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FLEAS (SIPHONAPTERA) AS VECTORS IN NATURAL PLAGUE FOCI WORLDWIDE: HOST-PARASITE RELATIONSHIPS, FAUNISTIC AND GEOGRAPHICAL ANALYSIS, EPIZOOTIC SIGNIFICANCE

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The fauna of fleas in the world is currently known by 2162 species, of which 262 species (12.1%) from 6 families are found infected with plague in nature. Fleas of the families Hystrichopsyllidae (74 species), Ceratophillidae (69 species) and Leptopsyllidae (40 species) are most involved in the epizootic. Among all flea species found infected with the plague pathogen, only 64 (24%) are considered as the main plague vectors. The species distribution by families is as follows: Ceratophillidae – 24 species, Pulicidae – 18 species, Hystrichopsyllidae – 10, Leptopsyllidae – 8, Rhopalopsyllidae – 4. The flea *Oropsylla silantiewi* takes the leading position among all main plague vectors. The approximate number of plague natural foci in the world is at least 316. *O. silantiewi* acts as the main vector and keeper of infection in 59 natural foci of plague. In 41 natural foci, this species is the only main vector, ensuring the circulation of the pathogen without significant assistance of other flea species. No other flea species is so powerfully involved in the plague pathogen circulation in any region of the world. *O. silantiewi* is a specific parasite of marmots, whose origin is associated with the mountain steppes of Central Asia, where the center of origin of the plague microbe is probably located. From this territory, the plague microbe began its further worldwide spread with penetration and development of new ecological niches in flea's populations of ground squirrels, mice, rats, voles and other small mammals.

Keywords: fleas, Siphonaptera, vectors, plague pathogen, host-parasite relationships, zoogeographic diversity, epizootic

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This article summarizes a series of publications analyzing the distribution features and host-parasite relationships of flea species, which are active vectors of the plague pathogen. The species composition, distribution, ecologic relationships, and epizootic significance of representatives of the genera *Citellophilus, Oropsylla, Rhadinopsylla, Neopsylla, Frontopsylla, Paradoxopsyllus,* and *Xenopsylla* have been considered earlier (Kotti, Zhiltsova, 2019; Medvedev et al., 2019, 2020, 2021, 2022, 2023a, 2023b; Medvedev, Verzhutsky, 2020; Verzhutsky et al., 2021).

Known plague pandemics have had a catastrophic impact on human civilization three times, taking millions of lives and destroying the economies of entire regions of the planet. Some euphoria associated with the invention of effective vaccines, the discovery and successful vast use of antibiotics quickly disappeared after the 1947 epidemic in Northeast China, when dozens of thousands of people fell ill in a short time, and the mortality rate exceeded 70%. This epidemic was suppressed mainly by strict quarantine measures (Kraminskij, 1953).

COVID-19 pandemic caused by the SARS-CoV-2 virus has clearly demonstrated that the most serious quarantine measures are practically powerless against highly contagious respiratory infections. The pneumonic form of plague had already shown its ability to spread rapidly on a global scale. However, the mortality rate from the COVID-19 virus was less than 1%: according to WHO data, as of January 2025, 777 million people worldwide had COVID-19, and about 7 million died[1]. With the pneumonic form of plague, the mortality rate exceeds 50% of the number of cases, even with timely treatment.

It can be assumed the emergence of new highly virulent clones of the plague pathogen, capable of rapid and uncontrolled spread among people, is due to the natural selection of the most pathogenic strains with an increase in genetic diversity in populations of the plague microbe.

The natural habitat of the plague pathogen is the gastrointestinal tract of fleas, where this microorganism spends most of its life. Here it can persist for a long time, weeks or even months, from one epizootic cycle to another. This applies only to the species that are the main vectors of plague in each particular natural focus. Accidental or secondary flea vectors, usually free themselves quickly from the pathogen and do not form a forestomach block (a specific effective mechanism for transmitting infection). As a rule, an infected flea (the main vector) with a formed forestomach block transmits the plague pathogen during bloodsucking on the first day of feeding. On the same day, the microbe overcomes the immune barriers of the warm-blooded host. On the second day, the plague pathogen intensively multiplies in the host's circulatory system, on the third day the death of the animal occurs. With intense bacteremia, on the second or third day, the microbe enters the bodies of other fleas that also feed on the infected animal. Some hosts recover, forming relatively long-term immunity to plague infection. Long-term hosting of plaque bacteria in warm-blooded animals occurs extremely rarely, so it cannot affect significantly the epizootic process. Block-free infection transmission is significantly less efficient than that with a formed forestomach block; as a rule, the first occurs only when the number of fleas on the host is high.

According to this scheme, with minor deviations, the entire vital activity of the plague microbe occurs in all known natural plague foci in the world without exception.

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[1] Coronavirus disease (COVID-19) Epidemiological Updates and Monthly Operational Updates: https://www.who.int/emergencies/diseases/novel-coronavirus-2019/situation-reports (date of circulation - 01.12.2024).

Since 2012, an explosive growth in the activity of natural plague foci has been observed along the perimeter of the Great Lakes Depression (northwestern Mongolia, southern Tuva, and the Altai Mountains). In addition, a transformation of the ecological structure of the foci and the penetration of highly virulent plague strains into new territories have been observed here (Korzun et al., 2017; Verzhutsky, 2018; Balahanov et al., 2019; Balahonov, Korzun, 2022). The epizootic state worsened and caused a sharp increase in the number of plague cases in humans, both in Mongolia and in the adjacent territories of Russia and China (Balahanov et al., 2021).

Ongoing aridization in Central Asia causes an increase in the number of the main plague vectors. The study of the efficiency of pathogen transmission by fleas in natural plague foci of Siberia has been conducted since the middle of the XX century. The results of these large-scale studies indicate a steady increase in the vector capacity of fleas (Verzhutsky et al., 2019). These factors probably determine the abnormal activity of plague foci in the region, so the tensions of the epidemiological state run high (Verzhutsky, 2018).

Evolutionarily honed mechanisms eliminate the plague pathogen from its alien habitat. However, it is possible that certain clones of the microbe may end up in slightly different, but sufficient conditions for its vital activity. The ability of the plague pathogen to occupy additional ecological niches is due to the multi-host nature of many flea species and their connection with certain habitats. Recently, it has been found experimentally that a number of flea species depends on the characteristics of the substrate – sand and loess particles from which the pupal cocoon is built, – and this affects their survival rates and biotope preferences (Krasnov et al., 2002). In addition to certain monoxenous species, most fleas may attack additional and accidental hosts. The plague pathogen enters the body of many mammal and bird species either periodically or accidentally. Apparently, such processes have occurred and are occurring in nature, and, consequently, there are prerequisites for the selection of new strains of the plague pathogen. Obviously, the epidemiological consequences of such processes are poorly predictable.

The entire diversity of parasite-host relationships of all types of plague-carrying fleas must be taken into account for global monitoring of the activity of the plague microbe. Nowadays, maintaining epidemiological safety should be based on an assessment of the possibility of involving the entire range of potential mammalian hosts of fleas in the circulation of the pathogen in all areas of the world.

Now let's look at some basic concepts related to the natural focality of the plague. First of all, it is necessary to define a natural focality of plague and its range.

The theory of natural focality of diseases was created by a Soviet Academician Evgeny N. Pavlovsky in 1939. He was the first to suggest that pathogens of many diseases, like any other biological species, arose through evolution and exist(ed) in nature completely independently of humans, being natural members of natural biocoenoses. His monograph "Natural Focality of Transmissible Diseases in Connection with Landscape Epidemiology of Zooanthroponoses" was published 25 years later, in 1964. In this work, E. Pavlovsky summarized and developed ideas about natural sources of human infection with pathogens of natural focal diseases and the ecological essence of the phenomenon itself (Pavlovsky, 1964).

The concept of a natural focus of disease is a central one in the theory of natural focality of diseases caused by pathogens of viral, bacterial and other etiologies.

Pavlovsky himself has several versions of the definition of a natural focus. One of those is a general definition of a natural focus of transmissible human diseases: "…a part of the territory of a certain geographic landscape, in which certain interspecies relationships have evolved between the causative agent of the disease, animal donors and recipients of the pathogen, and its vectors in the presence of environmental factors that favor or, in any case, do not interfere with the circulation of the pathogen" (Pavlovsky, 1955). In a broader sense, a short interpretation is presented, where a natural focus is understood as "…a section of a geographic landscape with its characteristic biocoenosis, among the individuals of which the causative agent of the disease circulates" (Pavlovsky, 1957, cited by Korenberg et al., 2013).

According to a later formulation of other authors, "…a natural focus is the smallest territory of one or several landscapes, where the circulation of the pathogen occurs in modern geobiocoenoses without its introduction from outside for an indefinitely long period (many epizootic cycles following one another). A natural focus is an individual phenomenon. Its boundaries can be determined on the ground and outlined on a map" (Kucheruk, Rositsky, 1984).

Currently, a concise formulation has been substantiated and accepted by most researchers, stating that "…a natural focus of an infectious disease is any natural ecosystem, where a pathogen population is a component" (Litvin, Korenberg, 1999).

A natural plague focus, like any other biological object, is a self-regulating system with its own internal structure and heterogeneous functional role of its constituent parts (Kucheruk, 1965; Verzhutsky, 1999; Korenberg, 2010; Balahonov et al., 2019). The population of the plague microbe should theoretically correspond territorially to the populations of the main vectors of the infection (certain flea species). Its range is tied to the main host (usually, the main vector in the focus). Nevertheless, the example of the Tuva and Gorno-Altai natural plague foci has clearly shown that the boundaries of individual vector populations are not the boundaries for the pathogen. As a rule, according to observations in these foci, as well as in the natural plague foci of Mongolia, the area of one population of the pathogen (homogeneous strains circulating in one territory) covers from several to several dozen population groups of infection vectors, as well as the main vectors. The current area of the Tuva natural focus is 10,830 km^2, the area of the Gorno-Altai focus is 11,650 km^2 (Balahonov et al., 2019; Balahonov, Korzun, 2022). There are 45 natural plague foci in Mongolia; most of them (82.2%) have an area from 4000 km^2 to 15,000 km^2, with a maximum of 25,000 km^2. We have used these data as a guide when identifying individual plague foci, considering larger formations in terms of area as several separate foci.

MATERIALS AND METHODS

Since 1995, the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) has been continuously working on creating an electronic resource on the flea world fauna as an information-analytical system 'IAS PARHOST1' [2] (Medvedev, Lobanov, 1999). This IAS has a number of fundamental features. Firstly, its factual tables of the PARHOST1 system are based on the classifier tables of the ZOOCOD3 standard (Lobanov, Smirnov, 1997). This standard reflects not only the required number of levels of classification hierarchy (including sub- and super-genera, families, etc., in addition to the main taxonomic categories), but also makes it possible to use synonymous names along

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[2] Information-analytical system 'IAS PARHOST1'. Internet address: http://www.zin.ru/Animalia/Siphonaptera.

with valid ones. Secondly, each classifier table in the PARHOST1 system defines both the hierarchical order of taxa of fleas and their hosts (mammals and birds) and morphological and structural features of the flea species. Thirdly, the hierarchy of subordination of physical-geographical objects and regions, administrative territories of countries, is also a part of the IAS.

Currently, the data on the systematic position of more than 2,200 species from 241 flea genera is stored in the IAS. More than 70 analytical programs, developed especially for IAS analysis, have made it possible to establish not only the parasite-host relationships of individual flea taxa and their hosts, but also the features of these relationships in the zoogeographic regions (Medvedev, 1996, 1997a, 1997b, 1998a, 1998b, 2000, 2002a, 2002b, 2009, 2013; Medvedev, Kotti, 2012, 2013).

Data on the species and taxonomic diversity of fleas and their hosts (mammals and birds), as well as the distribution of representatives of the order Siphonaptera in the world were obtained from more than 500 publications. We used monographs on the fauna of Russia and neighboring countries developed by I.G. Ioff and a team of his colleagues and followers (Ioff, Skalon, 1954; Ioff et al., 1965; Skalon, 1970; Tiflov et al., 1977). Extensive materials on the distribution of flea species of the Palaearctic fauna are contained in the "Catalogue of the Rothschild Flea Collection" (Hopkins, Rothschild, 1953, 1956, 1962, 1966, 1971; Mardon, 1981; Traub et al., 1983). Materials on the distribution and parasite-host relationships of flea species were presented by R. Lewis in a series of his publications (Lewis, 1972, 1973, 1974a, 1974b, 1974c, 1975, 1993; Lewis, Lewis, 1985). Information about the fauna of various regions is presented in monographs devoted to particular countries: China (Liu et al., 1986), Mongolia (Goncharov et al., 1989), France (Beaucournu, Launay, 1990), Greece (Beaucournu, 1988), Russia (Kotti, 2018), and Australia (Dunnet, Mardon, 1974).

