleupi</i>	<i>R. aegyptiacus</i>	Anciaux de Faveaux (1965)			
			<i>R. leschenaultii</i>	Ullah et al. (2019)			
			<i>R. aegyptiacus</i>	Amarga et al. (2017)			
		<i>Ancystropus</i> sp.	<i>R. leschenaultii</i>	Seneviratne et al. (2009)			
		<i>Ancystropus zeleborii</i>	<i>R. leschenaultii</i>	Advani & Vazirani (1981)			
		<i>Spinturnix americana</i>	<i>R. aegyptiacus</i>	Nartey (2015)			
		<i>Spinturnix delacruzi</i>	<i>R. aegyptiacus</i>	Estrada-Peña et al. (1992)			
		<i>Parameristaspis delfinadoi</i>	<i>R. leschenaultii</i>	Advani and Vazirani (1981)			
		<i>Periglischrus paracutisternus</i>	<i>R. aegyptiacus</i>	Nartey (2015)			
		<i>Periglischrus ojustii</i>	<i>R. aegyptiacus</i>	Nartey (2015)			
	Trombiculidae	<i>Whartonia kumaonensis</i>	<i>R. leschenaultii</i>	Bhat (1971)			
Flea	Ceratophyllidae	<i>Odontopsyllus</i> spp.	<i>R. aegyptiacus</i>	Dietrich et al. (2016)			
	Ischnopsyllidae	<i>Thaumapsylla breviceps</i>	<i>R. leschenaultii</i>	Seneviratne et al. (2009)			
Bug	Cimicidae	<i>Afrocmex constrictus</i>	<i>R. aegyptiacus</i>	Ferris and Usinger (1957)			
		<i>Leplocimex inordinatus</i>	<i>R. leschenaultii</i>	Advani and Vazirani (1981)			
Bat fly	Nycteribiidae	<i>Cyclopodia greefti</i>	<i>R. aegyptiacus</i>	Nartey (2015)	<i>Reoviridae</i>	<i>Mahlapitsi orthoreovirus</i>	Jansen van Vuren et al. (2016)
		<i>Eucampsipoda africana</i>	<i>R. aegyptiacus</i>	Braack (1989)	<i>Plasmodiidae</i>	<i>Polychromophilus dionisi</i>	Obame-Nkoghe et al. (2016)
				Braack (1989)	<i>Peribunyaviridae</i>	<i>Wolkberg orthobunyavirus</i>	Jansen van Vuren et al. (2017)
				Braack (1989)	<i>Bartonellaceae</i>	<i>Bartonella roussetti</i>	Bai et al. (2018)
				Braack (1989)	<i>Bartonellaceae</i>	<i>Bartonella</i> sp.	Qiu et al. (2020)

(continued on next page)

Table 2 (continued)

Groups	Ectoparasite family	Ectoparasites	Host species	References	Ectoparasite pathogen group	Ectoparasite pathogen	Refs.
				Braack (1989)	Laboulbeniaceae	<i>Arthrorhynchus eucampsipodae</i>	Haelewaters et al. (2017)
		<i>Eucampsipoda aegyptia</i>	<i>R. aegyptiacus</i>	Ševčík, Benda and Lučan (2013)			
		<i>Eucampsipoda hyrtlii</i>	<i>R. aegyptiacus</i>	Theodor (1955)	Laboulbeniaceae	<i>Arthrorhynchus eucampsipodae</i>	Haelewaters et al. (2017)
		<i>Eucampsipoda</i> spp.	<i>R. aegyptiacus</i>	Dietrich et al. (2016)	Bartonellaceae	<i>Bartonella</i> spp.	Dietrich et al. (2016)
		<i>Eucampsipoda sundaica</i>	<i>R. leschenaultii</i>	Maa (1971)	Peribunyaviridae	Kaeng Khoi orthobunyavirus	Feng et al. (2017)
		<i>Eucampsipoda latisterna</i>	<i>R. leschenaultii</i>	Weerakkody, Randeniya and Ratnasooriya (1999)	Bartonellaceae	<i>Bartonella</i> spp.	Morse et al. (2012)
		<i>Eucampsipoda theodori</i>	<i>R. obliviosus</i>	Tortosa et al. (2013)	Bartonellaceae	<i>Bartonella</i> spp.	Wilkinson et al. (2016)
		<i>Eucampsipoda theodori</i>	<i>R. obliviosus</i>	Tortosa et al. (2013)	Anaplasmatocae	<i>Ehrlichia</i> sp.	Wilkinson et al. (2016)
		<i>Eucampsipoda madagascariensis</i>	<i>R. madagascariensis</i>	Tortosa et al. (2013)	Bartonellaceae	<i>Bartonella</i> spp.	Wilkinson et al. (2016)
		<i>Eucampsipoda madagascariensis</i>	<i>R. madagascariensis</i>	Tortosa et al. (2013)	Rickettsiaceae	<i>Rickettsia</i> spp.	Wilkinson et al. (2016)
		<i>Nycteribia alternata</i>	<i>R. aegyptiacus</i>	Nartey (2015)			
		<i>Nycteribia schmidlii</i>	<i>R. aegyptiacus</i>	Theodor and Moscona (1954)	Plasmodiidae	<i>Polychromophilus dionisi</i>	Obame-Nkoghe et al. (2016)
		<i>Nycteribia pedicularia</i>	<i>R. aegyptiacus</i>	Theodor and Moscona (1954)			
Streblidae		<i>Brachytarsina allaudi</i>	<i>R. aegyptiacus</i>	Maa (1968)	Plasmodiidae	<i>Polychromophilus dionisi</i>	Obame-Nkoghe et al. (2016)
		<i>Brachytarsina gigantea</i>	<i>R. leschenaultii</i>	Advani and Vazirani (1981)			
		<i>Megastrebla parvior</i>	<i>R. leschenaultii</i>	Maa (1971)			
		<i>Megastrebla bequaerti</i>	<i>R. aegyptiacus</i>	Maa (1971)			
		<i>Megastrebla wenzeli</i>	<i>R. madagascariensis</i>	Maa (1971)			

