REVIEW ARTICLE
DOI: https://doi.org/10.36233/0507-4088-79

Viruses and bats: interdisciplinary issues

Aleksandr D. Botvinkin

FSBEI HE «Irkutsk State Medical University» of the Ministry of Health of Russia, 664003, Irkutsk, Russia

The virologists' attention to bats (*Chiroptera*) changed in the late 20th century as the concept of emerging infections grew in popularity. Since the beginning of the COVID-19 pandemic, the number of publications on bat viruses has increased profoundly.

History of the problem; biodiversity of *Chiroptera* and related viruses; medical and veterinary significance of some viral genera and subgenera (*Lyssavirus*, *Henipavirus*, *Marburgvirus*, *Ebolavirus*, *Sarbecovirus*, *Merbecovirus*), as well as problems of bat protection, are addressed in a concise form. Literature search was carried out in electronic databases, mainly for the period of 2000–2021. Publications in Russian that are poorly represented in English-language reviews are also included. The purpose of the review is to substantiate the importance of an interdisciplinary approach in the context of increased interest in the study of viral infections in bats. This review was written for researchers who have not previously dealt with this problem.

Since the beginning of this century, the number of known virus species associated with bats has increased by an order of magnitude (>200). The families *Rhabdoviridae*, *Coronaviridae*, *Paramyxoviridae* are in the first ranks according to the number of findings, and the highest diversity of viruses has been established for the families *Vespertilionidae*, *Pteropodidae*, *Molossidae*. Interdisciplinary cooperation positively influences the efficiency, biological safety and practical significance of the ongoing research. The best results were achieved by multidisciplinary teams with good cross-training in several specialties. Many papers emphasize the need to balance health and conservation interests.

The analysis of scientific publications indicates a change in research approaches in this area: from collecting individual facts within the framework of narrow specialties to a comprehensive assessment of new knowledge from ecological, evolutionary and socio-economic positions. Results of the research emphasize the need to maintain complex approaches addressing public health needs and environmental protection. The importance of bat-borne viral infections determines the necessity for correction and interdepartmental coordination of scientific research and surveillance of wildlife zoonoses in the Russian Federation.

Key words: *viruses, chiropterans; bats; interdisciplinary approach*

For citation: Botvinkin A.D. Viruses and bats: interdisciplinary issues. *Problems of Virology* (*Voprosy Virusologii*). 2021; 66(4): 259-268. DOI: https://doi.org/10.36233/0507-4088-79

For correspondence: Aleksandr D. Botvinkin, D.Sci. (Med.), Head of Epidemiology Department, FSBEI HE «Irkutsk State Medical University» of the Ministry of Health of Russia, 664003, Irkutsk, Russia. E-mail: botvinkin_ismu@mail.ru

Information about the author:

Botvinkin A.D., http://orcid.org/0000-0002-1324-7374

Funding. The work was carried out with funding from the Russian Foundation for Basic Researches (RFBR), project No. 20-115-50063/20.

Acknowledgement. The author gratefully acknowledges to Ivan V. Kuzmin (biomedical and consulting company Aravan LLC, Lilburn; CDC, Atlanta, GA, USA), and Sergey V. Kruskop (FSBEI HE «Lomonosov Moscow State University», Biology Department, Research Zoological Museum) for valuable advice and comments in preparing the text of the article.

Conflict of interest. The authors declare no conflict of interest.

Received 03 June 2021
Accepted 01 August 2021
Published 31 August 2021

НАУЧНЫЙ ОБЗОР
DOI: https://doi.org/10.36233/0507-4088-79

Вирусы и летучие мыши: междисциплинарные проблемы

Ботвинкин А.Д.

ФГБОУ ВО «Иркутский государственный медицинский университет» Минздрава России, 664003, Иркутск, Россия

Отношение вирусологов к рукокрылым (*Chiroptera*) изменилось в конце XX в. на фоне роста популярности концепции новых и возвращающихся (emerging) инфекций. После начала пандемии COVID-19 количество публикаций о вирусах рукокрылых резко возросло.
В обзоре рассмотрены история изучения, биологическое разнообразие этих животных и связанных с ними вирусов, медицинское и ветеринарное значение некоторых таксонов (*Lyssavirus*, *Henipavirus*, *Marburgvirus*, *Ebolavirus*, *Sarbecovirus*, *Merbecovirus*), а также проблемы охраны рукокрылых. Поиск информации проведён в электронных базах данных преимущественно за период 2000–2021 гг. Включены публикации на русском языке, недостаточно представленные в англоязычных обзорах.
Цель представляемой работы состоит в обосновании важности междисциплинарного подхода к изучению вирусных инфекций рукокрылых в условиях возросшего интереса к данной проблеме. Обзор адресован прежде всего исследователям, ранее непосредственно не занимавшимся этой областью научных знаний.
С начала текущего столетия число известных видов вирусов, ассоциированных с рукокрылыми, возросло на порядок (>200). Первые ранговые места по числу находок занимают семейства *Rhabdoviridae, Coronaviridae, Paramyxoviridae*, а наиболее высокое разнообразие вирусов установлено для рукокрылых семейств *Vespertilionidae*, *Pteropodidae*, *Molossidae*. Междисциплинарное взаимодействие положительно влияет на результативность, биологическую безопасность и практическую значимость проводимых исследований. Лучшие результаты достигнуты командами, в состав которых входили представители разных специальностей с хорошей подготовкой по смежным вопросам. Во многих работах подчёркивается необходимость соблюдения баланса интересов в сферах здравоохранения и охраны природы.
Анализ научных публикаций свидетельствует об изменении подходов к исследованиям в этой области: от сбора фактов в рамках отдельных специальностей к комплексной оценке новых знаний с экологических, эволюционных и социально-экономических позиций. Актуальность связанных с рукокрылыми вирусных инфекций определяет необходимость коррекции и межведомственной координации научной работы и эпидемиологического надзора за зоонозами в Российской Федерации.

Ключевые слова: *вирусы; рукокрылые; летучие мыши; междисциплинарный подход*

Для цитирования: Ботвинкин А.Д. Вирусы и летучие мыши: междисциплинарные проблемы. *Вопросы вирусологии*. 2021; 66(4): 259-268. DOI: https://doi.org/10.36233/0507-4088-79

Для корреспонденции**:** Ботвинкин Александр Дмитриевич, д-р мед. наук, заведующий кафедрой эпидемиологии, ФГБОУ ВО «Иркутский государственный медицинский университет» Минздрава России, 664003, Иркутск, Россия. E-mail: botvinkin_ismu@mail.ru

Финансирование. Работа выполнена при финансовой поддержке проекта Российского фонда фундаментальных исследований (РФФИ) № 20-115-50063/20.

Благодарности. Автор выражает благодарность И.В. Кузьмину (биомедицинская и консалтинговая компания Aravan LLC, Lilburn; CDC, Atlanta, GA, USA) и С.В. Крускопу (ФГБОУ ВО «Московский государственный университет имени М.В. Ломоносова», биологический факультет, научно-исследовательский зоологический музей) за ценные советы и замечания при подготовке текста статьи.

Конфликт интересов. Автор заявляет об отсутствии конфликта интересов.

Поступила 03.06.2021
Принята к печати 01.08.2021
Опубликована 31.08.2021

Relevance of the Issue

New knowledge regarding viruses associated with chiropterans (*Chiroptera*) has significantly changed the paradigm surrounding the reservoir of zoonotic infections. In the first half of the last century, it was a generally known fact that vampire bats (*Phyllostomidae*, *Desmodus rotundus*) were direct participants in the spread of rabies in the tropics of the American continent [1]. Due to the publication of the main provisions of the theory of the natural foci of diseases [2], study of vector-borne infections was initiated in different regions of the world and bats were examined using virological methods as were other warm-blooded animals [3, 4]. During the same period, bat rabies was being actively studied in the United States of America (USA) and Canada. As a result, data began to accumulate on the isolation from these animals of viruses from various systematic groups. In 1974, Edward Sulkin & Rae Allen published the first summary on bat-borne viruses [cit. by 5]. In most cases, new evidence was considered exotic and without practical value. The attitude of

DOI: https://doi.org/10.36233/0507-4088-79

virologists towards bats, however, was altered at the end of the 20th century after the publication of the Concept of Emerging Infections [6] and the growth in popularity of the subject [7–9].