The zoogeographic regions defined by Sclater-Wallace with modifications (Fig. 1) were taken as a basis (Medvedev, 1996). For example, according to this scheme, the Palearctic is divided into six subregions, three of which are the European-Siberian, Mediterranean, and Irano-Turanian, and these three are divided into two provinces each. This division scheme generally agrees well with the distribution features of fleas, and its divisions are characterized by a significant percentage of both species and genera endemism.

Fleas are characterized by a very high percentage of species endemic to individual zoogeographic regions (on average, 94% of species are endemic). Thus, only the analysis of flea faunas at the genus level allows one to assess the degree of their uniqueness / similarity to each other. Initially, Jaccard similarity index was applied (Pesenko, 1982). Later, other methods for constructing fauna dendrograms were used to calculate the similarity of faunas in zoogeographic regions. However, the similarity dendrograms, constructed using the Jaccard index and the Chekanovsky-Sørensen index, gave similar results.

Using the 'IAS PARHOST1' (Medvedev, Lobanov, 1999), the types of ranges and the families of the order Siphonaptera were analyzed. In total, 128 types of ranges belonging to 23 groups were identified. The titles of these range types are formed as a listing of the titles of zoogeographical sections in the order of their succession from north to south and from west to east. The same order of assigning geographical names is used when describing the species ranges.

Materials on natural plague foci and the epizootic significance of fleas were obtained from the literature. Data on 263 flea species that were mentioned as the main and secondary plague vectors in different zoogeographical regions of the world are given in Table1. These species belong to 78 genera of 6 families. More complicated data on the distribution and host-parasite relations of each of these species will be represented in the second part of this publication. As far as possible, summaries of the infection of individual flea species with plague have been verified with primary literary sources, the species names of infected insects have been brought into line with modern concepts, and the sequence of families and genera is also given in the currently accepted taxonomic system.

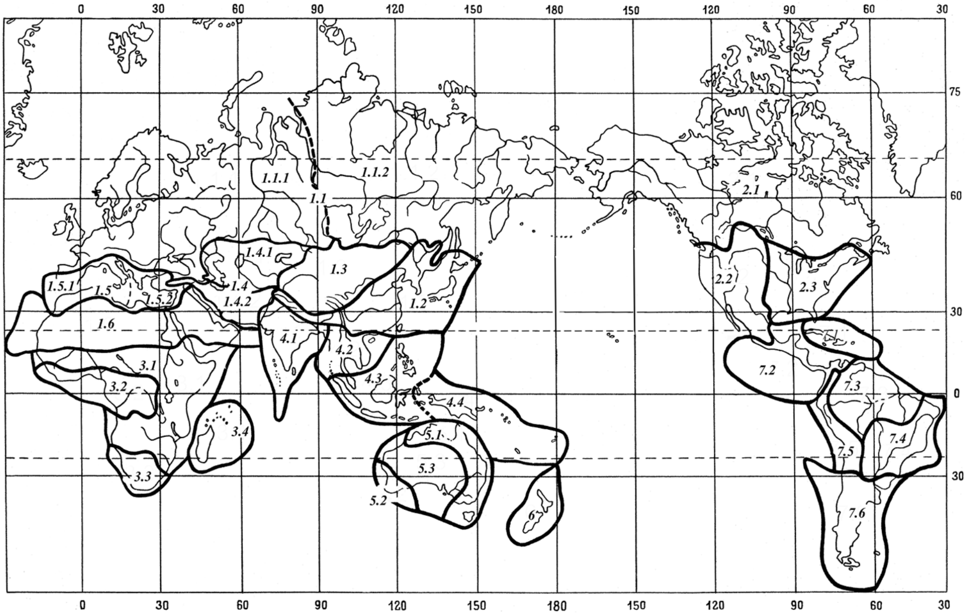

Figure 1. The zoogeographical regioning of land, modified after Sclater-Wallace. Modified from: Medvedev (1996).
Palaearctic region: *1.1* – Euro-Siberian [(*1.1.1*) European and (*1.1.2*) Siberian Provinces], *1.2* – East-Asian, *1.3* – Central-Asian, *1.4* – Turan-Persian [(*1.4.1*) Turan and (*1.4.2*) Persian Provinces], *1.5* – Mediterranean [(*1.5.1*) West-Mediterranean and (*1.5.2*) East-Mediterranean Provinces], and *1.6* – Sahara-Arabian subregions. Nearctic region: *2.1* – Canadian, *2.2* – West-American, and *2.3* – East-American subregions. Afro-Tropical region: *3.1* – East-African, *3.2* – West-African, *3.3* – Kapsk, and *3.4* – Madagascar subregions. Indo-Malayan region: *4.1* – Indian, *4.2* – Indochinese, *4.3* – Malayan, and *4.4* – Papuan subregions. Australian region: *5.1* – East-Australian, *5.2* – West-Australian, and *5.3* – Central-Australian subregions. *6* – New Zealand region. Neotropical region: *7.1* – Antilean, *7.2* – Caribbean. *7.3* – Amazonian, *7.4* – Brazilian, *7.5* – Andean, and *7.6* – Patagonian subregions.

Рисунок 1. Схема зоогеографического районирования суши по Склэтеру-Уоллесу с изменениями. По: Медведеву (1996), с изменениями.
Палеарктическая область: *1.1* – Европейско-Сибирская подобласть (*1.1.1* – Европейская провинция, *1.1.2* – Сибирская провинция), *1.2* – Восточноазиатская подобласть, *1.3* – Центральноазиатская подобласть, *1.4* – Турано-Иранская подобласть (*1.4.1* – Туранская провинция, *1.4.2* – Иранская провинция), *1.5* – Средиземноморская подобласть (*1.5.1* – Западносредиземноморская, *1.5.2* – Восточносредиземноморская), *1.6* – Сахаро-Аравийская). Неарктическая область: *2.1* – Канадская подобласть, *2.2* – Западноамериканская подобласть, *2.3* – Восточноамериканская подобласть. Афротропическая область: *3.1* – Восточноафриканская подобласть, *3.2* – Западноафриканская подобласть, *3.3* – Капская подобласть, *3.4* – Мадагаскарская подобласть. Индо-Малайская область: *4.1* – Индийская подобласть, *4.2* – Индокитайская подобласть, *4.3* – Малайская подобласть, *4.4* – Папуасская подобласть. *5* – Австралийская область: *5.1* – Восточноавстралийская подобласть, *5.2* – Западноавстралийская подобласть, *5.3* – Центральноавстралийская подобласть. *6* – Новозеландская область. Неотропическая область: *7.1* – Антильская подобласть, *7.2* – Карибская подобласть, *7.3* – Амазонская подобласть, *7.4* – Бразильская подобласть, *7.5* – Андийская подобласть, *7.6* – Патагонская подобласть.

Table 1. Epizootologic role of flea species found infected in natural plague foci in different zoogeographical regions of the world (flea species known as the main plague vectors in a single natural plague focus as minimum are highlighted in bold). Regions: PA – Palearctic, NA – Nearctic, AT – Afrotropical, NT – Neotropical, IM – Indomalayan. Taxonomy and sequence of families are given according to Medvedev (1998b, 2024).

Таблица 1. Эпизоотологическая роль видов блох, найденных инфицированными в природных очагах чумы, в разных зоогеографических регионах мира (жирным шрифтом обозначены виды блох, известные как основные переносчики, по меньшей мере, в одном природном очаге чумы). Регионы: ПА – Палеарктический, НА – Неарктический, АТ – Афротропический, НТ – Неотропический, ИМ – Индо-Малайский. Систематика и последовательность семейств приведены по Медведеву (1998б, 2024).

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
							Infraorder Pulicomorpha		
							Fam. Pulicidae		
1	*Cediopsylla spillmani* Jordan, 1930				+		*Sylvilagus*	Peru	Macchiavello, 1954; Plague…, 1963
2	*Ctenocephalides canis* (Curtis, 1826)	+					Carnivora	Cosmopolitan	Macchiavello, 1954; Pratt et al., 1993
3	*C. felis* (Bouché, 1835)		+	+		+	Felidae	Cosmopolitan	Macchiavello, 1954; Pratt et al., 1993
4	*C. orientis* (Jordan, 1925)	+				+	Carnivora	Thailand, India, Middle Asia	Velimirovic, 1972; Goncharov et al., 2013
5	*Echidnophaga gallinacea* (Westwood, 1875)		+				Insectivora	USA	Macchiavello, 1954; Pratt et al., 1993
6	*E. oschanini* Wagner, 1930	+					Gerbillinae	Kazakhstan, Mongolia	Naumov et al., 1972; Ajkimbaev et al., 1987; Martinevskij et al., 1987; Bolormaa et al., 2010
7	*Euchoplopsyllus andensis* (Jordan, 1933)				+		Lagomorpha	Peru, Ecuador	Macchiavello, 1954 (as *Hoplopsyllus andensis*); Laguna-Torres, Gómez-Benavides, 2004;
8	*E. glacialis* (Taschenberg, 1880)		+				Lagomorpha	USA	Macchiavello, 1954; Pratt et al., 1993 (as *Hoplopsyllaus glacialis*)
9	*E. manconis* (Jordan, 1950)				+		Lagomorpha	Peru, Ecuador	Macchiavello, 1954; Kozlov, Sultanov, 2000 (as *Hoplopsyllus manconis*); Laguna-Torres, Gómez-Benavides, 2004
10	***Hoplopsyllus anomalus* (Baker, 1904)**		+				*Spermophilus* (sensu lato)	USA	Pratt et al., 1993

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
15	*Pulex irritans* L., 1758	+	+	+	+	+	Polyhostal	Over the World	Ejgelis, 1980; Ajkimbaev et al., 1987; Pratt et al., 1993; Kozlov, Sultanov, 2000; The Atlas…, 2000; Goncharov et al., 2013
16	***P. simulans* Baker, 1895**		+				Sciuridae, Cricetidae	USA, North Mexico	Macchiavello, 1954; Zapata-Valdes et al., 2018
17	***Synosternus cleopatrae* (Rothschild, 1903)**	+					Cricetidae	North Africa	Dannis et al., 1999; Karimova, Neronov, 2007; Goncharov et al., 2013
18	*S. longispinus* (Wagner, 1893)	+					Insectivora, Carnivora, Rodentia	Middle Asia	Ajkimbaev et al., 1987; Goncharov et al., 2013
19	*S. pallidus* (Taschenberg, 1880)			+			Insectivora, Carnivora, Rodentia	Africa, Middle East, Middle Asia, India	Macchiavello, 1954; Ajkimbaev et al., 1987; Rajamannar et al., 2022
20	*Synopsyllus estradei* Klein, 1964			+			Muridae	Madagascar	Popova, Kutyrev, 2022
21	*S. fonquernii* Wagner et Roubaud, 1932						Muridae	Madagascar	Macchiavello, 1954; Goncharov et al., 2013 (as *Synopsyllus fonquerniei*)
	cheopis-group								
22	***Xenopsylla astia* Rothschild, 1911**	+				+	*Tatera indica*, Micromammalia	India, Middle East (Mesopotamia)	Macchiavello, 1954; Velimirovic, 1972; Rajamannar et al., 2022; Medvedev et al., 2023a
23	***X. buxtoni* Jordan, 1949**	+					*Meriones*	Iran, Iraq, Turkey, Syria	Varshavskij, Kozakevich, 1984; Shahraki et al., 2016; Maleki-Ravasan et al., 2017; Medvedev et al., 2022
24	***X. cheopis* (Rothschild, 1903)**	+	+	+	+	+	*Rattus*	Over the World	Macchiavello, 1954; Pratt et al., 1993; Medvedev et al., 2023a, b
25	*X. eridos* (Rothschild, 1904)			+			*Otomys*	South and East Africa	Goncharov et al., 2013; Medvedev et al., 2023b
26	***X. hipponax* De Meillon, 1942**			+			Gerbillinae, Micromammalia	Angola	Gracio, Gracio, 2011; Medvedev et al., 2023b