adult females (Dietrich et al., 2018b). Hence in bats, seasonal variation of the number of females in a colony and possible trade-offs between immunity, microbiota and reproduction can significantly affect pathogen infection dynamics (Dietrich et al., 2015; Plowright et al., 2015).

6.2. Experimental approaches

Rousettus aegyptiacus has been recently proposed as a model for the study of pathogenic infectious agents in captive breeding colonies (Wang et al., 2021) and also providing the means of continuous surveys of endogenous parasite ecology. Their relatively small size and their frugivorous diet facilitate the maintenance of captive breeding colonies. Colonies of *R. aegyptiacus* have been regularly used to evaluate the viral resistance, transmission mechanisms and infection dynamics for bats (e. g. Paweska et al., 2016; Halwe et al., 2021). For example, research employing a captive colony demonstrated that Sosuga virus is shed in body fluids after experimental infection of individual *R. aegyptiacus* (Amman et al., 2020).

Long-term infection dynamic studies associated with Ebola, Marburg and Sosuga viruses of captive *R. aegyptiacus* have provided details on temporal variation of their antibody levels (Schuh et al., 2019). Level of immunoglobulin G antibody specific to these viruses started to increase 10 days after infection and peak level was reached between 14 and 28 days after infection. For Marburg virus, the level of antibodies dropped below the seropositivity threshold three months after infection (Schuh et al., 2017a). This bat species still retains immunity to these filoviruses regardless of the antibody level. Such experimental studies are crucial for the estimation of parameters influencing infection dynamics with the aim of assessing spatial and temporal variation of pathogen spillover risk.

Cell lines have been established for *R. aegyptiacus* (Biesold et al., 2011) and *R. leschenaultii* (Lau et al., 2018). Experimental infection of *R. aegyptiacus* cells by Sendai virus (*Paramyxoviridae*) did not induce an immune response even after prolonged infection; only a limited inflammatory response was observed (Pavlovich et al., 2018). Viral

infection in *Rousettus* does not seem to affect their fitness, as they asymptotically host viruses that are, for example, pathogenic for humans and non-human primates (Jones et al., 2019). However, in the case of Marburg, Ebola and Sosuga viruses in *R. aegyptiacus*, antibody-mediated virus neutralization does not completely clear virus infection (Schuh et al., 2019). This may result from a certain tolerance of bat immunity to higher viral infection, limiting inflammatory reaction even at higher virus titres (Pavlovich et al., 2018). Study of Ebola and Marburg virus infected cell lines of *R. aegyptiacus* demonstrated a robust T-cell response and an anti-inflammatory state driven by M2 macrophages that likely control infection and limit pathological effects (Jayaprakash et al., 2020).

The majority of *in vivo* experiments performed with captive colony of *Rousettus* have been performed to study infection dynamics of viruses of public health importance. Information on the other endogenous parasite taxa were mostly obtained after non-invasive sampling and capture of animals from a wild colony (e.g. Gomard et al., 2016; Dietrich and Markotter, 2019), and available data about the ecology and temporal variation of infection are limited. Such aspects need to be explored to facilitate the control of the transmission rate for endogenous parasite communities associated with *Rousettus* colonies, a variable that can vary with the life history parameters of a given species and environmental changes.