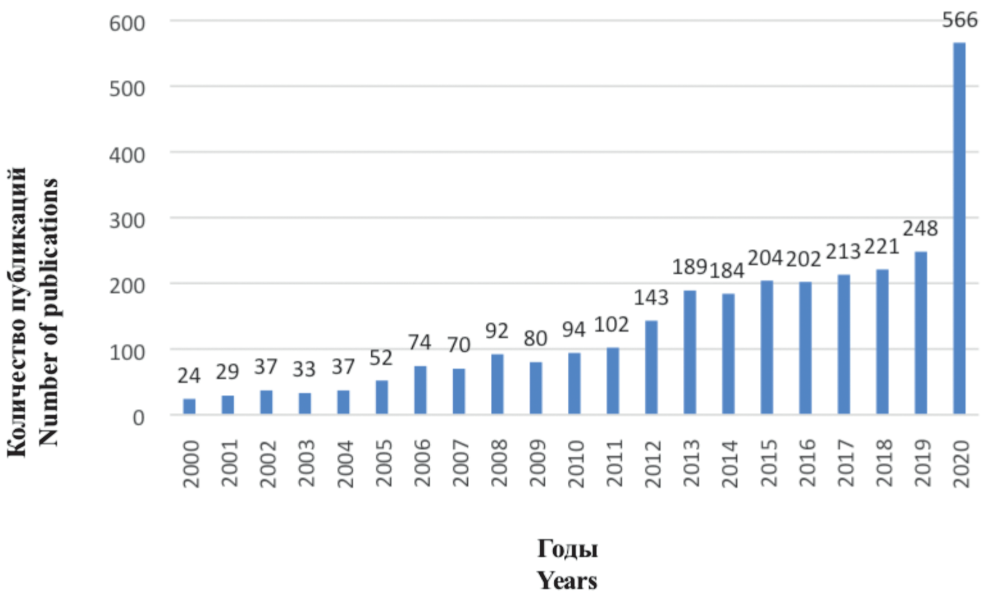
The COVID-19 pandemic has sharply aggravated the problem. The global spread of this new disease and the similarity of SARS-CoV, MERS-CoV and SARS-CoV-2 to bat coronaviruses has given rise to the interest of researchers who had not studied chiropteran viral diseases before. Finally, the overall number of publications related to the issue, all of varying quality, has sharply increased. Currently more than three thousand original and review articles on viruses associated with chiropterans have been published, including manuals, monographs [3, 8–10] and a series of recent reviews in the Russian language [4, 11–18].

The purpose of the review is to substantiate the importance of an interdisciplinary approach in the context of increased interest in the study of viral infections in bats. The need for an interdisciplinary approach is determined by the specifics of the objects under investigation and methods of field research, the full understanding of which is important in order to reach a consensus in the event of a conflict of interests between virologists and specialists in the field of environmental protection. However, this is no less important from the point of view of the efficiency, biological safety and the practical significance of the performed studies. Due to the presence of limited knowledge amongst researchers regarding chiropterans, errors inevitably occur in the names of species and taxa of different ranks, as well as in assessments given to the epidemiological significance of such animals [19, 20]. The data published on bat-borne viruses in the Russian Federation are scarce and mainly include review papers. It is expected that there will be an increase in the number of related scientific projects and an inflow of young scientific personnel who are acquainted with only one side of the issue. This review is primarily addressed to this category of researcher.

Our data search was conducted using the Web of Science, Scopus, PubMed, Google Scholar, eLIBRARY databases using the following keywords: «viruses and bats», «emerging diseases and bats», «bat biology», «bat conservation» within the 2000 to 2021 timeframe. Thereafter, the search was continued through lists of cited sources and other traditional methods, selecting publications confirming the importance of an interdisciplinary approach. The review includes national publications that are poorly represented in extra-national English-language scientific publications.

Virological studies

Since the beginning of the 21st century, the number of publications on chiropteran viruses has rapidly increased. During two periods of time the number of publications per year was observed to have more than doubled: 2004–2007 and 2020–2021 (**Figure**). There is also an obvious association with coronavirus epidemics caused by MERS-CoV, SARS-CoV and SARS-CoV-2 and attempts to establish their origin. At the beginning of this century, in the summary by Charles Calisher et al., there were data on 66 viruses that have been isolated from or detected in 74 species of chiropterans [5]. Rapid progress was traced when compared with later publications [7, 8, 12]. In the recently published monograph, more than 200 viruses of 27 families were identified [10]. A catalog of viruses discovered in chiropterans up to 2020 was published, which included 260 species of 19 orders, 28 families, 61 genera, and excluded a large number of unclassified viruses [22]. It is thus evident that an accurate calculation of their numbers



Number of publications on *Chiroptera* viruses during 2000–2020 (according to PubMed; keywords «viruses and bats»; accessed 07/26/2021).

Количество публикаций по вирусам рукокрылых на протяжении 2000–2020 гг. (по данным PubMed; ключевые слова «viruses and bats»; дата доступа 26.07.2021).

is impossible due to the rapid updating of knowledge and the different approaches to assessing biodiversity. It was not always possible to isolate viruses and identify them flawlessly; some findings were represented by fragments of the genome only [3, 10, 21]. The bat virom was studied with the help of metagenomic sequencing with an unclear assessment of the results [23]. Regardless, there was general understanding of the relation between different systematic groups of viruses and chiropterans. The families of the viruses *Rhabdoviridae, Coronaviridae, Paramyxoviridae* rank first in terms of the number of findings, and the highest diversity of viruses was observed in the chiropterans of the families *Vespertilionidae*, *Pteropodidae* and *Molossidae* [21]. The modern taxonomy of bat viruses is presented on the website of International Committee on Taxonomy of Viruses (ICTV) [24].

Biology of bats

Chiropterans (*Chiroptera*), in contrast to other warm-blooded animals such as rodents (*Rodentia*) and birds (*Aves*), did not become an object of close study by virologists until much later. It is important to note that this is one of the most successful and numerous orders of the *Mammalia* class, which includes more than 20% of all mammalian species known on the planet. Chiropterans are second only to rodents in the number of species and the geography of their distribution. The number of species of chiropterans known to science is constantly increasing, with more than 1,400 having been identified [25, 26] to date. On the territory of the Russian Federation, there are 57 species that have been registered which belong to four families: *Rhinolophidae*, *Vespertilionidae*, *Miniopteridae*, and *Molossidae*; the representatives of the first family are the most numerous and widespread in natural and anthropogenic landscapes (except for the Far North and highlands), the bats of the other three families only inhabit the southern borders of Russia [27].

The systematics and taxonomy of chiropterans have significantly undergone changes in recent decades due to the widespread use of molecular genetic methodologies. In the recent past, *Chiroptera* was subdivided into two large suborders, namely *Megachiroptera* (fruit bats) and *Microchiroptera* (bats). Currently, the suborder *Yinpterochiroptera* (*Pteropodiformes*) has been highlighted, and includes well-separated groups: *Pteropodoidea* (fruit bats) and *Rhinolophoidea* (horseshoe bats). The rest of the families belong to the suborder *Yangochiroptera* [3, 26]. The interpretation of many species of bats and the nomenclature of the domestic fauna have changed. The old names of species and taxa of chiropterans of different ranks continue to appear in publications on bat viruses, which can lead to an incorrect interpretation of the results. The names published by the International Union for Conservation of Nature (IUCN) after 2015 [28] should be adhered to. Listings of trivial and scientific names of bats, as well as a bibliography on chiropterans of the domestic fauna, are presented on the website [27].

What makes bats special as hosts for viruses? This is the leitmotif of many publications. The ability of bats to actively fly is unique to mammals. It is associated with the peculiarities of their metabolisms, the functioning of their immune systems, and finally with the pathogenesis and epidemiology of viral infections [3, 8–10, 29, 30]. From this point of view, the accumulations of millions of some species of bats in constraint environments, the close contacts of individuals of different age in brood colonies, the prolonged winter torpor, their relatively long life expectancy and their low rates of reproduction, all deserve attention. Methods of field work with chiropterans differ in their specificity, and difficulties in assessing bat population abundance should be especially noted [3, 25, 26].