27	*X. nubica* (Rothschild, 1903)			+			Gerbillinae	Sub-Saharan Africa; Middle East	Macchiavello, 1954; Varshavskij, Kozakevich, 1984; Dannis et al., 1999; Medvedev et al., 2022
28	***X. philloxera* Hopkins, 1949**			+			Gerbillinae, Cricetidae	South Africa, Angola	Macchiavello, 1954; Gracio, Gracio, 2011; Medvedev et al., 2022
29	*X. phyllomae* De Meillon, 1934			+			Cricetidae	South Africa	Macchiavello, 1954; Van Der Mescht, Matthee, 2017; Medvedev et al., 2022
30	***X. piriei* Ingram, 1928**			+			Cricetidae	South Africa	Macchiavello, 1954; Van Der Mescht, Matthee, 2017; Medvedev et al., 2022
31	*X. versuta* Jordan, 1925			+			*Rhabdomys*	South и Southwestern Africa	Kozakevich et al., 1972; Van Der Mescht, Matthee, 2017
32	***X. vexabilis* Jordan, 1925**					+	*Rattus*	Hawaii	Macchiavello, 1954; Dannis et al., 1999; Suntsov, Suntsova, 2013; Medvedev et al., 2022
	brasiliensis-group								
33	***X. brasiliensis* (Baker, 1904)**			+		+	Muridae	India, Africa	Macchiavello, 1954; Velimirovic, 1972; Rajamannar et al., 2022; Medvedev et al., 2023b
	conformis-group								
34	***X. conformis* (Wagner, 1903)**	+					*Meriones*	RF (Lower Volga), Azerbaijan, Armenia, Kazakhstan, Middle Asia; China (Erlian)	Naumov et al., 1972; Ejgelis, 1980; Ajkimbaev et al., 1987; The Atlas…, 2000; Goncharov et al., 2013; Medvedev et al., 2022
35	***X. gerbilli* (Wagner, 1903)**	+					*Rhombomys opimus*	Middle Asia	Ajkimbaev et al., 1987; Martinevskij et al., 1987; Medvedev et al., 2022, 2023a
36	*X. hirtipes* Rothschild, 1913	+					*Rhombomys opimus*	Middle Asia and Kazakhstan	Ajkimbaev et al., 1987; Medvedev et al., 2022, 2023a
37	*X. magdalinae* Ioff, 1935	+					Cricetidae	Uzbekistan	Ajkimbaev et al., 1987; Medvedev et al., 2023a, 2023b
38	***X. nuttalli* Ioff, 1930**	+					*Rhombomys opimus*	Middle Asia, Iran	Ajkimbaev et al., 1987; Medvedev et al., 2022, 2023a

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
39	***X. ramesis* (Rothschild, 1904)**	+					Gerbillinae	North Africa	Klein et al., 1975; Dannis et al., 1999; Karimova, Neronov, 2007; Medvedev et al., 2023a
40	***X. skrjabini* Ioff, 1930**	+					*Rhombomys opimus*	Middle Asia, Kazakhstan, China (Xinjiang), Mongolia	Naumov et al., 1972; Ajkimbaev et al., 1987; The Atlas…, 2000; Bolormaa et al., 2010; Medvedev et al., 2022b, 2023a
41	***X. taractes* J. et R., 1913**	+					Gerbillinae	NorthAfrica	Varshavskij et al., 1971; Klein et al., 1975; Karimova, Neronov, 2007; Medvedev et al., 2023b
	hirsute group								
42	*X. hirsuta* Ingram, 1928			+			Cricetidae	East и South Africa	Macchiavello, 1954; Medvedev et al., 2023b
	Fam. Tungidae								
43	*Hectopsylla eskeyi* Jordan, 1933				+		Caviidae	Peru, Ecuador, Argentina	Macchiavello, 1954; Kozakevich et al., 1970; Kozlov, Sultanov, 2000; Laguna-Torres, Gómez-Benavides, 2004
44	*H. gemina* Jordan, 1939				+		Caviidae	Peru, Ecuador, Argentina	Plague…, 1963; Laguna-Torres, Gómez-Benavides, 2004
45	*H. suarezi* C. Fox, 1929				+		Caviidae	Ecuador, Peru	Macchiavello, 1954; Rall’, 1958
46	*Tunga* (Brevidigita) penetrans L., 1758			+			Polyhostal	Central Africa, USA	Macchiavello, 1954
	Fam. Malacopsyllidae – there is no data on the infection rate of representatives of the family with plague pathogen								
	Fam. Rhopalopsyllidae								
47	***Delostichus talis* (Jordan, 1936)**				+		Caviidae, Micromammalia	Argentina	Macchiavello, 1954; Kozakevich et al., 1970; Kozlov, Sultanov, 2000
48	*Ectinorus* (*Panallius*) *galeanus* (Jordan, 1939)				+		Caviidae	Argentina	Plague…, 1963; Kozakevich et al., 1970

49	***Polygenis* (*Polygenis*) *bohlsi*** **(Wagner, 1901)**				+		Caviidae, Cricetidae, Didelphidae	Nearly over entire South America	Macchiavello, 1954; Plague…, 1963; Kozakevich et al., 1970
50	*P. (P.) brachinus* Jordan, 1950				+		Cricetidae	Ecuador	Macchiavello, 1954
51	***P. (P.) byturus*** **(Jordan et Rothschild, 1923)**				+		Caviidae, Cricetidae	Argentina	Plague…, 1963; Kozakevich et al., 1970
52	*P. (P.) gwyni* (C.Fox, 1914)				+		Cricetidae	Peru, Ecuador	Macchiavello, 1954; Laguna-Torres, Gómez-Benavides, 2004
53	***P. (P.) litargus*** **(Jordan et Rothschild, 1923)**				+		Cricetidae	Peru, Ecuador	Macchiavello, 1954; Kozlov, Sultanov, 2000
54	***P. (P.) platensis*** **(Jordan et Rothschild, 1908)**				+		Caviidae	Argentina	Macchiavello, 1954; Kozlov, Sultanov, 2000
55	*P. (P.) tripus* (Jordan, 1933)				+		Cricetidae	Brazil	Plague…, 1963; Fernandes et al., 2020
	Rhopalopsyllus sp.				+		Vermilingua	Argentina	Plague…, 1963
56	*Rhopalopsyllus casicus* J. et R., 1908				+		Cricetidae, Caviidae	Peru	Plague…, 1963; Laguna-Torres, Gómez-Benavides, 2004
57	*Tiamastus cavicola* (Weyenbergh, 1881)				+		Cricetidae, Caviidae	Argentina, Brazil, Ecuador, Peru	Macchiavello, 1954; Rall', 1958; Kozlov, Sultanov, 2000
							Fam. Vermipsyllidae		
58	*Chaetopsylla* (*Chaetopsylla*) *homoea* Rothschild, 1906	+					Micromammalia, *Ochotona*, Carnivora	RF (Mountain Altai); Mongolia	Zhovtyj, 1969; Bolormaa et al., 2010; Balahonov, Korzun, 2022
							Fam. Coptopsyllidae		
59	*Coptopsylla* (*Coptopsylla*) *bairamaliensis* Wagner, 1928	+					Gerbillinae	RF (Lower Volga, Dagestan), Kazakhstan, Middle Asia, China (Xinjiang)	Ajkimbaev et al., 1987; Popova, Kutyrev, 2022
60	*C.* (*C.*) *caucasica* Isayeva-Gurvich, 1950	+					Gerbillinae	Azerbaijan	Ejgelis, 1980; Goncharov et al., 2013
61	*C.* (*C.*) *lamellifer* (Wagner, 1895)	+					Gerbillinae	RF (Lower Volga), Kazakhstan, Middle Asia, North China	Naumov et al., 1972; Ajkimbaev et al., 1987; Martinevskij et al., 1987; Popova, Kutyrev, 2022

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
62	*C.* (*C.*) *olgae* Argyropulo, 1946	+					*Rhombomys opimus*	Turkmenia, Uzbekistan	Ajkimbaev et al., 1987
	Fam. Ancistropsyllidae – there is no data on the infection rate of representatives of the family with plague pathogen								
	Infraorder Hystrichopsyllomorpha								
	Fam. Hystichopsyllidae								
	Subfam. Anomiopsyllinae								
63	*Anomiopsyllus hiemalis* Eads et Menzies, 1948		+				*Neotoma*	USA (Texas)	Pratt et al., 1993
64	*A. nudatus* (Baker, 1898)		+				Cricetidae	USA	Eskey, Haas, 1940; Pratt et al., 1993
65	*Stenistomera alpina* (Baker, 1895)		+				Cricetidae	USA	Pratt et al., 1993
66	*S. macrodactyla* Good, 1942		+				*Peromyscus*	USA	Pratt et al., 1993
67	*Wagnerina* (*Wagnerina*) *longicauda* Scalon, 1953	+					*Ochotona*, *Alticola*	RF (Mountain Altai)	Balahonov, Korzun, 2022
68	*W.* (*W.*) *tuvensis* Ioff et Scalon, 1953	+					*Ochotona*, *Alticola*	RF (Mountain Altai)	Balahonov, Korzun, 2022
	Subfam. Ctenophthalminae								
69	***Ctenophthalmus* (*Euctenophthalmus*) *assimilis* (Taschenberg, 1880)**	+					Microtinae	Kirgizia, Kazakhstan	Goncharov et al., 2013
70	*C.* (*E.*) *bogatschevi* Wagner et Argyropulo, 1934	+					Cricetidae	Azerbaijan	Goncharov et al., 2013
71	*C.* (*E.*) *breviatus* Wagner et Ioff, 1926	+					*Spermophilus*, Micromammalia	Kazakhstan, Lower Volga	Ioff, 1941; Kutyrev, Popova, 2016
72	*C.* (*E.*) *congener* Rothschild, 1907	+					Micromammalia	Azerbaijan	Goncharov et al., 2013
73	*C.* (*E.*) *intermedius* Argyropulo, 1935	+					*Microtus arvalis*	Georgia, Azerbaijan, RF (Dagestan)	Goncharov et al., 2013

74	*C.* (*E.*) *iranus* Argyropulo, 1935	+					Cricetidae	Azerbaijan	Goncharov et al., 2013
75	*C.* (*E.*) *orientalis* Wagner, 1898	+					*Spermophilus*	RF (North Caucasus, Caspian Sea region)	Goncharov et al., 2013; Kutyrev, Popova, 2016
76	*C.* (*E.*) *pollex* Wagner et Ioff, 1926	+					*Spermophilus*	RF (Lower Volga), North-West Kazakhstan	Macchiavello, 1954; Goncharov et al., 2013
77	*C.* (*E.*) *secundus* Wagner, 1916	+					Microtinae	Azerbaijan	Ejgelis, 1980; Kutyrev, Popova, 2016
78	*C.* (*E.*) *teres* Ioff et Argyropulo, 1934	+					*Microtus arvalis*	Azerbaijan, Armenia	Goncharov et al., 2013
79	*C.* (*E.*) *wladimiri* Isayeva-Gurvich, 1948	+					*Microtus arvalis*	Azerbaijan, Armenia	Ejgelis, 1980; Kutyrev, Popova, 2016
80	*C.* (*Ethioctenophthalmus*) *calceatus* Waterston, 1912			+			*Arvacanthis*	Zaire	Macchiavello, 1954 (as *Ctenophthalmus cabirus*)
81	*C.* (*E.*) *nyikensis* Smit, 1962			+			Muridae	Tanzania	Varshavskij et al., 1971; Ziwa et al., 2013; Popova, Kutyrev, 2022
82	*C.* (*E.*) *phyris* Jordan, 1941			+			Micromammalia	Zaire	Macchiavello, 1954
83	*C.* (*Paractenophthalmus*) *dolichus* Rothschild, 1913	+					Gerbillinae	Kazakhstan, Middle Asia, Mongolia (Gobi)	Naumov et al., 1972; Ajkimbaev et al., 1987; Martinevskij et al., 1987; Goncharov et al., 2013; Popova, Kutyrev, 2022
84	*C.* (*Medioctenophthalmus*) *golovi* Ioff et Tiflov, 1930	+					*Spermophilus*, Micromammalia	Azerbaijan, RF, Middle Asia	Popova, Kutyrev, 2022
85	*C.* (*Metactenophthalmus*) *wagneri* Tiflov, 1928	+					Micromammalia	RF (Lower Volga, Dagestan), Azerbaijan	Goncharov et al., 2013
86	***C.* (*Sinoctenophthalmus*) *quadratus* Liu Chiying et Wu Houyong, 1960**	+					Micromammalia	China (NorthYunnan)	Popova, Kutyrev, 2022
87	*Neotyphloceras rosenbergi* (Rothschild, 1904)				+		Didelphidae	Ecuador, Peru	Macchiavello, 1954
88	*Atyphloceras multidentatus* (C.Fox, 1909)		+				*Neotoma*	USA (southwest)	Macchiavello, 1954; Pratt et al., 1993