6.3. The new era of bat genomes

Genome sequences are currently available for a limited number of bat species. On-going efforts are being made by the Bat1K consortium to generate reference-quality genomes for all living bat species (Teeling et al., 2018). The genus *Rousettus* is among the few genera for which a complete genome has been sequenced and include both *R. aegyptiacus* and *R. leschenaultii* (Pavlovich et al., 2018; Nikaido et al., 2020). In addition, complete mitochondrial genomes have also been obtained for *R. leschenaultii* (Szcześniak et al., 2013) and *R. amplexicaudatus* (Mendoza and Fontanilla, 2019). More recently, an ongoing project of the

DNAZoo (2022) (www.dnazoo.org/assemblies/Rousettus_madagascariensis) have provided details on the full genome of *R. madagascariensis*.

Such data are essential for evaluating variation in bat genetic diversity at the population level and to better understand levels of dispersal, as well as the transmission of pathogens. Further, details on bat genomics are important for the analysis of immunity evolution and responses to pathogens. Sequence analyses of *Rousettus* genomes indicate that the tolerance of species of this genus to viral infection might be linked with their distinctly short genomes relative to most other groups of Pteropodidae (Smith and Gregory, 2009; Nikaido et al., 2020). Studies on vertebrate evolution have shown that larger genomes favour an increase in cellular metabolic activities (Organ and Shedlock, 2009). Hence in the case of *Rousettus*, the genome may have evolved to maintain a smaller size in order to reduce metabolic activities particularly given the high energy expenditure during flight (Smith and Gregory, 2009). Transposable element sequences that can change position and are responsible for mutations (Bourque et al., 2018), are also significantly smaller in pteropodid genomes (Kapusta et al., 2017). These sequences are generally associated with viral genome replication and antiviral responses (Nikaido et al., 2020). Roy et al. (2020) suggested that chronic viral infection could inhibit the activities of transposable elements; and the large number of viruses in *Rousettus* may be linked to the small size of their transposable elements. Also, *Rousettus* genes associated with antibody production and immune system regulation are significantly different from other mammals, with expanded and diversified antiviral loci (Nikaido et al., 2020). This reinforces the hypothesis that bats have co-evolved with viruses and acquire a state of virus tolerance even towards virulent strains.

7. Effect of habitat fragmentation on zoonoses and conservation challenges

Although there is good evidence that *Rousettus* co-evolved with different plant species and floral communities that provide fruit and pollen in their diet, there is no evidence of any species in the genus being completely forest dependent. This may explain their often broad geographical distributions, the range of habitats they occur in and their dispersal patterns, as well as their significant role in ecosystem services. They use different day roost sites that include caves, rock shelters, buildings in public spaces, wells, abandoned houses, ancient monuments and mines (Kumar et al., 2015; Lučan et al., 2016); and in many cases these sites are outside of natural habitats. The use of human-built structures for roosting is a form of adaptation, whether this has been caused by natural habitat loss or range expansion, and in either case attest to their ability to modify aspects of their life history, as is also the case with their foraging on cultivated plants.

Fifty-four percent of plants consumed by *R. aegyptiacus* on Cyprus (Del Vaglio et al., 2011) and 56% of those consumed by *R. madagascariensis* in Northern Madagascar, occur in forested areas (Vololona, 2020; Vololona et al., 2020). Deforestation can change these proportions towards feeding more on cultivated fruit, which in turn brings members of this genus in closer proximity to people (Vogeler and Tschapka, 2021), and may increase the possibility of bat pathogen spillover. This underlines the importance of conserving natural forests and other native habitats in order to maintain the services of *Rousettus* for indigenous tree regeneration through seed dispersal and flower pollination, as well as reduce contact with humans (Plowright et al., 2021). The daily nutrient needs of *Rousettus* can be found in figs especially minerals (calcium, potassium, sodium), nitrogen, and carbohydrate (Wendeln and Runkle, 2000; Valvi and Rathod, 2011), as well as other types of native fruits. Some species of *Rousettus* can supplement energy intake by consuming other plant parts (pollen, leaves) or occasionally by feeding on insects such as their ectoparasites (Ramanantsalama et al., 2019; Vololona et al., 2020).