Medicine and veterinary medicine

Chiropterans serve as a reservoir for viruses that have a high epidemiological danger, and this is the main incentive for expanding studies. The mortality due to rabies and other lyssavirus encephalitis is almost 100% [3, 31]; the frequency of fatal outcomes of diseases caused by filoviruses reaches 50–90% [8, 11, 12]. The outbreaks of diseases caused by Hendra (*Hendra henipavirus*) and Nipah (*Nipah henipavirus*) viruses are accompanied by the death of farm animals and diseases in people with a high level of mortality [9, 13, 32]. The mortality rate for new coronavirus infections caused by MERS-CoV, SARS-CoV and SARS-CoV-2 is not so high, but due to the pandemic spread of COVID-19, more than 4 million people have died from this infection by the middle of 2021 [33].

The medical and veterinary significance of chiropterans is ambiguous. They can serve as a direct source of sporadic diseases in human and domestic animals. Moreover, sometimes outbreaks and epidemics initiate from them, although bats are not a part of their further spread. As a rule, the incidence of human infectious diseases after contact with chiropterans is low [8, 10]. A role in the pathology of human and companion animals was not established for the majority of viruses detected in chiropterans. Many of these viruses are closely related but not identical to the causative agents of viral infections circulating in human population [3, 7, 8, 10]. The geography of epidemiological manifestations is peculiar, but in general, the problem is more relevant for tropical and subtropical countries, where the frequency of contacts by the populations with chiropterans is much higher.

Let us consider this using the example of four taxa of viruses (*Lyssavirus, Paramyxoviridae, Filoviridae, Coronaviridae*), whose representatives have the greatest epidemiological significance.

***Lissaviruses* (*Rhabdoviridae, Lyssavirus*).** In the first half of the last century, the study of bat viruses started from this group [1, 3, 5]. The most famous representative of the genus, the rabies virus (*Rabies lyssavirus*), is widespread among bats on the American continent only, where outbreaks of paralytic rabies among cattle, after being bitten by vampire bats (*Phyllostomidae*, *Desmodus rotundus*), are registered almost every year along with sporadic human diseases after contact not only with these animals, but also with insectivorous bats. Several distinct genetic variants of the rabies virus associated with different bat species were identified in the North and South America, but other types of lyssaviruses have not been found in the New World [31, 34]. On other continents, both in temperate latitudes and in the tropics, 17 species of lyssaviruses are currently known to exist, however, there is no reliable data on rabies virus isolation. Such a peculiarity of the geographical distribution of lyssaviruses has not been satisfactorily explained yet [34]. The first findings in Africa in the middle of the last century were primarily designated as «rabies-like» and «rabies-related» viruses. Human connected diseases are not known for any of them and are registered extremely rarely [3, 10, 31]. For example, in all of Eurasia (including Russia), only eight cases were recorded and two of the diseased persons were bat researchers [35]. Reports were obtained on the detection of rabies virus in bats in Ukraine, Russia and China, nevertheless they were either not confirmed by genotyping [36] or based on the detection of short genome fragments [37, 38]. Rabies virus variants adapted to insectivorous bats in Americas, like the Old World chiropteran lyssaviruses, are isolated from time to time in dogs, cats, farm and wild animals without evidence of the further spread of infection among them [54]. However, the possibility of overcoming the interspecies barrier cannot be completely excluded. There are good reasons to believe that chiropteran lyssaviruses have served as the ancestral forms for the rabies virus, numerous variants of which are common among carnivorous mammals around the world and which cause tens of thousands of lethal diseases among humans and enormous damage to animal husbandry every year [3, 7, 31].

***Paramyxoviruses* (*Paramyxoviridae*).** The best known viruses are the Hendra virus (*Hendra henipavirus)*, the Nipah virus (*Nipah henipavirus*) and the Menangle virus (*Menangle rubulavirus*), first isolated during outbreaks among horses and pigs and which were accompanied by human diseases. People contracted the viruses while caring for the animals; cases of human-to-human transmission of the virus were also described [3, 7–9, 13]. The above-mentioned viruses and antibodies to them were most often detected in fruit bats of different species (*Pteropodidae*) in Australia and Asia [32]. The list of known chiropteran paramyxoviruses is constantly growing, and the geography of their detection is expanding [10, 21, 22]. Outbreaks caused by the Nipah virus are observed almost every year in India, Bangladesh, Malaysia, Singapore and result in significant economic loss [39, 40]. Outbreaks of Hendra-viral etiology continue to be registered in Australia [41]. Based on the genetic similarity of chiropteran paramyxoviruses with measles and carnivorous plague viruses, and other pathogens affecting human and domestic animals, assumptions have been made about their evolutionary relationships [32, 39].

Filoviruses (*Filoviridae*). From year to year, the number of facts increases confirming the participation of chiropterans in the reservation of viruses of this family. The viruses of two genera, *Marburgvirus* and *Ebolavirus* are considered to be the causative agents of the most dangerous infections for human [5, 7, 11, 12, 18] and the fact of their existence is constantly present in the focused attention of biosafety specialists [15]. The Marburg virus (*Marburg marburgvirus*) was repeatedly isolated from fruit bats (*Rousettus aegyptiacus*) in Africa [11, 12, 42]. Although there are difficulties in isolating ebolaviruses from chiropterans, viral RNA was detected in biomaterial obtained from several species of fruit bats (*Pteropodidae*) and other chiropterans in Africa and Asia. Numerous serological confirmations of the relation of marburgviruses and ebolaviruses with chiropterans have been documented [14, 15, 42]. In modern zoogeographic studies, the habitats of fruit bats with the territories of western and central Africa, where outbreaks caused by the *Zaire ebolavirus* are registered [43] and their coincidence have been established. New data on the diversity and geographical distribution of filoviruses outside the African continent has been documented mainly after the examination of bats [14, 18]. Recently, new filovirus (*Lloviu cuevavirus*) was discovered in bats in Europe [44]. Primates and other wild animals are systematically involved in the circulation of filoviruses, contacts with which can also lead to infection among humans [7, 12, 15]. Due to the high contagiousness of viruses, outbreaks and epidemics develop sans the participation of chiropterans and involving tens, and sometimes thousands of people [11, 12, 15]. The significance of filoviruses in veterinary medicine has been confirmed by the isolation of *Reston ebolavirus* from pigs [9, 13].

***Coronaviruses* (*Coronaviridae*).** A crucial moment in the study of chiropteran coronaviruses was a publication concerning the detection of a coronavirus, genetically closest to the virus of severe acute respiratory syndrome-related coronavirus, SARS-CoV, in the organs of Chinese horseshoe bats (*Rhinolophus sinicus*) in the south of China [45]. The goal of this work, performed by a multidisciplinary team organized by the World Health Organization (WHO), was to find the reservoir of the virus which had caused the SARS epidemic from 2002 to 2003. Since 2005, new data has been rapidly accumulating in the course of studies conducted in different parts of the world. These works have established the significant biodiversity, the wide range of hosts and the global spread of viruses from this family [10, 46].

The coronaviruses of two genera are associated with chiropterans, *Alphacoronavirus* and *Betacoronavirus*, which include viruses that can cause long-known respiratory infections in humans [16, 17]. The SARS-CoV and SARS-CoV-2 viruses are combined into the *Sarbecovirus* subgenus together with viruses isolated from bats. Of these, the most similar genetically, but not identical to SARS-CoV and SARS-CoV-2, are viruses isolated from various species of horseshoe bats (*Rhinolophidae*) widespread in Asia, as well appearing as in Europe and Africa [16, 17, 45]. The Middle East respiratory syndrome-related coronavirus – MERS-CoV is assigned to the *Merbecovirus* subgenus, which includes coronaviruses isolated from several species of bats of two families, *Vespertilionidae* and *Nycteridae*, which enjoy a wide distribution [7, 16, 46]. The chiropteran sarbekoviruses and merbecoviruses are considered as ancestral forms from which coronavirus infections occur and became epidemic at the beginning of the 21st century [16, 17, 46, 47].