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
							Subfam. Dinopsyllinae		
89	*Dinopsyllus* (*Dinopsyllus*) *brachypecten* Smit, 1951			+			*Rattus*	Madagascar	Popova, Kutyrev, 2022 (as *Dinopsyllus brachypectus*)
90	*D.* (*D.*) *ellobius* (Rothschild, 1905)			+			Micromammalia	South Africa, Botswana, Zambia, Angola	Macchiavello, 1954; Gracio, Gracio, 2011
91	***D.* (*D.*) *lypusus* Jordan et Rothschild, 1913**			+			Muridae	Kongo; Kenya; Tanzania	Kozakevich et al., 1971; Ziwa et al., 2013
							Subfam. Doratopsyllinae		
92	*Adoratopsylla* (*Tritopsylla*) *intermedia* (Wagner, 1901)				+		Didelphidae	Ecuador	Macchiavello, 1954 (as *Tritopsylla intermedia*)
	Subfam. Hystrichopsyllinae								
93	*Hystrichopsylla* (*Hystrichopsylla*) *dippiei* Rothschild, 1902		+				Cricetidae	USA	Macchiavello, 1954; Pratt et al., 1993
94	*H.* (*H.*) *occidentalis Holland*, 1949		+				Cricetidae	USA	Pratt et al., 1993 (as *Hystrichopsylla linsdalei*)
95	*H.* (*H.*) *talpae* (Curtis, 1826)	+					Insectivora	RF (Dagestan)	Goncharov et al., 2013
							Subfam. Listropsyllinae		
96	*Listropsylla dorippae* (Rothschild, 1904)			+			Gerbillinae, *Tatera*	South Africa	Van Der Mescht, Matthee, 2017
							Subfam. Rhadinopsyllinae		
97	*Rhadinopsylla* (*Actenophthalmus*) *altaica* (Wagner, 1901)	+					*Ochotona*, *Alticola*	RF (Mountain Altai), Mongolia	Bolormaa et al., 2010; Balahonov, Korzun, 2022; Medvedev et al., 2020
98	*Rh.* (*A.*) *altifrons* Labunets et Kafarskaya, 1961	+					*Microtus juldaschi*	Kirgizia	Goncharov et al., 2013; Medvedev et al., 2020
99	*Rh.* (*A.*) *angusta* Traub, 1972	+					Cricetinae	Middle Asia	Goncharov et al., 2013; Kutyrev, Popova, 2016; Medvedev et al., 2020

100	***Rh.* (*A.*) *dahurica* Jordan et Rothschild, 1923**	+					*Ochotona*, Micromammalia	RF (Mountain Altai), Mongolia, North China	Zhovtyj, 1969; Popova, Kutyrev, 2022; Bolormaa et al., 2010; Balahonov, Korzun, 2022; Medvedev et al., 2020
101	*Rh.* (*A.*) *dives* Jordan, 1929	+					*Spermophilus*, Micromammalia	China (South Manchuria)	The Atlas…, 2000; Medvedev et al., 2020
102	*Rh.* (*A.*) *insolita* Jordan, 1929	+					Micromammalia	China (South Manchuria, Erlian)	The Atlas…, 2000; Medvedev et al., 2020
103	*Rh.* (*A.*) *caucasica* Argyropulo, 1941						Cricetinae	RF (Dagestan), Azerbaijan	Goncharov et al., 2013 (as *Rhadinopsylla integella caucasica*); Medvedev et al., 2020
104	*Rh.* (*A.*) *rothschildi* Ioff, 1940	+					*Lasiopodomys brandtii*	RF (Transbaikalia)	Zhovtyj, 1969; Medvedev et al., 2020
105	*Rh.* (*A.*) *tenella* Jordan, 1929	+					Micromammalia	China (Erlian)	The Atlas…, 2000; Medvedev et al., 2020
106	*Rh.* (*A.*) *integella* Jordan et Rothschild, 1921	+					Micromammalia	RF (North Caucasus), China (South Manchuria)	The Atlas…, 2000; Goncharov et al., 2013; Popova, Kutyrev, 2022
107	*Rh.* (*Rhadinopsylla*) *bivirgis* Rothschild, 1913	+					*Meriones*	Caspian Sea region, Middle Asia, Kazakhstan, Iran	Goncharov et al., 2013; Maleki-Ravasan et al., 2017; Medvedev et al., 2020
108	*Rh.* (*Rh.*) *cedestis* Rothschild, 1913	+					*Meriones*, *Rhombomys opimus*	Middle Asia, Kazakhstan, Transcaucasia	Naumov et al., 1972; Ejgelis, 1980; Ajkimbaev et al., 1987; Martinevskij et al., 1987; Goncharov et al., 2013; Medvedev et al., 2020
109	*Rh.* (*Rh.*) *socia* Wagner, 1930	+					*Meriones*	Middle Asia, Kazakhstan	Ajkimbaev et al., 1987; Medvedev et al., 2020
110	*Rh.* (*Rh.*) *ucrainica* Wagner et Argyropulo, 1934	+					Gerbillinae, *Microtus socialis*	Azerbaijan, Armenia	Ejgelis, 1980; Goncharov et al., 2013; Medvedev et al., 2020
111	***Rh.* (*Ralipsylla*) *li* Argyropulo, 1941**	+					Marmotinae	RF (Tuva, Mountain Altai), Kazakhstan, Kirgizia, Mongolia, China (Tibet, Xinjiang)	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022; Medvedev et al., 2020
112	*Stenischia angustifrontalis* Xie Baoqi et Gong Zhengda, 1983					+	Micromammalia	China (Yunnan)	The Atlas…, 2000

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
113	*S. humilis* Xie Baoqi et Gong Zhengda, 1983					+	Cricetidae	China (Yunnan)	The Atlas…, 2000
							Subfam. Neopsyllinae		
114	*Paraneopsylla ioffi* Smit, 1953	+					*Ochotona*, *Alticola*	RF (Mountainous Altai), Kazakhstan, Middle Asia, Mongolia, North China	The Atlas…, 2000; Bolormaa et al., 2010; Balahonov, Korzun, 2022
115	*Catallagia decipiens* Rothschild, 1915		+				Cricetidae	USA	Eskey, Haas, 1940; Pratt et al., 1993
116	*C. sculleni* Hubbard, 1940		+				Micromammalia	USA	Popova, Kutyrev, 2022
117	*C. wymani* (C.Fox, 1909)		+				Micromammalia	USA	Macchiavello, 1954; Pratt et al., 1993
118	*Epitedia stanfordi* Traub, 1944		+				Cricetidae	USA	Pratt et al., 1993 (as *Epitedia stenfordi*)
119	*E. wenmanni* (Rothschild, 1904)		+				Cricetidae	USA	Pratt et al., 1993
120	*Meringis shannoni* (Jordan, 1929)		+				Micromammalia	USA (Washington)	Pratt et al., 1993
121	***Neopsylla abagaitui* Ioff, 1946**	+					*Spermophilus dauricus*	RF (Transbaikalia), China (Manchuria, Ordos), Mongolia	The Atlas…, 2000; Bolormaa et al., 2010; Medvedev et al., 2021
122	*N. bidentatiformis* (Wagner, 1893)	+					Micromammalia	RF (Transbaikalia) China (Manchuria, Xyling, Erlian)	Macchiavello, 1954; Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Medvedev et al., 2021
123	*N. galea* Ioff, 1946	+					Micromammalia	China (Erlian)	The Atlas…, 2000; Medvedev et al., 2021
124	*N. hongyangensis* Li Kueichen, Bai Xueli et Chen Baifang, 1986	+					Micromammalia	China (Tibet)	The Atlas…, 2000; Medvedev et al., 2021
125	*N. inopina* Rothschild, 1915		+				*Spermophilus* (sensu lato)	USA	Macchiavello, 1954; Pratt et al., 1993; Medvedev et al., 2021

126	*N. mana* Wagner, 1927	+					Polyhostal	RF (Tuva, Mountain Altai), Mongolia, China (Xinjiang)	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov, Korzun, 2022; Medvedev et al., 2021
127	*N. meridiana* Tiflov et Kolpakova, 1937	+					*Microtus juldaschi*	Kirgizia, Tajikistan	Goncharov et al., 2013; Kutyrev, Popova, 2016; Medvedev et al., 2021
128	***N. pleskei* Ioff, 1928**	+					Micromammalia	RF (Tuva, Transbaikalia), Kazakhstan, Middle Asia, North China, Mongolia	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022; Medvedev et al., 2021
129	***N. setosa* (Wagner, 1898)**	+					*Spermophilus*	RF (Lower Volga, North Caucasus), Middle Asia; Kazakhstan	Ioff, 1941; Macchiavello, 1954; Ajkimbaev et al., 1987; Medvedev et al., 2021
130	***N. specialis* Jordan, 1932**	+					Muridae	China (NorthYunnan)	Popova, Kutyrev, 2022; Guo et al., 2020; Medvedev et al., 2021
131	***N. teratura* Rothschild, 1913**	+					*Cricetulus migratorius*	Middle Asia, China (Xinjiang), West Mongolia	Goncharov et al., 2013; The Atlas…, 2000; Bolormaa et al., 2010; Medvedev et al., 2021
132	*Phalacropsylla allos* Wagner, 1936		+				Cricetidae	USA	Pratt et al., 1993 (as *Phalacropsylla allos*)
							Subfam. Stenoponiinae		
133	*Stenoponia conspecta* Wagner, 1926	+					Gerbillinae	Middle Asia, Kazakhstan	Ajkimbaev et al., 1987; Martinevskij et al., 1987
134	*S. ivanovi* Ioff et Tiflov, 1934	+					*Microtus arvalis*	Transcaucasia, China (Xinjiang)	The Atlas…, 2000; Karimova, Neronov, 2007; Goncharov et al., 2013
135	***S. tripectinata* (Tiraboschi, 1902)**	+					*Meriones*	RF (Dagestan), Azerbaijan, Middle East	Ejgelis, 1980; Dannis et al., 1999; Karimova, Neronov, 2007; Goncharov et al., 2013
136	*S. vlasovi* Ioff et Tiflov, 1934	+					*Meriones*	RF (Caspian Sea region, Dagestan), Middle Asia	Ajkimbaev et al., 1987; Martinevskij et al., 1987; Goncharov et al., 2013

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
Fam. Chimaeropsyllidae									
Subfam. Chiastopsyllinae									
137	*Chiastopsylla* (*Chiastopsylla*) *numae* (Rothschild, 1904)			+			Muridae	South Africa, Botswana	Van Der Mescht, Matthee, 2017
138	*Ch.* (*Ch.*) *rossi* (Waterston, 1909)			+			Gerbillinae, *Tatera*, *Otomys*	South Africa	Macchiavello, 1954
Fam. Macropsyllidae – there is no data on the infection rate of representatives of the family with plague pathogen									
Fam. Stephanocircidae									
Subfam. Craneopsyllinae									
139	*Craneopsylla minerva* (Rothschild, 1903)				+		Cricetidae	Argentina	Plague…, 1963; Kozakevich et al., 1970
140	*Plocopsylla* (*Plocopsylla*) *hector* Jordan, 1931				+		*Tomasomys* sp.	Ecuador	Macchiavello, 1954
141	*Sphinctopsylla mars* (Rothschild, 1898)				+		Hesperomys	Peru	Macchiavello, 1954 Laguna-Torres, Gómez-Benavides, 2004
Infraorder Pygiopsyllamorpha									
Fam. Lycopsyllidae – there is no data on the infection rate of representatives of the family with plague pathogen									
Fam. Pygiopsyllidae – there is no data on the infection rate of representatives of the family with plague pathogen									
Fam. Stivaliidae									
142	*Lentistivalius* (*Lentistivalius*) *ferinus* (Rothschild, 1908)					+	Micromammalia	China (Yunnan)	The Atlas…, 2000
143	*Stivalius ahalae* (Rothschild, 1904)					+	Muridae	India, Java	Macchiavello, 1954; Velimirovic, 1972
144	*S. aporus* Jordan et Rothschild, 1922					+	Muridae	India	Velimirovic, 1972; Ramalingaswami, 1995
145	*S. cognatus* Jordan et Rothschild, 1922					+	Muridae	Java	Macchiavello, 1954

Infraorder Ceratophyllomorpha

Fam. Ceratophyllidae

146	*Aetheca wagneri* (Baker, 1904)		+					*Peromyscus*	USA (New Mexico)	Macchiavello, 1954 (as *Monopsyllus wagneri*); Goncharov et al., 2013 (as *Megabothris wagneri*)
147	*Amalareus dissimilis* (Jordan, 1938)	+						*Microtus arvalis*	RF (North Caucasus)	Goncharov et al., 2013
148	*Amalareus penicilliger* (Grube, 1851)	+						Micromammalia	RF (Tuva); Mongolia (Bayan-Ulgii)	Bolormaa et al., 2010, Balahonov et al., 2019
149	*A. bitterrootensis* (Dunn, 1923)		+					Cricetidae (*Neotoma*)	USA	Pratt et al., 1993 (as *Malaraeus biterrotensis*)
150	***Amphalius runatus* (Jordan et Rothschild, 1923)**	+						*Ochotona*	RF, Mongolia, North China	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022
151	***Callopsylla* (*Callopsylla*) *caspia* (Ioff et Argyropulo, 1934)**	+						Micromammalia	RF (Mountain Altai), Armenia, Kirgizia, Tajikistan	Ejgelis, 1980; Goncharov et al., 2013; Balahonov, Korzun, 2022
152	***C.* (*C.*) *dolabris* (Jordan et Rothschild, 1911)**	+						*Marmota hymalayana*, *M. baibacina*	China (Tibet, Qinghai, East Tien Shan)	The Atlas..., 2000; Karimova, Neronov, 2007
153	*C.* (*C.*) *saxatilis* (Ioff et Argyropulo, 1934)	+						Cricetidae	RF (North Caucasus)	Goncharov et al., 2013
154	***C.* (*C.*) *sparsilis* (Jordan et Rothschild, 1922)**	+						*Neodon* (*Microtus*) *fuscus*	China (Qinghai, Sichuan)	The Atlas…, 2000
155	*Ceratophyllus* (*Amonopsyllus*) *ciliatus* Baker, 1904		+					*Eutamias*	USA (California)	Macchiavello, 1954 (as *Monopsyllus ciliatus*); Traub et al., 1983
156	*C.* (*Emmareus*) *borealis* Rothschild, 1907	+						Aves	Armenia	Goncharov et al., 2013
157	*C.* (*Ceratophyllus*) *styx* Rothschild, 1900	+						Aves	RF (Tuva, Mountain Altai), Mongolia, North China	Zhovtyj, 1969 (as *Ceratophyllus avicitelli*); The Atlas…, 2000; Bolormaa et al., 2010; Goncharov et al., 2013