Raising public awareness to protect bats remains challenging, even for species that do not live in close proximity to people. The circulation

of negative information on the role of bats in the spread of current emerging and zoonotic diseases impacting public health has directly increased their persecution, including incorrect decisions on the regulation of bat populations (Rocha et al., 2020). For instance, roosts of vampire bats *Desmodus rotundus* and *Diphylla ecaudata* (Phyllostomidae) are continuously destroyed in Central and South America due to the fear of rabies, and even bat species that are not involved in rabies transmission are killed (Shapiro et al., 2020). Hence, popularizing information related to the ecology and the role of different bat species with regards to ecosystem services, whether closed-canopy forest or other vegetation formations, is critical for bat conservation. Instead of highlighting the role of human activities as the principal cause of bat borne zoonotic disease spillover, bats are often presented as the culprit of transmission (López-Baucells et al., 2017). Moreover, circulation of information on the role of bats in ecosystem functioning is not widely disseminated as compared to information that warn people on the pathogens they harbour (Rocha et al., 2020).

In different areas of the Old World, *Rousettus* are considered as a crop pest. In China and Sri Lanka, *R. leschenaultii* is persecuted for feeding on different commercial fruits such as banana, longan, litchi and mango, and reducing fruit harvests (Fujita and Tuttle, 1991; Yapa et al., 1999). On Madagascar, *R. madagascariensis* has been cited to feed massively on ripening litchis (Andrianaivoarivelo et al., 2007). On Cyprus, hunting campaigns between 1927 and 1988 were organized against *R. aegyptiacus* to protect commercial fruit crops, and cave roosts were fumigated, which killed all inhabiting bats (Hadjisterkotis, 2006). Field research has shown that in many cases *Rousettus* prefer native and non-commercial fruits of native trees and they only forage in fruit orchards when wild food resources are scarce (Thomas and Fenton, 1978; Andrianaivoarivelo et al., 2012).

In certain countries it is challenging to stop people from consuming fruit bats in the form of bushmeat, particularly in areas where local people need to supplement protein in their diet, as is the case in Madagascar (Jenkins and Racey, 2008). *Rousettus leschenaultii* are reported to be served at restaurants in Thailand (Mickleburgh et al., 2009).

Multidisciplinary conservation actions involving researchers, people working on conservation, human health and public awareness, are needed to protect *Rousettus* and their habitats. During these last decades, several bat-harboured pathogens have been identified, but evidence of transmission of most of the isolated infectious agents to people remains scarce. Many of these endogenous parasites may shift host taxa and their capacity to survive in different vertebrate taxa hosts need to be understood.

Across portions of the Old World where *Rousettus* occur, the results of ecological research should be popularized at the local and national level to increase awareness of the role of fruit bats in ecosystem functioning. Further, clear dissemination of information on the potential risks of hunting and consuming these bats with regards to possible pathogen spillover is important from the side of public health. Future research and conservation programs should incorporate monitoring aspects of seasonal and annual variation in pteropodid life-history traits. Given that *Rousettus* are excellent study models, aspects including shifts in foraging range size and dispersal patterns should be examined in greater detail, as well as the cascade effects on their ecology, epidemiology and evolution of their associated infectious agents.

8. Conclusion

- (1) Throughout portions of the Old World, *Rousettus* are important members of local vertebrate communities and provide ecosystem services in the form of seed dispersal and flower pollination that are essential for the maintenance and regeneration of forest habitats. Members of this genus play a significant role in extending forest cover across large areas of tropical and subtropical habitats.

- (2) *Rousettus* host a diversity of viruses, bacteria, protozoa and fungi, including some affecting human health, such as filoviruses. As with other taxonomic groups of bats, they appear to have certain levels of immunity to a range of pathogens, which translates to their limited fitness costs associated with infection. This tolerance, particularly for *Rousettus*, has been hypothesised to be related to their genome, which is significantly shorter as compared to other mammals.
- (3) *Rousettus* infectious diseases, such as filovirus and paramyxovirus, are mainly transmitted to people via direct physical contact and bat body fluids (saliva, urine, faeces). Transmission of vector-borne pathogens, like those of *Peribunyaviridae*, by hematophagous ectoparasites, might be possible. However, this transmission route requires further investigation. Infectious agent spillover through bridging intermediate hosts to domesticated animals and humans should not be underestimated especially endogenous parasites that have already been detected in other group of vertebrates (mammals, birds), as the case of the astroviruses, coronaviruses, herpesviruses, influenza viruses or rhabdoviruses, and bacteria like *Bartonella* or *Leptospira*.
- (4) Decrease in the range of natural forest and destruction of natural habitats of *Rousettus* via human activities result in reduced food resources for *Rousettus*. This can affect their feeding behaviour with increased consumption of cultivated fruits and contact with people and, in turn, the possibility of bat infectious disease spillover. Conservation programs should be promoted to increase protection of *Rousettus* and their natural habitats, so that they continue their role with respect to ecosystem services and reduce their proximity to people. Further multidisciplinary research on infection dynamics, transmission mode and evolution of *Rousettus* pathogens is also critical to understand and prevent any risk of future outbreaks.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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