DOI: https://doi.org/10.36233/0507-4088-79

Regardless of these facts, there is no consensus on how this actually occurred. From the perspective of coronavirus infection through the aspiration transmission mechanism and widespread subclinical forms of the disease, it is difficult to obtain rigorous evidence regarding the indexed patient and source of their infection. There are widely discussed variable options and schemes including; direct infection by chiropterans, the participation of other animals (palm civets (*Nandinia binotata*), one-humped camels (*Camelus dromedaries)*, pangolins (*Pholidota*), and other) and the alteration of the virus under laboratory conditions [16, 47–49].

Even a brief summary of the data on selected groups of viruses shows the importance of a multidisciplinary approach to their study and the theoretical contribution to the development of ideas about the relation between the diseases of wild animals and those of humans. It has become clear that different variants of the epidemiological manifestations of viral infections, the reservoir of which are chiropterans, are possible:

1. A human is a biological dead end for the virus, and under natural conditions, its further spread does not occur (for example, lyssaviruses). This is a typical situation for many zoonoses.
2. A human becomes infected from a bat directly or with the participation of animals from other species, after which chains of successive transmission of the virus from human to human are formed with a gradual attenuation of the epidemic process (for example, filoviruses and henipaviruses).
3. The virus overcomes the interspecies barrier and acquires the ability to circulate among people indefinitely (for example, SARS-CoV-2). This process can end with the formation of new anthroponosis.

A similar scheme is considered in monographs [3, 8, 10] and several review works within the framework of the origin of infectious diseases in human and domestic animals from the zoonoses of wild animals [16, 46, 50]. The COVID-19 pandemic has been the first event of «biblical proportions» after humanity had achieved the adequate technical capabilities to analyze the situation. Of principle importance remains the issue of mechanisms for overcoming the interspecies barrier. The process of the transition of viruses from the population of the main host to other species of animals and human («spillover») is being intensively studied at the molecular-genetic level [8, 10, 18]. However ecological relationships and patterns are also important [3, 7, 10].

Epidemiological surveillance and monitoring

The accumulation of knowledge about viral infections in chiropterans is dependent on the organization of studies and the quality of surveillance systems. In the USA and Canada, monitoring of bat rabies for decades (since the middle of the last century) was conducted by the laboratories of public health institutions with the assistance of a population that is well informed about the dangers of the infection. As a result, in North America, rabies in chiropterans is detected more often than in other animal species, and more than a thousand cases are confirmed every year [51]. In Europe, a similar system was applied much later. In recent years, dozens (sometimes hundreds) of cases of lyssavirus infection in bats have been indicated in WHO reports [52]. The surveillance system for viral infections in chiropterans in Europe continues to be improved [52]. In the Russian Federation, laboratory diagnostics of rabies is executed by veterinary laboratories, and such cases are detected very rarely [9, 13]. Staff members of the sanitary-epidemiological services have no experience in field work with bats, since zoological and parasitological studies were focused mainly on monitoring zoonoses associated with rodents and blood-sucking arthropods [54]. In most countries of the world, including the Russian Federation, targeted scientific studies with the participation of specialists who have experience in working with chiropterans are the most effective [3, 36, 45].

The effectiveness of different surveillance systems also depends on the characteristics of specific infections. Lissavirus infections are accompanied by characteristic symptoms and the death of the diseased bats, therefore, passive monitoring is quite effective. Nevertheless, most other viral infections in bats are subclinical, so there is a need for selective capture and examination of the animals. Moves to active monitoring occur when conducting serological studies. Recommendations have been developed for the examination of chiropterans, including using non-invasive protocols [3], as well as for the capture of these animals [3, 25, 26].

Ecology and environmental protection

Chiropterans play an important role in the biosphere [25, 55]. In a number of countries, bats and their habitats are strictly protected, and associations of experts on chiropterans are successfully working in this direction [56, 57]. Since the outbreak of the COVID-19 pandemic, the activities of experts on chiropteran protection have sharply increased. In addition to the above-mentioned reasons, the possibility of infection with new coronavirus in bats in Europe and America from diseased people («spillback») has been supposed. To prevent such transmissions, zoologists have been recommended to use personal protective equipment and limit field work with chiropterans [56–58]. The Russian Federation is not among the parties of the Bonn Convention (Convention on Migratory Species, CMS) [56], so the restrictions during field and experimental studies with these animals are not as severe as in most European countries. Some bat species are represented in the regional Red Data Books of many territorial subjects of the Russian Federation [26, 27], and penalties are provided and in effect for damage caused to rare species[1]. Generally accepted ethical standards and requirements for biological safety are applied during field and experimental work with chiropterans [58].

One of the main reasons for a decrease in biodiversity and the number of chiropterans is the anthropogenic

[1]«The Code of Administrative Offenses of the Russian Federation» of 30.12.2001 No. 195-FZ (as edited on 30.04.2021; as amended on 17.05.2021). Article 8.35. Destruction of rare and endangered species of animals and plants).

DOI: https://doi.org/10.36233/0507-4088-79

transformation of their natural habitat [25, 55]. Emerging zoonoses are in second place in the list of threats to the existence of these animals [55]. Viral infections rarely lead to the death of bats [8, 10], but against the background of epidemics, virological scientific projects are well funded, and large numbers of chiropterans are caught for studies. In these cases, some of the animals are inadvertently killed. However, even the intravital collection of biomaterial is accompanied by an increase in mortality among bats, especially during critical periods of their life cycle (reproduction, hibernation, etc.) [3, 55]. The distribution of information about dangerous diseases associated with bats forms a negative attitude towards these animals which then may provoke the destruction of their habitats and colonies [56–58].

The pursuit of bats as potential carriers of zoonotic infections is considered by some as futile and even counterproductive [3, 6, 7]. On a limited scale, extermination measures are used only against vampire bats [1]. The main efforts should be aimed at limiting contact between people and bats, using personal protective equipment and specific prophylaxis during professional and casual contacts, as well as providing for environmental and hygienic education [26, 35, 56–58]. It is emphasized that deforestation, unsustainable agricultural production systems, and trade in wild animals (including game) not only threaten the existence of some species of chiropterans, but can contribute to the spread of emergent zoonoses [3, 8, 55]. One of the ways to solve interdisciplinary issues is the concept of «One Health», aimed at developing a balanced approach to the fight against emerging zoonoses [60].

Conclusion

At the beginning of the 21st century, chiropterans, as a reservoir of viruses, became the focus of interests of various experts. The summary of scientific publications testifies to a gradual alteration regarding approaches to studies in this area: from collecting data and its «sensationalized» presentation, to comprehending new knowledge from ecological, evolutionary and socio-economic points of view. The best results were achieved by teams, which included representatives of different specialties with good training in related issues. The results of studies underline the need to adhere to a balance of interests in the fields of health care and environmental protection. In the Russian Federation, due to the increased relevance of the issue of viral infections in bats, interdepartmental coordination of scientific research and surveillance activities for zoonotic infections is required.