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
158	*C.* (*Monopsyllus*) *anisus* Rothschild, 1907	+					*Rattus norvegucus*	RF (Transbaikalia, Primorsky Krai), China (Manchuria, Yunnan)	Macchiavello, 1954 (as *Monopsyllus anisus*); The Atlas..., 2000; Goncharov et al., 2013
159	***Citellophilus lebedewi* (Wagner, 1933)**	+					*Marmota caudata*, *M. baibacina*	Kirgizia, Tajikistan, China (West Xinjiang)	The Atlas…, 2000; Goncharov et al., 2013
160	***C. tesquorum* (Wagner, 1898)**	+					*Spermophilus*, *Urocitellus*	RF, Mongolia, Middle Asia, Kazakhstan, China (Manchuria, Xylignol, Ordos, East Tien Shan)	Macchiavello, 1954; Zhovtyj, 1969; Traub et al., 1983; Ajkimbaev et al., 1987; Martinevskij et al., 1987; The Atlas…, 2000; Bolormaa et al., 2010; Goncharov et al., 2013; Medvedev et al., 2019a
161	*C. trispinus* (Wagner et Ioff, 1926)	+					*Spermophilus fulvus*	Middle Asia	Ajkimbaev et al., 1987; Martinevskij et al., 1987; Goncharov et al., 2013; Medvedev et al., 2019a
162	*C. ullus* (Mikulin, 1957)	+					*Spermophilus erythrogenys*	Kazakhstan, China (Xinjiang)	The Atlas…, 2000; Goncharov et al., 2013; Medvedev et al., 2019a
163	*Eumolpianus eumolpi* (Rothschild, 1905)		+				*Eutamias*	USA (Washington)	Macchiavello, 1954 (as *Monopsyllus eumolpi*); Traub et al., 1983; Dannis et al., 1999 (as *Monopsyllus eumolpi*)
164	*E. fornacis* (Jordan, 1937)		+				*Eutamias*	USA (California)	Dannis et al., 1999 (as *Monopsyllus fornacis*)
165	*Malaraeus sinomus* (Jordan, 1925)		+				Cricetidae	USA (south and southwest)	Traub et al., 1983; Pratt et al., 1993
166	*M. telchinus* (Rothschild, 1905)		+				*Microtus californicus*	USA (California, Oregon, Nevada)	Macchiavello, 1954; Traub et al., 1983
167	*Megabothris* (*Amegabothris*) *abantis* (Rothschild, 1905)		+				Cricetidae	USA	Macchiavello, 1954; Traub et al., 1983
168	*M.* (*A.*) *clantoni* Hubbard, 1949		+				Micromammalia	USA (Washington)	Macchiavello, 1954; Traub et al., 1983

169	*M.* (*Gebiella*) *turbidus* (Rothschild, 1909)	+					Micromammalia	RF (Dagestan)	Goncharov et al., 2013
170	*Nosopsyllus* (*Gerbillophilus*) *aralis* (Argyropulo, 1946)	+					*Meriones tamariscinus*	Middle Asia, Kazakhstan	Ajkimbaev et al., 1987; Goncharov et al., 2013
171	***N.* (*G.*) *iranus* Wagner et Argyropulo, 1934**	+					Gerbillinae	Syria, Arabian Peninsula, Iran, Azerbaijan	Ejgelis, 1980; Karimova, Neronov, 2007; Goncharov et al., 2013; Maleki-Ravasan et al., 2017
172	***N.* (*G.*) *laeviceps* (Wagner, 1909)**	+					*Meriones*	Azerbaijan, RF (Dagestan), China (Manchuria, Xyling, Erlian), Middle Asia, Kazakhstan, Iran	Naumov et al., 1972; Ejgelis, 1980; Ajkimbaev et al., 1987; Martinevskij et al., 1987; The Atlas…, 2000; Karimova, Neronov, 2007; Goncharov et al., 2013
173	***N.* (*Nosopsyllus*) *consimilis* (Wagner, 1898)**	+					Micromammalia	Armenia, Azerbaijan	Ejgelis, 1980; Goncharov et al., 2013; Kutyrev, Popova, 2016
174	*N.* (*N.*) *fasciatus* (Bosc, 1800)	+	+	+			*Rattus*	Over the World	Ioff, 1941; Macchiavello, 1954; Traub et al., 1983; The Atlas…, 2000
175	*N.* (*N.*) *fidus* (Jordan et Rothschild, 1915)	+					Muridae	Middle Asia	Ajkimbaev et al., 1987; Sludskij, 2014
176	*N.* (*N.*) *londiniensis* (Rothschild, 1903)				+		Muridae	Brazil, Ecuador	Macchiavello, 1954; Traub et al., 1983
177	*N.* (*N.*) *mokrzeckyi* (Wagner, 1916)	+					*Mus musculus*	RF (Lower Volga, North Caucasus), Kazakhstan	Ioff, 1941; Ejgelis, 1980; Ajkimbaev et al., 1987; Goncharov et al., 2013
178	*N.* (*N.*) *monstrosus* (Wagner, 1928)	+					*Meriones*	Middle Asia (Karakums)	Ajkimbaev et al., 1987; Goncharov et al., 2013
179	*N.* (*Nosopsyllus*) *nicanus* Jordan, 1937	+					*Rattus*	China (Manchuria)	The Atlas…, 2000
180	*N.* (*Nosopsyllus*) *nilgiriensis* (Jordan et Rothschild, 1921)					+	Muridae, *Bandicota*	India	Macchiavello, 1954; Rajamannar et al., 2022
181	*N.* (*N.*) *punjabensis* (Jordan et Rothschild, 1921)	+				+	Muridae	India, South-East Asia	Traub et al., 1983; Popova, Kutyrev, 2022
182	*N.* (*Gerbillophilus*) *tersus* (Jordan et Rothschild, 1915)	+					*Rhombomys opimus*	Middle Asia, Kazakhstan	Ajkimbaev et al., 1987; Martinevskij et al., 1987
183	*N.* (*G.*) *turkmenicus* (Vlasov et Ioff, 1937)	+					*Meriones*	Middle Asia	Traub et al., 1983; Ajkimbaev et al., 1987

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
184	*Opisodasys* (*Oxypsylla*) *keeni* (Baker, 1896)		+				Cricetidae	USA (California)	Eskey, Haas, 1940; Pratt et al., 1993
185	*O.* (*O.*) *nesiotus* Augustson, 1941		+				Cricetidae	USA (California)	Macchiavello, 1954; Pratt et al., 1993
186	*Orchopeas howard*i (Baker, 1895)		+				Cricetidae	USA	Eskey, Haas, 1940; Pratt et al., 1993; Dannis et al., 1999
187	*O. leucopus* (Baker, 1904)		+				*Peromyscus*	USA (New Mexico)	Traub et al., 1983; Pratt et al., 1993
188	***O. neotomae* (Augustson, 1943)**		+				*Neotoma*	USA (New Mexico) и North Mexico	Traub et al., 1983; Pratt et al., 1993; Dannis et al., 1999
189	***O. sexdentatus* (Baker, 1904)**		+				Cricetidae	USA, North Mexico	Traub et al., 1983; Macchiavello, 1954; Pratt et al., 1993; Dannis et al., 1999
190	***Oropsylla* (*Diamanus*) *montana* (Baker, 1895)**		+				Marmotinae	USA (West)	Macchiavello, 1954; Pratt et al., 1993 (as *Diamanus montanus*); Medvedev, Verzhutsky, 2019b
191	*O.* (*Oropsylla*) *alaskensis* Baker, 1904	+					*Urocitellus*, *Spermophilus*	RF (Tuva, Altai, Transbaikalia); Mongolia	Zhovtyj, 1969 (as *Oropsylla asiatica*); Bolormaa et al., 2010; Medvedev, Verzhutsky, 2019b
192	*O.* (*O.*) *ilovaiskii* Wagner et Ioff, 1926	+					*Spermophilus*	RF (Lower Volga), Middle Asia, North-West Kazakhstan	Traub et al., 1983; Ajkimbaev et al., 1987; Medvedev, Verzhutsky, 2019b
193	*O.* (*O.*) *rupestris* (Jordan, 1929)		+				*Urocitellus*, *Spermophilus*	USA (West), Canada	Eskey, Haas, 1940; Traub et al., 1983; Pratt et al., 1993; Medvedev, Verzhutsky, 2019b
194	***O.* (*O.*) *silantiewi* (Wagner, 1898)**	+					*Marmota*	RF (Tuva, Mountain Altai, Transbaikalia), Kazakhstan, Kirgizia, Mongolia, China	Ioff, 1941; Macchiavello, 1954; Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Medvedev, Verzhutsky, 2019b

195	***O.* (*O.*) *bruneri* (Baker, 1895)**		+				*Ictidomys tridecimlineatus*	USA	Macchiavello, 1954; Pratt et al., 1993 (as *Opisocrostis bruneri*); Medvedev, Verzhutsky, 2019b
196	***O.* (*Opisocrostis*) *hirsuta* (Baker, 1895)**		+				*Cynomys*	USA (West)	Macchiavello, 1954; Pratt et al., 1993 (as *Opisocrostis hirsutus*); Dannis et al., 1999; Medvedev, Verzhutsky, 2019b
197	***O.* (*O.*) *tuberculata* (Baker, 1904)**		+				Marmotinae	USA	Macchiavello, 1954; Pratt et al., 1993 (as *Opisocrostis tuberculatus*); Medvedev, Verzhutsky, 2019b
198	***O.* (*O.*) *labis* (Jordan et Rothschild, 1922)**		+				*Urocitellus*, *Spermophilus*	USA (West)	Macchiavello, 1954; Traub et al., 1983; Pratt et al., 1993 (as *Opisocrostis labia*); Dannis et al., 1999; Medvedev, Verzhutsky, 2019b
199	***O.* (*O.*) *idahoensis* (Baker, 1904)**		+				*Urocitellus*, *Spermophilus*	USA (northwest)	Macchiavello, 1954; Traub et al., 1983; Pratt et al., 1993; Dannis et al., 1999; Medvedev, Verzhutsky, 2019b
200	*Paramonopsyllus scalonae* (Vovchinskaya, 1950)		+				*Ochotona*, *Alticola*	RF (Tuva, Mountainous Altai), Mongolia, North China	Zhovtyj, 1969 (as *Ceratophyllus scalonae*); The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022
201	*Pleochaetis exilis* (Jordan, 1937)		+				Micromammalia	USA	Traub et al., 1983; Pratt et al., 1993 (as *Megabothris exilis*)
202	***Plusaetis dolens* (Jordan et Rothschild, 1914)**				+		Cricetidae, *Sciurus*	Peru	Macchiavello, 1954; Traub et al., 1983; Kozlov, Sultanov, 2000
203	*P. equatoris* (Jordan, 1933)				+		Cricetidae, Caviidae	Peru	Macchiavello, 1954; Traub et al., 1983
204	*P. sibynus*(Jordan, 1925)				+		Cricetidae	USA	Pratt et al., 1993; Goncharov et al., 2013 (as *Pleochaetis sibinus*)
205	*Rostropsylla daca* (Jordan et Rothschild, 1911)	+					*Spermophilopsys leptodactylus*	Middle Asia, Southern Kazakhstan	Ajkimbaev et al., 1987
206	***Thrassis acamantis* (Rothschild, 1905)**		+				Marmotinae	USA	Macchiavello, 1954; Traub et al., 1983 (as *Oropsylla acamanthis*); Pratt et al., 1993
207	*Th. arizonensis* (Baker, 1898)		+				*Spermophilus lateralis*, *S. variegatus*	USA (California, Arizona)	Macchiavello, 1954; Pratt et al., 1993