REFERENCES

1. Baer G.M., ed. *The Natural History of Rabies*. New York, San Francisco, London: Academic press; 1975.
2. Pavlovsky E.N. Fundamentals of the doctrine of the natural focus of vector-borne human *[Osnovy ucheniya o prirodnoy ochagovosti transmissivnykh bolezney cheloveka]*. *Zhurnal obshchey biologii*. 1946; (7): 3–33. (in Russian)
3. Newman S.H., Field H.E., de Long C.E., Epstein J.N., eds. *Food and Agriculture Organization of the United Nations. Investigating the Role of Bats in Emerging Zoonozes. Balancing Ecology, Conservation and Public Health Interest*. *Manual No 12*. Rome: FAO Animal Production and Health; 2011.
4. Lenshin S.V., Romashin A.V., Vyshemirsky O.I., Lvov D.K., Alkhovsky S.V. Bats of the subtropical climate zone of the Krasnodar Territory of Russia as a possible reservoir of zoonotic viral infections *[Letuchie myshi subtropicheskoy zony Krasnodarskogo kraya kak vozmozhnyy rezervuar zoonoznykh virusnykh infektsiy]*. *Voprosy virusologii*. 2021; 66(2): 112–22. https://doi.org/10.36233/0507-4088-41 (in Russian)
5. Calisher C.H., Childs J.E., Field H.E., Holmes K.V., Schountz T. Bats: important reservoir hosts of emerging viruses. *Clin. Microbiol. Rev*. 2006; 19(3): 531–45. https://doi.org/10.1128/CMR.00017-06
6. Lederberg J., Shope R.E., Oaks S.C., eds. *Emerging Infections: Microbial Threats to Health in the United States*. Washington: National Academies Press; 1992.
7. Moratelli R., Calisher C.H. Bats and zoonotic viruses: can we confidently link bats with emerging deadly viruses? *Mem. Inst. Oswaldo Cruz*. 2015; 110(1): 1–22. https://doi.org/10.1590/0074-02760150048
8. Wang L.-F., Cowled C., eds. *Bats and Viruses: A New Frontier of Emerging Infectious Diseases*. Hoboken, New Jersey: John Wiley & Sons, Inc.; 2015. https://doi.org/10.1002/9781118818824
9. Makarov V.V., Lozovoy D.A. *New Especially Dangerous Infections Associated with Bats [Novye osobo opasnye infektsii, assotsiirovannye s rukokrylymi]*. Vladimir; 2016. (in Russian)
10. Corrales-Aguilar E., Schwemmle M., eds. *Bats and Viruses: Current Research and Future Trends*. Caister: Academic Press; 2020.
11. Porshakov A.M., Kononova Yu.V., Loktev V.B., Boiro M.I. *Chiroptera* as a potential reservoir of dangerous for humans viruses in the territory of the Republic of Guinea. Part 1 *[Rukokrylye kak vozmozhnyy rezervuar opasnykh dlya cheloveka virusov na territorii Gvineyskoy Respubliki. Chast' 1]*. *Problemy osobo opasnykh infektsiy*. 2018; (3): 32–9. https://doi.org/10.21055/0370-1069-2018-3-32-39 (in Russian)
12. Porshakov A.M., Kononova Yu.V., Loktev V.B., Boiro M.I. *Chiroptera* as a potential reservoir of dangerous for humans viruses in the territory of the Republic of Guinea. Part 2 *[Rukokrylye kak vozmozhnyy rezervuar opasnykh dlya cheloveka virusov na territorii Gvineyskoy Respubliki. Chast' 2]*. *Problemy osobo opasnykh infektsiy*. 2018; (4): 20–6. https://doi.org/10.21055/0370-1069-2018-4-20-26 (in Russian)
13. Makarov V.V., Barsukov O.Yu. Emerging zoonoses associated with *Chiroptera [Emerdzhentnye zoonozy, assotsiirovannye s rukokrylymi]*. *Pest-menedzhment*. 2019; (2): 18–2. https://doi.org/10.25732/PM.2019.110.2.003 (in Russian)
14. Porshakov A.M., Kononova Yu.V., Lyong T.M. Filoviruses of Southeast Asia, China and Europe (the literature review) *[Filovirusy Yugo-Vostochnoy Azii, Kitaya i Evropy (obzor literatury)]*. *Zhurnal infektologii*. 2019; 11(2): 5–13. https://doi.org/10.22625/2072-6732-2019-11-2-5-13 (in Russian)
15. Sizikova T.E., Boyarskaya N.V., Kovalchuk A.V., Lebedev V.N., Borisevich S.V. The new members of *Filoviridae* family: distribution, natural reservoirs, potential epidemic danger *[Novye predstaviteli semeystva Filoviridae: rasprostranenie, prirodnye rezervuary, potentsial'naya epidemicheskaya opasnost']*. *Vestnik voysk RKHB zashchity*. 2019; 3(4): 329–36. https://doi.org/10.35825/2587-5728-2019-3-4-329-336 (in Russian)
16. Lvov D.K., Alkhovsky S.V. Source of the COVID-19 pandemic: ecology and genetics of coronaviruses (*Betacoronavirus*: *Coronaviridae*) SARS-CoV, SARS-CoV-2 (subgenus *Sarbecovirus*), and MERS-CoV (subgenus *Merbecovirus*) *[Istoki pandemii COVID-19: ekologiya i genetika koronavirusov (Betacoronavirus: Coronaviridae) SARS-CoV, SARS-CoV-2 (podrod Sarbecovirus), MERS-CoV (podrod Merbecovirus)]*. *Voprosy virusologii*. 2020; 65(2): 62–70. https://doi.org/10.36233/0507-4088-2020-65-2-62-70 (in Russian)
17. Shestopalov A.M., Kononova Yu.V., Gadzhiev A.A., Gulyaeva M.A., Marandi M.V., Alekseev A.Yu., et al. Biodiversity and epidemic potential of *Chiroptera* coronaviruses (*Nidovirales*: *Coronaviridae*) *[Bioraznoobrazie i epidemicheskiy potentsial koronavirusov (Nidovirales: Coronaviridae) rukokrylykh]*. *Yug Rossii: ekologiya, razvitie*. 2020; 15(2): 17–34. https://doi.org/10.18470/1992-1098-2020-2-17-34 (in Russian)
18. Dolzhikova I.V., Shcherbinin D.N., Logunov D.Yu., Gintsburg A.L. Ebola virus (*Filoviridae*: *Ebolavirus*: *Zaire ebolavirus*): fatal adaptation mutations *[Virus Ebola (Filoviridae: Ebolavirus: Zaire ebolavirus): fatal'nye adaptatsionnye mutatsii]*. *Voprosy virusologii*. 2021; 66(1): 7–16. https://doi.org/10.36233/0507-4088-23 (in Russian)