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
208	***Th. bacchi*** **(Rothschild, 1905)**		+				Marmotinae, Cricetidae	USA (Colorado, Montana, South Dakota)	Macchiavello, 1954; Pratt et al., 1993
209	***Th. fotas*** **(Jordan, 1925)**		+				Onychomys	USA (Colorado)	Macchiavello, 1954; Traub et al., 1983; Pratt et al., 1993 (as *Thrassis fotus*)
210	***Th. francisi*** **(C.Fox, 1927)**		+				Marmotinae	USA (Utah, Nevada, Oregon)	Macchiavello, 1954; Traub et al., 1983 (as *Oropsylla francisi*); Pratt et al., 1993
211	***Th. pandorae Jellison*****, 1937**		+				*Urocitellus armatus*	USA (Montana, Oregon)	Macchiavello, 1954; Pratt et al., 1993
212	*Th. petiolatus* (Baker, 1904)		+				Marmotinae	USA (Idaho, Montana, Oregon, Washington)	Macchiavello, 1954; Pratt et al., 1993
213	*Th. stanfordi* Wagner, 1936		+				*Marmota*	USA	Eskey, Haas, 1940; Traub et al., 1983 (as *Oropsylla stanfordi*); Pratt et al., 1993
							Subfam. Dactylopsyllinae		
214	*Foxella ignota* (Baker, 1895)		+				Geomyidae	USA (Colorado)	Macchiavello, 1954; Traub et al., 1983; Pratt et al., 1993 (as *Dactylopsylla ignota*)
							Fam. Xiphiopsyllidae		
215	*Xiphiopsylla lippa* Jordan, 1933			+			Laphuromys	East Africa	Macchiavello, 1954, Varshavskij et al., 1971; Popova, Kutyrev, 2022
							Fam. Leptopsyllidae		
							Subfam. Leptopsyllinae		
216	*Leptopsylla aethiopica* (Rothschild, 1908)			+			Muridae	East Africa	Macchiavello, 1954; Goncharov et al., 2013
217	*L. nana* Argyropulo, 1946	+					Micromammalia	RF, Tajikistan	Goncharov et al., 2013
218	*L. segnis* (*Schönherr*, 1811)	+					*Mus musculus*	RF, China (Yunnan),	Macchiavello, 1954; Popova, Kutyrev, 2022; Karimova, Neronov, 2007

219	*L. taschenbergi* (Wagner, 1898)	+					Micromammalia	North-West Kazakhstan	Ajkimbaev et al., 1987
220	*Pectinoctenus nemorosa* Tiflov, 1937	+					Micromammalia	Kirgizia	Goncharov et al., 2013
221	*P. pavlovskii* Ioff, 1928	+					*Phodopus* и др. Micromammalia	Mongolia, China (Xylignol)	The Atlas…, 2000; Bolormaa et al., 2010 (as *Leptopsylla pavlovskii*)
222	*Peromyscopsylla bidentata* (Kolenati, 1863)	+					Cricetidae	Azerbaijan	Goncharov et al., 2013
223	*P. hesperomys* (Baker, 1904)		+				*Peromyscus*	USA	Eskey, Haas, 1940; Pratt et al., 1993
224	*Amphipsylla anceps* Wagner, 1930	+					Micromammalia	Tajikistan	Goncharov et al., 2013; Popova, Kutyrev, 2022
225	*A. asiatica* Ioff, 1928	+					*Lasiopodomys* (*Microtus*) *gregalis*	Kirgizia	Goncharov et al., 2013; Popova, Kutyrev, 2022
226	*A. kuznetzovi* Wagner, 1912	+					*Microtus*	RF (Mountain Altai)	Zhovtyj, 1969; Balahonov, Korzun, 2022
227	*A. longispina* Scalon, 1950	+					*Phodopus sungorus*	RF (Tuva, Mountain Altai)	Balahonov et al., 2019; Balahonov, Korzun, 2022
228	*A. montana* Argyropulo, 1946	+					*Alticola argentatus*	Tajikistan	Goncharov et al., 2013
229	***A. phaiomydis* Ioff, 1946**	+					*Microtus juldaschi*	Kirgizia, Tajikistan	Goncharov et al., 2013
230	***A. primaris* Jordan et Rothschild, 1915**	+					*Alticola*, *Ochotona*	RF (Mountain Altai, Tuva, Transbaikalia), Mongolia, China (Xylignol)	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022
231	*A. rossica* Wagner, 1912	+					*Microtus arvalis*	RF (Dagestan), Armenia	Ejgelis, 1980; Ajkimbaev et al., 1987; Goncharov et al., 2013
232	*A. schelkovnikovi* Wagner, 1909	+					*Cricetulus migratorius*	RF (Dagestan), Armenia	Goncharov et al., 2013
233	***A. tuta*Wagner, 1928**	+					*Neodon* (*Microtus*) *fuscus*	China (Qinghai)	Nikitin et al., 2009; Wang et al., 2009 (as *Amphipsylla tutua*)
234	*Mesopsylla apscheronica* Wagner et Argyropulo, 1934	+					Dipodidae	Azerbaijan	Ejgelis, 1980; Goncharov et al., 2013

Table 1. *Continuation*
Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
235	*Mesopsylla eucta Dampf*, 1910	+					Dipodidae	RF (Lower Volga, Middle Asia, Kazakhstan, China (Xinjiang)	Ajkimbaev et al., 1987; The Atlas…, 2000; Ajkimbaev et al., 1987 (as *Mesopsylla lenis*)
236	*M. hebes* Jordan et Rothschild, 1915	+					*Allactaga jaculus*	RF (Caspian Sea region), Middle Asia, Kazakhstan, China (Xinjiang)	The Atlas…, 2000; Goncharov et al., 2013; Popova, Kutyrev, 2022
237	*M. tuschkan* Wagner et Ioff, 1926	+					Dipodidae	Kazakhstan, China (Xinjiang)	The Atlas…, 2000; Goncharov et al., 2013
238	*Acropsylla episema* Rothschild, 1911					+	Micromammalia	India	Velimirovic, 1972; Popova, Kutyrev, 2022
							Subfam. Paradoxopsyllinae		
239	***Ctenophyllus hirticrus* (Jordan et Rothschild, 1923)**	+					*Ochotona*	RF (Tuva, Mountain Altai, Transbaikalia), West Mongolia	Zhovtyj, 1969; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022
240	*Frontopsylla* (*Frontopsylla*) *caucasica* Ioff et Argyropulo, 1934	+					*Microtus arvalis*	RF (North Caucasus), Armenia, Azerbaijan	Ejgelis, 1980; Goncharov et al., 2013; Medvedev et al., 2021a
241	***F.* (*F.*) *elata* (Jordan et Rothschild, 1915)**	+					Micromammalia	RF (Tuva, Mountain Altai), Azerbaijan, Mongolia, China (Ordos)	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Goncharov et al., 2013; Popova, Kutyrev, 2022
242	*F.* (*F.*) *elatoides* Wagner, 1928	+					*Urocitellus undulatus*	RF (Tuva), China (Xinjiang - East Tian Shan)	Zhovtyj, 1969; The Atlas…, 2000; Balahonov et al., 2019; Medvedev et al., 2021a
243	*F.* (*F.*) *hetera* Wagner, 1933	+					*Ochotona* и Micromammalia	RF (Tuva, Mountain Altai), Mongolia	Zhovtyj, 1969; Bolormaa et al., 2010; Balahonov et al., 2019; Medvedev et al., 2021a

244	*F.* (*F.*) *glabra* Ioff, 1946	+					Micromammalia	Middle Asia (Tien Shan, Pamir-Alai), China (Kunlun)	Onishchenko, Kutyrev, 2004; Sludskij et al., 2003; Medvedev et al., 2021a
245	***F.* (*F.*) *luculenta* (Jordan et Rothschild, 1923)**	+					Micromammalia	RF (Transbaikalia) Mongolia, China (Manchuria, Xylignol)	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Medvedev et al., 2021a
246	*F.* (*F.*) *semura* Wagner et Ioff, 1926	+					*Spermophilus*	RF (North Caucasus, Caspian Sea region), Middle Asia, Kazakhstan	Macchiavello, 1954; Ajkimbaev et al., 1987; Medvedev et al., 2021a
247	*F.* (*F.*) *spadix* (Jordan et Rothschild, 1921)	+					Micromammalia	China (NorthYunnan)	The Atlas…, 2000; Goncharov et al., 2013; Medvedev et al., 2021a
248	*F.* (*F.*) *wagneri* Ioff, 1928	+					Dipodidae	RF (Tuva), China (Tibet)	The Atlas…, 2000; Balahonov et al., 2019; Medvedev et al., 2021a
249	*F.* (*Profrontia*) *protera* Wagner, 1933	+					*Alticola argentatus*	Kirgizia	Goncharov et al., 2013; Medvedev et al., 2021a
250	*F.* (*P.*) *ornata* Tiflov, 1937	+					Micromammalia	Kirgizia	Goncharov et al., 2013; Medvedev et al., 2021a
251	*F.* (*Orfrontia*) *frontalis* (Rothschild, 1908)	+					*Oenanthe*	RF (Tuva, Mountain Altai), Kirgizia, China, Mongolia	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022; Medvedev et al., 2020
252	*Odontopsyllus sp.*				+		*Sylvilagus*	Peru	Macchiavello, 1954
253	*Ophthalmopsylla* (*Cystipsylla*) *kasakiensis* Ioff, 1929	+					*Dipus sagitta*	RF (Volga-Urals), North-West Kazakhstan	Goncharov et al., 2013; Popova, Kutyrev, 2022
254	*O.* (*C.*) *kiritschenkovi* (Wagner, 1930)	+					Dipodidae	China (Xinjiang), Middle Asia	The Atlas…, 2000; Goncharov et al., 2013
255	*O.* (*Ophthalmopsylla*) *kukuschkini* Ioff, 1928	+					Micromammalia	China (Manchuria)	The Atlas…, 2000
256	*O.* (*O.*) *praefecta* (Jordan et Rothschild, 1915)	+					Dipodidae	Mongolia, China (Manchuria, Xyling, Ordos)	The Atlas…, 2000; Bolormaa et al., 2010

Table 1. *Continuation*

Таблица.1. *Продолжение*

№	Species	PA	NA	AT	NT	IM	Mail hosts	Countries and regions	References
257	*O.* (*O.*) *volgensis* (Wagner et Ioff, 1926)	+					Dipodidae	RF (Caspian Sea region)	Goncharov et al., 2013
258	*Paradoxopsyllus curvispinus* Miyajima et Koidzumi, 1909	+					*Rattus*	China (Manchuria)	Macchiavello, 1954; The Atlas…, 2000; Medvedev et al., 2022a
259	*P. custodis* Jordan, 1932	+					*Eothenomys custos*	China (Sichuan, Yunnan)	Popova, Kutyrev, 2022; Medvedev et al., 2022a
260	***P. dashidorzhii* Scalon, 1953**	+					*Ochotona*, *Alticola*	RF (Mountain Altai), Mongolia (Sailugem, Mongolian Altai)	Zhovtyj, 1969; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022; ; Medvedev et al., 2022a
261	*P. hisperius* Ioff, 1946	+					*Ochotona*, Micromammalia	RF (Mountain Altai), Mongolia, China (Erlian)	The Atlas…, 2000; Balahonov, Korzun, 2022; Medvedev et al., 2022a
262	*P. integer* Ioff, 1946	+					*Ochotona*	North-West Mongolia	Bolormaa et al., 2010; Balahonov, Korzun, 2022; Medvedev et al., 2022a
263	*P. repandus* (Rothschild, 1913)	+					Gerbillinae	Middle Asia	Ajkimbaev et al., 1987; Martinevskij et al., 1987; Medvedev et al., 2022a
264	*P. scalonae* Violovich, 1964	+					*Alticola*	Mongolia (Mongolian Altai)	Balahonov, Korzun, 2022; Medvedev et al., 2022a
265	***P. scorodumovi* Scalon, 1935**	+					Micromammalia	RF (Tuva, Mountain Altai), Mongolia, North China	Zhovtyj, 1969; The Atlas…, 2000; Bolormaa et al., 2010; Balahonov et al., 2019; Balahonov, Korzun, 2022; Medvedev et al., 2022a
266	*P. teretifrons* (Rothschild, 1913)	+					*Rhombomys opimus*	Middle Asia, Kazakhstan, China (Xinjiang)	Ajkimbaev et al., 1987; The Atlas…, 2000; Medvedev et al., 2022a

Fam. Ischnopsyllidae – there is no data on the infection rate of representatives of the family with plague pathogen.

GENERAL CHARACTERISTICS OF THE FLEAS AND THEIR WORLD FAUNA

GENERAL CHARACTERISTICS OF FLEAS

The order of Fleas (Siphonaptera) unites secondarily wingless obligate blood-sucking insects with complete metamorphosis. Currently, the world fauna of the order includes about 2,162 species and 800 subspecies of fleas, which belong to 241 genera and 97 subgenera from 19 families, according to the ‛IAS PARHOST1’ data on the world fauna of fleas (Zoological Institute, Russian Academy of Sciences).

Flea imagoes are highly specialized ectoparasites of mammals (94% of flea species) and, to a lesser extent, of birds (6%). Most representatives of the order lead a nest-burrow lifestyle, being on the body of a warm-blooded host periodically or permanently. The flea morphology firstly ensures that the adult insect is held on the host during bloodsucking; secondly, it allows a parasite to move quickly around the host and leave it with a jump; thirdly, it facilitates the stay of the parasite outside the host in the nest litter, in burrows and outside them (for example, on the paths of the host routes).

The nesting and burrowing lifestyle has resulted in small size (about 4–5 mm on average) and a laterally flattened body, complete reduction of wings and compound eyes, mobile articulation of the middle and posterior segments of the thorax, as well as developed rear jumping legs and intersegmental and dorsoventral muscles. Flea imagoes are characterized by a developed chaetome, elongated protective collars and ctenidia on the posterior edges of the thorax and abdomen segments. The thorax and abdomen segments of fleas are movably connected, they are completely open from the back, due to which they can move inside each other. The thorax of fleas, consisting of three completely separate and movably articulated segments, has well-developed longitudinal dorsal and ventral muscles. The 10th abdominal segment carries a separate shield, called pygidium (sensillium), which is a unique sensory organ. Sensillium is armed with a large number of filiform receptors (trichobothria), which detect air vibrations.

The chaetome of the outer surface of the head, thorax, and abdomen is represented by setae of varying length and thickness, which are adjacent to the body or are located at a slight angle to it, diverting the hair of the hosts. The ctenidia teeth, unlike the setae, do not have a movable articulation with the body. They can be present on the head, the posterior edge of the notum prothorax and metathorax, as well as on the 1st, 3rd, and some other tergites of the abdomen.

Geographical distribution of Siphonaptera is preconditioned not only by the adaptations of fleas to live on the body of a warm-blooded host, but also to the microbiotope conditions of its nest. It should be noted that the development of preimaginal phases of fleas takes place in the nest litter. As a result, the distribution of fleas is greatly influenced by temperature and humidity. These indicators determine the biotope confinement of many flea taxa, as well as their absence on host species that live in waterlogged biotopes or lead an aquatic lifestyle. This causes the emergence of complex parasite-host relationships and coevolution of fleas and hosts, with most flea taxa characterized by a wide range of hosts.

According to the degree of attachment to the host body, flea species are divided into four ecological groups: “nest fleas”, “fur fleas”, “semi-stationary”, and “stationary” parasites (Ioff, 1941). The duration of stay of “nest fleas” on the host body is limited to the time required for them to consume food. Fleas of this group maintain a connection with the host’s shelter during all periods of life. Actually, “fur fleas” are represented by a narrow range of species. Having got on a suitable host, they remain on the host’s body constantly, but do not lose the ability to move and change hosts. Most flea species occupy an intermediate position in the type of parasitism between typical "nest fleas" and "fur fleas". The total number of species of "semi-stationary" and "stationary" parasites does not exceed 70. It should be noted that the "fur fleas" group is formed by genera and species belonging to different families.

PARASITE-HOST RELATIONSHIPS OF FLEAS

Earlier, it has been found that the number of species of parasites and their hosts relates as 1.1 : 1 for mammals and 1 : 2.5 for birds. At the genus rank, this ratio is 1 : 2.1 for mammals and 1 : 4.2 for birds; at the family rank, 1 : 5.1 and 1 : 7.4, respectively (Medvedev, 1997a) Such ratios, when the number of flea species slightly predominate over the number of mammal hosts and the opposite pattern observed for birds, might be explained by two reasons. Firstly, relatively small number of flea species parasitize on birds; secondly, the bird flea species are less host-specific. At the same time, many mammal species are the hosts for several flea species belonging to different genera and families. Higher ratios observed at the family rank testify to a great influence of environmental conditions on the distribution of flea species, i.e., several host species belonging to different genera and families can live in the same biotopes.

In our opinion, the ancestors of fleas were closely related to modern parasites of shrews. The habitat of modern shrews is also limited to a hunting area of several dozen square meters. Already wingless ancestors of fleas, like those of the genus Palaeopsylla, could wait for their hosts on the permanent migration routes of the latter. The presence of brood burrows in mammals with their relatively stable microclimate contributed to the formation of an even more stable connection between wingless fleas and warm-blooded hosts. The nest-burrow lifestyle contributed to the spread of fleas in various landscape zones, including boreal ones.

In particular, mammal hosts for fleas may be divided into several groups: (1) have nesting and brood shelters (most rodents and some Lagomorpha); (2) do not have nesting and brood shelters (Soricidae); (3) are characterized by a particularly mobile way of life (Microchiroptera, ungulates Euungulata, and Carnivora); (4) lead an ecologically isolated (e.g. underground) lifestyle. Birds form a separate group (Medvedev, 2017).

Traditionally, flea species are divided into monoxenous, mesoxenous, oligoxenous, euryxenous, and polyxenous parasites according to their degree of host specificity. At present, this feature of nearly every flea species may only be assessed by indirect data, which is the frequency of occurrence on various host species, the degree of range overlapping of the fleas and their hosts, and by the ecological characteristics of host(s). It should be noted that the parasite-host relationships of many flea species are currently studied insufficiently. According to specially written analytical programs, it is found that 39–46% of all flea species are euryxenous within the 10 largest families of the order Siphonaptera (Pulicidae, Tungidae, Rhopalopsyllidae, Pygiopsyllidae, Stivaliidae, Hystrichopsyllidae, Stephanocircidae, Ceratophyllidae, and Leptopsyllidae), i.e., they are found on the hosts belonging to different orders. Polyxenous species, parasitizing on the hosts of different families belonging to the same order, make up a significantly smaller number in each of these families, from 2 to 15%. Mesoxenous species (a flea species found on several genera of hosts from the same family) make up from 11 to 25%, true oligoxenous species (a flea species parasitizes several host species from the same genus), from 3 to 9% (Medvedev, 2009).

Typically, specific and basic relationships arise between certain species of fleas and their hosts. Monoxenous parasites include a small group of flea species, which parasitize both mammals and birds and which are ecologically isolated from their hosts. For example, these are the fleas of animals leading an underground way of life and the flea *Ceratophyllus styx* Rotschild, 1900 of the sand martin *Riparia riparia* (L., 1758). The flea *Ctenophthalmus spalacis* J. et R., 1911 is found on the greater blind mole-rat *Spalax microphthalmus* Güldenstädt, 1770, the flea *C. inornatus* Wagner, 1916, on long-clawed mole vole *Prometheomys schaposchnikowi* Satunin, 1901; flea *Xenopsylla magdalinae* Ioff, 1935, on mole voles of tribe Ellobiusini. The fleas from family Ischnopsyllidae are extremely closely related to order Chiroptera (bats), with an example of the flea genus *Thaumapsylla* found only on Old World fruit bats (Pteropodidae). Sloths and anteaters (order Pilosa) serve as hosts mainly for the flea family Malacopsyllidae (Patagonian Province); elephant shrews (Macroscelididae) host mainly the fleas of the family Chimaeropsyllidae (Cape Province). The fleas of the genus *Procaviopsylla* (Pulicidae) parasitize only on hyraxes (Procaviidae), genus *Bradiopsylla* (Lycopsyllidae), only on echidnas (Tachyglossidae). The flea tribe Doratopsyllini (Hystrichopsyllidae) are the parasites of Eulipotyphla only (hedgehogs, gymnures, moles, shrew moles, desmans, solenodons, and shrews); fleas of tribe Spilopsyllini and of genera *Moeopsylla* (Pulicidae) and *Odontopsyllus* (Leptopsyllidae) parasitize on rabbits, hares, and pikas (Lagomorpha) only. Fleas of the genera *Uropsylla* and *Lycopsylla* (Lycopsyllidae) are mainly associated with marsupials (Marsupialia), genus *Chaetopsylla*, with carnivores (Carnivora), genera *Moeopsylla* and *Ancistropsylla*, with artiodactyls (Artiodactyla), genus *Neotunga*, with pangolins (Pholidota). In rodents (Rodenta), gerbils, jirds, and sand rats (subfamily Gerbillinae) relate the most closely with flea family Coptopsyllidae; representatives of genus *Calomyscus* (mouse-like hamsters of Cricetidae family), with flea genus *Phaenopsylla*; birch mice, jumping mice, and jerboas (Dipodidae family), with flea genera *Mesopsylla* and *Desertopsylla*. In addition, fleas of genus *Caenopsylla* parasitize many mammals exclusively on gundis, or comb rats (family Ctenodactylidae); fleas of genera *Foxella*, *Dactylopsylla*, and *Spicata*, on pocket gophers (Geomyidae family); fleas of the subgenus *Geoctenophthalmus* (genus *Ctenophthalmus*), on bamboo rats (Spalacidae family); and fleas of genus *Paryodontis*, on the Old-World porcupines (Hystricidae).

According to faunistic analysis, 78 oligoxenous flea species are known from several host species belonging to the same genus, which is 4% of the total species number in the order Siphonaptera. Mesoxenous fleas are represented by 234 species (13%) found on the hosts of several genera from the same family. Polyxenous fleas (259 species, or 15%) are found on the hosts from several families of the same order, and euryxenous fleas (609 species, or 34%), on the hosts belonging to different orders (Medvedev, 2002a, 2002b).

Oligoxenous parasites can occur on hosts from different taxonomic groups, but their association with hosts of a certain taxonomic group is a distinctive feature. This group of parasites includes, for example, fleas *Xenopsylla conformis* (Wagner, 1903) and *Nosopsyllus laeviceps* (Wagner, 1909), parasites of the gerbil genus *Meriones*, and the flea *Citellophilus tesquorum* (Wagner, 1898), a parasite of ground squirrels. According to our data, the flea *Xenopsylla conformis* is also found on a total of 62 host species belonging to 38 genera and 8 orders, including even such random ones as bats and birds, in addition to various gerbils of the genus *Meriones*. The flea *Nosopsyllus laeviceps* is found on a wide range of not only primary, but also secondary and accidental hosts (50 species belonging to 35 genera and 9 orders). The primary hosts of the flea *Citellophilus tesquorum* are ground squirrels of the genus *Spermophilus*. However, fleas of this species have been recorded on 22 species of mammals and birds belonging to 19 genera of 6 orders. Polyxenous species of fleas inhabit a wide range of hosts. Many of them are confined to a specific landscape, where they use various mammals leading a similar lifestyle as hosts. This group includes species of the genera *Ctenophthlamus*, *Rhadinopsylla*, *Frontopsylla*, and *Amphipsylla*.

Fleas have been found on the mammals (in 16 orders out of 20) and on the birds (21 orders out of 31). However, two host orders are of the greatest importance: Rodenta (70.3% of the host-parasite pairs in mammals) and Passeridae, or Old-World sparrows (55.2% of the host-parasite pairs in birds). The other mammal orders are characterized by less degree of host-parasite relationships with fleas: 9.5% in Carnivora, 6.5% in Eulipotyphla, 4.2% in Lagomorpha, and 3.7% in Chiroptera. An even more significant dominance of rodents and passerines as the main hosts of flea species is revealed by comparing the ratios of the number of specific / primary types of host-parasite pairs, making up 82% of their total number with rodents, and 66% with passerines.

On all continents, there is a predominant association of flea species with different groups of rodents. This is explained by the fact that rodents have the greatest taxonomic diversity, they lead a burrowing lifestyle, and different species and genera inhabit the same biotopes. However, in addition to rodents, other subdominant host groups can also be indicated for fleas of each zoogeographic region. In general, the main host species of fleas in the Nearctic are Arvicolinae and the New World – Cricetidae, Geomyidae, Heteromyidae, Eulipotyphla, and Lagomorpha; in the Neotropical region, these are Cricetidae of the New World, Caviomorpha, Didelphidae, and Caenolestidae (Marsupiales); in the African region, Muridae, Rhizomyini, Bathyergidae, Procaviidae, and Macroscelididae; in the Indo-Malayan region, Muridae, Sciuridae, carnivorous marsupials, Petauridae, Peroryctinae (New Guinean long-nosed bandicoots), and Pseudocheiridae (ring-tail possums); in the Australian region, carnivorous marsupials, Peramelidae (bandicoots), Phalangeridae (cuscuses, brushtail possums), Vombatidae (wombats), and Muridae (mice). In the Palearctic, the main rodent hosts of fleas are Arvicolinae and Gerbillinae, to a lesser extent, Cricetidae, as well as Lagomorpha and Eulipotyphla.