19. Puechmaille S.J., Ar Gouilh M., Dechmann D., Fenton B., Geiselman C., Medellin R., et al. Misconceptions and misinformation about bats and viruses. *Int. J. Infect. Dis*. 2021; 105: 606–7. https://doi.org/10.1016/j.ijid.2021.02.097
20. Egorov A.Yu., Romanova Yu.R. The impact of the global distribution of bats on mortality in COVID-19 patients *[Vliyanie global'nogo raspredeleniya letuchikh myshey na smertnost'u patsientov s COVID-19]*. *Microbiol. Indep. Res. J*. 2020; 7(1): 34–41. https://doi.org/10.18527/2500-2236-2020-7-1-34-41(in Russian)
21. Chen L., Liu B., Yang J., Jin Q. DBatVir: the database of bat-associated viruses. *Database*. 2014; 2014: bau021. https://doi.org/10.1093/database/bau021
22. Shchelkanov M.Yu., Dunaeva M.N., Moskvina T.V., Voronova A.N., Kononova Yu.V., Vorobyeva V.V., et al. Catalogue of Chiropteran viruses (2020) *[Katalog virusov rukokrylykh (2020)]*. *Yug Rossii: ekologiya, razvitie*. 2020; 15(3): 6–30. https://doi.org/10.18470/1992-1098-2020-3-6-30 (in Russian)
23. Hermida Lorenzo R.J., Cadar D., Koundouno F.R., Juste J., Bialonski A., Baum H., et al. Metagenomic snapshots of viral components in Guinean bats. *Microorganisms*. 2021; 9(3): 599. https://doi.org/10.3390/microorganisms9030599
24. International Committee on Taxonomy of Viruses. Available at: https://talk.ictvonline.org (accessed 24 July 2021).
25. Wilson D.E., Mittermeier R.A. *Handbook of the Mammalians of the World*. *Volume 9: Bats*. Barcelona: Lynx Ediciones. 2019. Available at: https://www.lynxeds.com/product/handbook-of-the-mammals-of-the-world-volume-9/ (accessed 24 July 2021).
26. Tiunov M.P., Kruskop S.V., Orlova M.V. *Bats of Russian Far East and their ectoparasies [Rukokrylye Dal'nego Vostoka Rossii i ikh ektoparazity]*. Moscow: Pero; 2021. (in Russian)
27. Russian Working Group on Bats *[Rossiyskaya rabochaya gruppa po rukokrylym]*. Available at: https://zmmu.msu.ru/bats/rbgrhp/rbrg.htm (Accessed 20 July 2021). (in Russian)
28. IUCN: International Union for Conservation of Nature. Available at: https://www.iucn.org (accessed 24 July 2021).
29. Luis A.D., Hayman D.T.S., O'Shea T.J., Cryan P.M., Gilbert A.T., Pulliam J.R.C., et al. A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proc. Biol. Sci*. 2013; 280: 20122753. https://doi.org/10.1098/rspb.2012.2753
30. Gorbunova V., Seluanov A., Kennedy B.K. The world goes bats: living longer and tolerating viruses. *Cell Metabolism*. 2020; 32(1): 31–43. https://doi.org/10.1016/j.cmet.2020.06.013
31. Rupprecht C., Kuzmin I., Meslin F. Lyssaviruses and rabies: current conundrums, concerns, contradictions and controversies. *F1000Research*. 2017; 6: 184. https://doi.org/10.12688/f1000research.10416.1
32. Epstein J.H., Anthony S.J., Islam A., Kilpatrick A.M., Ali Khan S., Balkey M.D., et al. Nipah virus dynamics in bats and implications for spillover to humans. *Proc. Natl. Acad. Sci. USA*. 2020; 117(46): 29190–201. https://doi.org/10.1073/pnas.2000429117
33. WHO. Coronavirus (COVID-19) Dashboard. Available at: https://covid19.who.int (Accessed 17 July 2021).
34. Banyard A.C., Evans J.S., Luo T.R., Fooks A.R. Lyssaviruses and bats: emergence and zoonotic threat. *Viruses*. 2014; 6(8): 2974–90. https://doi.org/10.3390/v6082974
35. Botvinkin A.D. Fatal human cases of rabies in Eurasia after contacts with *Chiroptera* (the literature review) *[Smertel'nye sluchai zabolevaniya lyudey beshenstvom v Evrazii posle kontaktov s rukokrylymi (obzor literatury)]*. *Plecotus et al*. 2011; (14): 75–86. Available at: https://zmmu.msu.ru/bats/biblio/rabies.pdf (accessed 17 July 2021). (in Russian)
36. Kuzmin I.V., Botvinkin A.D., Poleschuk E.M., Orciari L.A., Rupprecht C.E. Bat rabies surveillance in the former Soviet Union. *Dev. Biol. (Basel)*. 2006; 125: 273–82.
37. Ternovoy V.A., Zaykovskaya A.V., Tomilenko A.A., Aksenov V.I., Chausov E.V., Shestopalov A.M. Lissavirus in bats residing in the south of West Siberia *[Lissavirusy u letuchikh myshey, obitayushchikh na yuge Zapadnoy Sibiri]*. *Voprosy virusologii*. 2005; 50(1): 31–4. (in Russian)
38. Lu Z.L., Wang W., Yin W.L., Tang H.B., Pan Y., Liang X., et al. Lyssavirus surveillance in bats of southern China's Guangxi Province. *Virus Genes*. 2013; (2): 293–301. https://doi.org/10.1007/s11262-012-0854-2
39. Drexler J.F., Corman V.M., Muller M.A., Maganga G.D., Vallo P., Binger T., et al. Bats host major mammalian paramyxoviruses. *Nat. Commun*. 2012; 3: 796. https://doi.org/10.1038/ncomms1796
40. Sharma V., Kaushik S., Kumar R., Yadav J.P., Kaushik S. Emerging trends of Nipah virus: A review. *Rev. Med. Virol*. 2019; (1): e2010. https://doi.org/10.1002/rmv.2010
41. Williamson K.M., Wheeler S., Kerr J., Bennett J., Freeman P., Kohlhagen J., et al., BatOneHealth field team. Hendra in the Hunter Valley. *One Health*. 2020; 10: 100162. https://doi.org/10.1016/j.onehlt.2020.100162
42. Kuzmin I.V., Niezgoda M., Franka R., Agwanda B., Markotter W., Breiman R.F., et al. Marburg virus in fruit bat, Kenya. *Emerg. Infect. Dis*. 2010; 16(2): 352–4. https://doi.org/10.3201/eid1602.091269
43. Koch L.K., Cunze S., Kochmann J., Klimpel S. Bats as putative *Zaire ebolavirus* reservoir hosts and their habitat suitability in Africa. *Sci. Rep*. 2020; 10(1): 14268. https://doi.org/10.1038/s41598-020-71226-0
44. Negredo A., Palacios G., Vázquez-Morón S., González F., Dopazo H., Molero F., et al. Discovery of an ebolavirus-like filovirus in Europe. *PLoS Pathog*. 2011; 7(10): e1002304. https://doi.org/10.1371/journal.ppat.1002304
45. Li W., Shi Z., Yu M., Ren W., Smith C., Epstein J.H., et al. Bats are natural reservoirs of SARS-like coronaviruses. *Science*. 2005; 310(5748): 676–9. https://doi.org/10.1126/science.1118391
46. Luk H.K.H., Li X., Fung J., Lau S.K.P., Woo P.C.Y. Molecular epidemiology, evolution and phylogeny of SARS coronavirus. *Infect. Genet. Evol*. 2019; 71: 21–30. https://doi.org/10.1016/j.meegid.2019.03.001
47. Leitner T., Kumar S. Where did SARS-CoV-2 come from? *Mol. Biol. Evol*. 2020; 37(9): 2463–4. https://doi.org/10.1093/molbev/msaa162
48. Ji W., Wang W., Zhao X., Zai J., Li X. Cross-species transmission of the newly identified coronavirus 2019-nCoV. *J. Med. Virol*. 2020; 92(4): 433–40. https://doi.org/10.1002/jmv.25682
49. Olival K.J., Cryan P.M., Amman B.R., Baric R.S., Blehert D.S., Brook C.E., et al. Possibility for reverse zoonotic transmission of SARS-CoV-2 to free-ranging wildlife: A case study of bats. *PLoS Pathog*. 2020; 16(9): e1008758. https://doi.org/10.1371/journal.ppat.1008758
50. Wolfe N.D., Dunavan C.P., Diamond J. Origins of major human infectious diseases. *Nature*. 2007; 447(7142): 279–83. https://doi.org/10.1038/nature05775
51. Patyk K., Turmelle A., Blanton J.D., Rupprecht C.E. Trends in national surveillance data for bat rabies in the United States: 2001–2009. *Vector. Borne. Zoonotic. Dis*. 2012; 12(8): 666–73. https://doi.org/10.1089/vbz.2011.0839
52. Schatz J., Fooks A.R., McElhinney L., Horton D., Echevarria J., Vázquez-Moron S., et al. Bat rabies surveillance in Europe. *Zoonoses Public Health*. 2013; 60(1): 22–34. https://doi.org/10.1111/zph.12002
53. Phelps K.L., Hamel L., Alhmoud N., Ali S., Bilgin R., Sidamonidze K., et al. Bat research networks and viral surveillance: gaps and opportunities in Western Asia. *Viruses*. 2019; 11(3): 240. https://doi.org/10.3390/v11030240
54. Trankvilevskiy D.V., Zhukov V.I., Tsarenko V.A. The probability of infection of the population by pathogens associated with *Chiroptera* in the Russian Federation *[Veroyatnost' zarazheniya naseleniya vozbuditelyami, assotsiirovannymi s rukokrylymi, v Rossiyskoy Federatsii]*. *Zdorov'e naseleniya i sreda obitaniya*. 2018; (3): 32–7. https://doi.org/10.35627/2219-5238/2018-300-3-32-37 (in Russian)
55. Voigt C.C., Kingston T., eds. *Bats in the Anthropocene: conservation of bats in a changing world*. Cham: Springer; 2016. https://doi.org/10.1007/978-3-319-25220-9_1
56. Bat Concervation International. Available at: https://www.batcon.org (accessed 24 July 2021).
57. UNEP/EUROBATS. Agreement on the conservation of populations of European bats. Available at: https://www.eurobats.org/ (accessed 24 July 2021).
58. Melber M., Gloza-Rausch F., Voigt C.C. Statement on handling of bats in times of Covid-19 regarding the IUCN Bat Specialists Groups recommendations of field activities for the protection of bats. Available at: https://bvfledermaus.de/wp-content/uploads/2020/04/BVF_Statement_on_Handling_of_Bats_in_times_of_Covid_19.pdf (accessed 24 July 2021).
59. Germanchuk V.G., Semakova A.P., Shavina N.Yu. Ethical Principles for Handling Laboratory Animals in an Experiment with Pathogenic Biological Agents of the I–II Groups *[Eticheskie printsipy pri obrashchenii s laboratornymi zhivotnymi v eksperimente s pato-*

gennymi biologicheskimi agentami I–II grupp]. *Problemy osobo opasnykh infektsiy*. 2018; (4): 33–8. https://doi.org/10.21055/0370-1069-2018-4-33-38 (in Russian)
60. Cunningham A.A., Daszak P., Wood J.L.N. One Health, emerging infectious diseases and wildlife: two decades of progress? *Philos. Trans. R. Soc. Lond. B. Biol. Sci*. 2017; 372(1725): 20160167. https://doi.org/10.1098/rstb.2016.0167

ЛИТЕРАТУРА

1. Baer G.M., ed. *The Natural History of Rabies*. New York, San Francisco, London: Academic press; 1975.
2. Павловский Е.Н. Основы учения о природной очаговости трансмиссивных болезней человека. *Журнал общей биологии*. 1946; (7): 3–33.
3. Newman S.H., Field H.E., de Long C.E., Epstein J.N., eds. *Food and Agriculture Organization of the United Nations. Investigating the Role of Bats in Emerging Zoonozes. Balancing Ecology, Conservation and Public Health Interest*. *Manual No 12.* Rome: FAO Animal Production and Health; 2011.
4. Леншин С.В., Ромашин А.В., Вышемирский О.И., Львов Д.К., Альховский С.В. Летучие мыши субтропической зоны Краснодарского края как возможный резервуар зоонозных вирусных инфекций. *Вопросы вирусологии*. 2021; 66(2): 112–22. https://doi.org/10.36233/0507-4088-41
5. Calisher C.H., Childs J.E., Field H.E., Holmes K.V., Schountz T. Bats: important reservoir hosts of emerging viruses. *Clin. Microbiol. Rev*. 2006; 19(3): 531–45. https://doi.org/10.1128/CMR.00017-06
6. Lederberg J., Shope R.E., Oaks S.C., eds. *Emerging Infections: Microbial Threats to Health in the United States*. Washington: National Academies Press; 1992.
7. Moratelli R., Calisher C.H. Bats and zoonotic viruses: can we confidently link bats with emerging deadly viruses? *Mem. Inst. Oswaldo Cruz*. 2015; 110(1): 1–22. https://doi.org/10.1590/0074-02760150048
8. Wang L.-F., Cowled C., eds. *Bats and Viruses: A New Frontier of Emerging Infectious Diseases*. Hoboken, New Jersey: John Wiley & Sons, Inc.; 2015. https://doi.org/10.1002/9781118818824
9. Макаров В.В., Лозовой Д.А. *Новые особо опасные инфекции, ассоциированные с рукокрылыми.* Владимир; 2016.
10. Corrales-Aguilar E., Schwemmle M., eds. *Bats and Viruses: Current Research and Future Trends.* Caister: Academic Press; 2020.
11. Поршаков А.М., Кононова Ю.В., Локтев В.Б., Boiro M.I. Рукокрылые как возможный резервуар опасных для человека вирусов на территории Гвинейской Республики. Часть 1. *Проблемы особо опасных инфекций*. 2018; (3): 32–9. https://doi.org/10.21055/0370-1069-2018-3-32-39
12. Поршаков А.М., Кононова Ю.В., Локтев В.Б., Boiro M.I. Рукокрылые как возможный резервуар опасных для человека вирусов на территории Гвинейской Республики. Часть 2. *Проблемы особо опасных инфекций*. 2018; (4): 20–6. https://doi.org/10.21055/0370-1069-2018-4-20-26
13. Макаров В.В., Барсуков О.Ю. Эмерджентные зоонозы, ассоциированные с рукокрылыми. *Пест-менеджмент*. 2019; (2): 18–2. https://doi.org/10.25732/PM.2019.110.2.003
14. Поршаков А.М., Кононова Ю.В., Льюнг Т.М. Филовирусы Юго-Восточной Азии, Китая и Европы (обзор литературы). *Журнал инфектологии*. 2019; 11(2): 5–13. https://doi.org/10.22625/2072-6732-2019-11-2-5-13
15. Сизикова Т.Е., Боярская Н.В., Ковальчук А.В., Лебедев В.Н., Борисевич С.В. Новые представители семейства *Filoviridae*: распространение, природные резервуары, потенциальная эпидемическая опасность. *Вестник войск РХБ защиты*. 2019; 3(4): 329–36. https://doi.org/10.35825/2587-5728-2019-3-4-329-336
16. Львов Д.К., Альховский С.В. Истоки пандемии COVID-19: экология и генетика коронавирусов (*Betacoronavirus*: *Coronaviridae*) SARS-CoV, SARS-CoV-2 (подрод *Sarbecovirus*), MERS-CoV (подрод *Merbecovirus*). *Вопросы вирусологии*. 2020; 65(2): 62–70. https://doi.org/10.36233/0507-4088-2020-65-2-62-70
17. Шестопалов А.М., Кононова Ю.В., Гаджиев А.А., Гуляева М.А., Маранди М.В., Алексеев А.Ю., и др. Биоразнообразие и эпидемический потенциал коронавирусов (*Nidovirales*: *Coronaviridae*) рукокрылых. *Юг России: экология, развитие*. 2020; 15(2): 17–34. https://doi.org/10.18470/1992-1098-2020-2-17-34
18. Должикова И.В., Щербинин Д.Н., Логунов Д.Ю., Гинцбург А.Л. Вирус Эбола (*Filoviridae*: *Ebolavirus*: *Zaire ebolavirus*): фатальные адаптационные мутации. *Вопросы вирусологии*. 2021; 66(1): 7–16. https://doi.org/10.36233/0507-4088-23
19. Puechmaille S.J., Ar Gouilh M., Dechmann D., Fenton B., Geiselman C., Medellin R., et al. Misconceptions and misinformation about bats and viruses. *Int. J. Infect. Dis*. 2021; 105: 606–7. https://doi.org/10.1016/j.ijid.2021.02.097
20. Егоров А.Ю., Романова Ю.Р. Влияние глобального распределения летучих мышей на смертность у пациентов с COVID-19. *Microbiol. Indep. Res. J.* 2020; 7(1): 34–41. DOI:10.18527/2500-2236-2020-7-1-34-41
21. Chen L., Liu B., Yang J., Jin Q. DBatVir: the database of bat-associated viruses. *Database*. 2014; 2014: bau021. https://doi.org/10.1093/database/bau021
22. Щелканов М.Ю., Дунаева М.Н., Москвина Т.В., Воронова А.Н., Кононова Ю.В., Воробьёва В.В., и др. Каталог вирусов рукокрылых (2020). *Юг России: экология, развитие.* 2020; 15(3): 6–30. https://doi.org/10.18470/1992-1098-2020-3-6-30
23. Hermida Lorenzo R.J., Cadar D., Koundouno F.R., Juste J., Bialonski A., Baum H., et al. Metagenomic snapshots of viral components in Guinean bats. *Microorganisms*. 2021; 9(3): 599. https://doi.org/10.3390/microorganisms9030599
24. International Committee on Taxonomy of Viruses. Available at: https://talk.ictvonline.org (accessed 24 July 2021).
25. Wilson D.E., Mittermeier R.A. *Handbook of the Mammalians of the World*. *Volume 9: Bats*. Barcelona: Lynx Ediciones. 2019. Available at: https://www.lynxeds.com/product/handbook-of-the-mammals-of-the-world-volume-9/ (accessed 24 July 2021).
26. Тиунов М.П., Крускоп С.В., Орлова М.В. *Рукокрылые Дальнего Востока России и их эктопаразиты*. М.: Перо; 2021.
27. Российская рабочая группа по рукокрылым. Available at: https://zmmu.msu.ru/bats/rbgrhp/rbrg.htm (accessed 20 July 2021).
28. IUCN: International Union for Conservation of Nature. Available at: https://www.iucn.org (accessed 24 July 2021).
29. Luis A.D., Hayman D.T.S., O’Shea T.J., Cryan P.M., Gilbert A.T., Pulliam J.R.C., et al. A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proc. Biol. Sci*. 2013; 280: 20122753. https://doi.org/10.1098/rspb.2012.2753
30. Gorbunova V., Seluanov A., Kennedy B.K. The world goes bats: living longer and tolerating viruses. *Cell Metabolism*. 2020; 32(1): 31–43. https://doi.org/10.1016/j.cmet.2020.06.013
31. Rupprecht C., Kuzmin I., Meslin F. Lyssaviruses and rabies: current conundrums, concerns, contradictions and controversies. *F1000Research*. 2017; 6: 184. https://doi.org/10.12688/f1000research.10416.1
32. Epstein J.H., Anthony S.J., Islam A., Kilpatrick A.M., Ali Khan S., Balkey M.D., et al. Nipah virus dynamics in bats and implications for spillover to humans. *Proc. Natl. Acad. Sci. USA*. 2020; 117(46): 29190–201. https://doi.org/10.1073/pnas.2000429117
33. WHO. Coronavirus (COVID-19) Dashboard. Available at: https://covid19.who.int (Accessed 17 July 2021).
34. Banyard A.C., Evans J.S., Luo T.R., Fooks A.R. Lyssaviruses and bats: emergence and zoonotic threat. *Viruses*. 2014; 6(8): 2974–90. https://doi.org/10.3390/v6082974
35. Ботвинкин А.Д. Смертельные случаи заболевания людей бешенством в Евразии после контактов с рукокрылыми (обзор литературы). *Plecotus et al*. 2011; (14): 75–86. Available at: https://zmmu.msu.ru/bats/biblio/rabies.pdf (accessed 17 July 2021).
36. Kuzmin I.V., Botvinkin A.D., Poleschuk E.M., Orciari L.A., Rupprecht C.E. Bat rabies surveillance in the former Soviet Union. *Dev. Biol. (Basel)*. 2006; 125: 273–82.
37. Терновой В.А., Зайковская А.В., Томиленко А.А., Аксёнов В.И., Чаусов Е.В., Шестопалов А.М. Лиссавирусы у летучих мышей, обитающих на юге Западной Сибири. *Вопросы вирусологии*. 2005; 50(1): 31–4.
38. Lu Z.L., Wang W., Yin W.L., Tang H.B., Pan Y., Liang X., et al. Lyssavirus surveillance in bats of southern China’s Guangxi Province. *Virus Genes*. 2013; (2): 293–301. https://doi.org/10.1007/s11262-012-0854-2
39. Drexler J.F., Corman V.M., Muller M.A., Maganga G.D., Vallo P., Binger T., et al. Bats host major mammalian paramyxoviruses. *Nat. Commun*. 2012; 3: 796. https://doi.org/10.1038/ncomms1796
40. Sharma V., Kaushik S., Kumar R., Yadav J.P., Kaushik S. Emerging trends of Nipah virus: A review. *Rev. Med. Virol*. 2019; (1): e2010. https://doi.org/10.1002/rmv.2010

41. Williamson K.M., Wheeler S., Kerr J., Bennett J., Freeman P., Kohlhagen J., et al., BatOneHealth field team. Hendra in the Hunter Valley. *One Health*. 2020; 10: 100162. https://doi.org/10.1016/j.onehlt.2020.100162
42. Kuzmin I.V., Niezgoda M., Franka R., Agwanda B., Markotter W., Breiman R.F., et al. Marburg virus in fruit bat, Kenya. *Emerg. Infect. Dis*. 2010; 16(2): 352–4. https://doi.org/10.3201/eid1602.091269
43. Koch L.K., Cunze S., Kochmann J., Klimpel S. Bats as putative *Zaire ebolavirus* reservoir hosts and their habitat suitability in Africa. *Sci. Rep*. 2020; 10(1): 14268. https://doi.org/10.1038/s41598-020-71226-0
44. Negredo A., Palacios G., Vázquez-Morón S., González F., Dopazo H., Molero F., et al. Discovery of an ebolavirus-like filovirus in Europe. *PLoS Pathog*. 2011; 7(10): e1002304. https://doi.org/10.1371/journal.ppat.1002304
45. Li W., Shi Z., Yu M., Ren W., Smith C., Epstein J.H., et al. Bats are natural reservoirs of SARS-like coronaviruses. *Science*. 2005; 310(5748): 676–9. https://doi.org/10.1126/science.1118391
46. Luk H.K.H., Li X., Fung J., Lau S.K.P., Woo P.C.Y. Molecular epidemiology, evolution and phylogeny of SARS coronavirus. *Infect. Genet. Evol*. 2019; 71: 21–30. https://doi.org/10.1016/j.meegid.2019.03.001
47. Leitner T., Kumar S. Where did SARS-CoV-2 come from? *Mol. Biol. Evol*. 2020; 37(9): 2463–4. https://doi.org/10.1093/molbev/msaa162
48. Ji W., Wang W., Zhao X., Zai J., Li X. Cross-species transmission of the newly identified coronavirus 2019-nCoV. *J. Med. Virol*. 2020; 92(4): 433–40. https://doi.org/10.1002/jmv.25682
49. Olival K.J., Cryan P.M., Amman B.R., Baric R.S., Blehert D.S., Brook C.E., et al. Possibility for reverse zoonotic transmission of SARS-CoV-2 to free-ranging wildlife: A case study of bats. *PLoS Pathog*. 2020; 16(9): e1008758. https://doi.org/10.1371/journal.ppat.1008758
50. Wolfe N.D., Dunavan C.P., Diamond J. Origins of major human infectious diseases. *Nature*. 2007; 447(7142): 279–83. https://doi.org/10.1038/nature05775
51. Patyk K., Turmelle A., Blanton J.D., Rupprecht C.E. Trends in national surveillance data for bat rabies in the United States: 2001–2009. *Vector. Borne. Zoonotic. Dis*. 2012; 12(8): 666–73. https://doi.org/10.1089/vbz.2011.0839
52. Schatz J., Fooks A.R., McElhinney L., Horton D., Echevarria J., Vázquez-Moron S., et al. Bat rabies surveillance in Europe. *Zoonoses Public Health*. 2013; 60(1): 22–34. https://doi.org/10.1111/zph.12002
53. Phelps K.L., Hamel L., Alhmoud N., Ali S., Bilgin R., Sidamonidze K., et al. Bat research networks and viral surveillance: gaps and opportunities in Western Asia. *Viruses*. 2019; 11(3): 240. https://doi.org/10.3390/v11030240
54. Транквилевский Д.В., Жуков В.И., Царенко В.А. Вероятность заражения населения возбудителями, ассоциированными с рукокрылыми, в Российской Федерации. *Здоровье населения и среда обитания*. 2018; (3): 32–7. https://doi.org/10.35627/2219-5238/2018-300-3-32-37
55. Voigt C.C., Kingston T., eds. *Bats in the Anthropocene: conservation of bats in a changing world*. Cham: Springer; 2016. https://doi.org/10.1007/978-3-319-25220-9_1
56. Bat Concervation International. Available at: https://www.batcon.org (accessed 24 July 2021).
57. UNEP/EUROBATS. Agreement on the conservation of populations of European bats. Available at: https://www.eurobats.org/ (Accessed 24 July 2021).
58. Melber M., Gloza-Rausch F., Voigt C.C. Statement on handling of bats in times of Covid-19 regarding the IUCN Bat Specialists Groups recommendations of field activities for the protection of bats. Available at: https://bvfledermaus.de/wp-content/uploads/2020/04/BVF_Statement_on_Handling_of_Bats_in_times_of_Covid_19.pdf (accessed 24 July 2021).
59. Германчук В.Г., Семакова А.П., Шавина Н.Ю. Этические принципы при обращении с лабораторными животными в эксперименте с патогенными биологическими агентами I–II групп. *Проблемы особо опасных инфекций*. 2018; (4): 33–8. https://doi.org/10.21055/0370-1069-2018-4-33-38
60. Cunningham A.A., Daszak P., Wood J.L.N. One Health, emerging infectious diseases and wildlife: two decades of progress? *Philos. Trans. R. Soc. Lond. B. Biol. Sci*. 2017; 372(1725): 20160167. https://doi.org/10.1098/rstb.2016.0167