WORLD FAUNA OF ORDER SIPHONAPTERA

The fleas' distribution and the parasite-host relationships could have been affected significantly by the glaciation of a significant part of Eurasia and North America and the subsequent changes in their landscapes due to glacier regression, the glaciation of Antarctica, and aridization of most of Australia. The release of vast areas of Eurasia and North America from the glacier led to extensive species divergence in the families Hystrichopsyllidae, Ceratophyllidae, Leptopsyllidae, and Ischnopsyllidae. As a result, the diversity of the known flea fauna of the Palearctic turned out to be several times larger than the flea faunas of any other region.

The flea faunas of the Palearctic and Nearctic regions have the highest similarity index (*SI*) at the genera level (*SI* 22.3%). The flea fauna of the Nearctic is also close to that of the Neotropical region (*SI* 21.7%) and to the Indo-Malayan region (*SI* 17.4%). The similarity index between the Indo-Malayan and Afrotropical region is 11.7%, between the Indo-Malayan and Australian regions, 13.0%.

According to our classification, the infraorder Pulicomorpha unites five superfamilies and seven families. The modern distribution of taxa of the infraorder Pulicomorpha indicates the connections between the faunas of Africa and Asia, Africa and South America. The representatives of this infraorder are less closely tied to rodents than the representatives of the other three infraorders. We assume that the ancestral group of the infraorder Pulicomorpha existed in Africa. Probably, the fleas of the monotypic family Coptopsyllidae are now the closest to the common ancestor of this infraorder. From Africa through Europe, the ancestral taxa of the families Vermipsyllidae and Ancistropsyllidae penetrated into Asia. Modern representatives of the Holarctic family Vermipsyllidae (39 species belonging to 3 genera) parasitize on carnivores and ungulates, the East Asian-Indochinese family Ancistropsyllidae (3 species, 1 genus), on ungulates only. The tropical-subtropical family Pulicidae (156 species, 22 genera) and Neotropical-Holarctic family Tungidae (23 species, 4 genera) have a wide range of hosts. Family Pulicidae is most widespread in Africa, where its species have widely mastered various groups of animals: Procaviidae, Pedetidae, Rodenta, Lagomorpha, warthogs (genus *Phacochoerus*), and predators. In family Pulicidae, the fleas of genera *Echidnophaga* and *Xenopsylla* penetrated into Asia. Some species of the genus *Echidnophaga* have spread further to Australia, where 10 endemic species of this genus parasitize echidnas (Tachyglossidae), marsupials, and rodents. The connections between Africa and South America are evidenced by the distribution of fleas belonging to the family Tungidae. The genus *Neotunga* is represented in Africa, its representatives are parasites of pangolins (Pholidota). Two other genera, *Hectopsylla* and *Rhynchopsyllus*, are found in South America. The distribution of the genus *Tunga* attracts much attention, since the species of this genus are found both in South and North Americas, Japan, and China.

South American families Rhopalopsyllidae and Malacopsyllidae have a number of characteristics similar to those of the Pulicidae and Tungidae families. Most likely, the ancestors of these two families penetrated into South America together with hystricognaths (Caviomorpha) from Africa. Representatives of the predominantly neotropical family Rhopalopsyllidae (more than 120 species belonging to 14 genera) are parasites of Cricetidae (subfamily Hesperomiinae), Caviomorpha, anteaters and sloths (order Pilosa), armadillos (Cingulata), and birds (Aves). Family Malacopsyllidae (2 species, 2 genera) is tied to armadillos in the Patagonian subregion of the Neotropical region.

Taxa of the infraorders Ceratophyllomorpha, Hystrichopsyllomorpha, and Pygiopsyllomorpha have a Eurasian-American and American-Australian types of distribution; their ties with rodents are most developed. The infraorder Hystrichopsyllomorpha was separated by homoplasy characters that have although formed on a similar basis (Medvedev, 1995, 1998b). Three superfamilies were identified in this infraorder: Hystrichopsylloidea (Hystrichopsyllidae and Chimaeropsyllidae), Macropsylloidea (Macropsyllidae) and Stephanocircidoidea (Stephanocircidae). The family Hystrichopsyllidae is the central family of the infraorder, as accepted by Hopkins and Rothschild (Hopkins, Rothschild, 1962, 1966); it is one of the largest in the order (more than 610 species belonging to 10 subfamilies). The family Hystrichopsyllidae is currently considered as conditionally monophyletic until a comprehensive assessment of its morphological diversity is completed (Medvedev, 2006a, 2006b, 2007, 2008, 2010). Preliminary, the family Hystrichopsyllidae is brought closer to the African family Chimaeropsyllidae. It has a wide Holarctic-Afrotropical-Neotropical distribution, but quite patchy and uneven. In particular, family Hystrichopsyllidae is represented by only 16 species in the Indo-Malayan fauna and 2 species in the Australian fauna, while its Palearctic fauna includes more than 330 species from 19 genera, Nearctic fauna – 120 species from 25 genera, Afrotropical fauna – 84 species from 3 genera, and Neotropical fauna – 39 species from 12 genera. Representatives of the family Hystrichopsyllidae have mastered the widest range of hosts, including the species of 16 genera belonging to Eulipotyphla, 7 genera of marsupials, 65 genera of rodents (9 genera in Sciuridae, 37 in Cricetidae, and 19 in Muridae) and 5 genera of Carnivora. Fleas of the family Hystrichopsyllidae are most frequently observed on Cricetidae and Muridae, much less often, on Sciuridae; Eulipotyphla (families Soricidae and Talpidae) is the third largest host group in regard to the species number.

The absence of features, which help to distinguish clearly the family Hystrichopsyllidae, is probably explained by the fact that this family is paraphyletic. Along with large number of Holarctic genera, it includes certain taxa that are the representatives of the ancient flea fauna of the Southern Hemisphere. The family Hystrichopsyllidae had three main centers of taxonomic diversity (Medvedev, 2007). In addition, Australia could have been another hotspot. The number of tribes formed within the subfamily Hystrichopsyllinae and subfamily Doratopsyllinae, parasitizing Eulipotyphla, is associated with the most ancient South American (extra-Caribbean) biodiversity hotspot. Monotypic Afrotropical subfamilies Listropsyllinae and Dinopsyllinae, and genera *Palaeopsylla* and *Ctenophthalmus* (Ctenophthalminae) belong to the Afro-European biodiversity hotspot, subfamilies Neopsyllinae, Rhadinopsyllinae, Anomiopsyllinae, Stenoponiinae, and Liuopsyllinae, to North American-Asian biodiversity hotspot.

The infraorder Pygiopsyllomorpha comprises more than 170 species belonging to 37 genera in three families. Close relationships between the infraorder Pygiopsyllomorpha and the representatives of the family Hystrichopsyllidae have been confirmed by molecular analysis data (Zhu et al., 2015) According to the morphological analysis and the classification we proposed earlier (Medvedev, 1998b, 2024), the infraorder Pygiopsyllomorpha is represented by three separate families, but not subfamilies, as was previously believed (Dunnet, Mardon, 1974; Mardon, 1981). The infraorder Pygiopsyllomorpha exhibits extensive ties with marsupials. Many genera of this infraorder are confined to the Indo-Malayan region (26 out of 37 genera in total, or 62% of the species number). Most of them (22 genera) are representatives of the family Stivaliidae. At the same time, the largest part of the endemic genera (13 genera) is found exclusively in the Papuan subregion, in particular, in New Guinea. Some genera of the family Stivaliidae are presented in the fauna of South-East Asia and in Africa, where they parasitize mice and tree shrews. The family Pygiopsyllidae is more widely represented in Australia (7 genera out of 10 known), 4 genera of this family are also distributed in New Zealand.

The infraorder Ceratophyllomorpha is represented by one superfamily Ceratophylloidea, comprising four families (Xiphiopsyllidae, Ceratophyllidae, Leptopsyllidae, and Ischnopsyllidae).

The Xiphiopsyllidae family is represented by only one genus, *Xiphiopsylla*. The species of this genus are found in Muridae in East Africa (Tanzania, Kenya, and Uganda). Unfortunately, its representatives have not yet been studied by molecular genetic methods.

The family Ceratophyllidae comprises over 400 species belonging to 44 genera. Most species are the representatives of the Palearctic fauna (49% of the total number of species) and the Nearctic fauna (30%). In the Neotropical region, the species of this family contribute as 11% of total flea fauna, in the Indo-Malayan region, 7%, and in the Afrotropical region, 4%. In the family Ceratophyllidae, 96% of species found on rodents do not parasitize on birds (Traub et al., 1983). At the same time, 42% flea species were found on Sciuridae (including representatives of the tribe Marmotini) and 39% flea species, on Cricetidae. According to our data, fleas of 21 genera (out of 42) were found on species from 20 genera of the family Sciuridae. At the same time, this family is associated with 27 genera of Cricetidae (13 genera belonging to subfamily Hesperomiinae) and 11 genera of Muridae (Medvedev, 2009).

The Leptopsyllidae family comprises more than 240 species belonging to 30 genera. The family systematics has been described earlier (Medvedev, Kotti, 1992), with three subfamilies distinguished: monotypic subfamily Dolichopsyllinae and extensive subfamilies Paradoxopsyllinae and Leptopsyllinae. Most of the species of the family Leptopsyllidae belong to the tribes Leptopsyllini (68 species), Amphipsyllini (36 species), and Paradoxopsyllini (125 species). Fleas of genus *Dolichopsyllus*, identified as an independent subfamily, parasitize on the relict genus of mountain beavers (Aplodontidae family).

The fleas of the family Ischnopsyllidae parasitize exclusively on Chiroptera. This family comprises two subfamilies of unequal size and more than 120 species belonging to 20 genera. Representatives of the monotypic subfamily Thaumapsyllinae (3 species) parasitize Old World fruit bats (Pteropodidae) in the tropics of the Old World. The second subfamily, Ischnopsyllinae, contains 19 genera parasitizing Microchiroptera. The taxonomy and phylogeny of this group have been described in detail earlier (Medvedev, 1985). Later, the patterns of parasite-host relationships and geographic distribution of taxa of this family have been considered (Medvedev, 1989).

The disappearance of the Transantarctic Bridge between South America and Australia and the glaciation of Antarctica led to the disappearance of a significant part of the flea fauna of the Southern Hemisphere. Therefore, only the family Stephanocircidae remained from probably historically rich fauna, now represented by the Neotropical subfamily Craneopsyllinae and Australian subfamily Stephanocircinae. The family Macropsyllidae is also a fragment of the Australian paleofauna of fleas. In general, opposite to the Holarctic, families with a relatively small number of taxa are characteristic of the modern fauna of fleas of the Southern Hemisphere. For South America, these are the families Malacopsyllidae and Rhopalopsyllidae and subfamily Craneopsyllinae (Stephanocircidae), for Africa, families Xiphiopsyllidae and Chimaeropsyllidae, for Australia, families Macropsyllidae and Lycopsyllidae, and subfamily Stephanocircinae. At the same time, flea families Hystrichopsyllidae, Ceratophyllidae, and Leptopsyllidae, which are the most diverse both in terms of genera and species, are confined to the Northern Hemisphere, Eurasia, and North America. It should be noted that fleas of the Afrotropical, Neotropical and Australian regions are most likely to have head ctenidia, which were inherent in the ancestors of modern representatives of the order Siphonaptera (Medvedev, 2001). This allows us to assume that these regions have nowadays preserved elements of the ancient flea fauna the most.

CHARACTERISTICS OF FLEA FAUNAS OF VARIOUS ZOOGEOGRAPHIC REGIONS

PALEARCTIC REGION

Diversity and composition of flea fauna

The Palearctic flea fauna is the largest among the faunas of zoogeographic regions. According to our data, it includes 921 species and 594 subspecies, belonging to 96 genera from 10 families (Medvedev, 1998a). The ranges of 858 species (94%) from 43 genera are intra-Palearctic. Only 5% of species are characterized by wide ranges extending beyond the Palearctic region, and only 1% of species can be attributed to that with a cosmopolitan type of distribution. However, the Palearctic fauna has 53 genera in common with other zoogeographic regions.

While stating the fact of the high fauna diversity in the Palearctic compared to the fauna of other zoogeographic regions, one should take into account the fact that it has been studied most actively not only in the past, but also continues to be studied at the present time by specialists, mostly from the PRC.

Most species of the Palaearctic fauna (83%) belong to 3 families – Hystrichopsyllidae, Ceratophyllidae, and Leptopsyllidae, – which are represented by a rich and diverse fauna here. In the family Hystrichopsyllidae, Palaearctic endemic genera make up more than 50%, in Ceratophyllidae, 46%, in Leptopsyllidae, 65%. The Palaearctic fauna also includes the species of six other flea families: Ischnopsyllidae, Pulicidae, Vermipsyllidae, Coptopsyllidae, Stivaliidae, and Tungidae.

The largest genera of the family, such as *Leptopsylla*, *Peromyscopsylla*, *Pectinoctenus* (tribe Leptopsyllini), and *Ctenophyllus*, *Frontopsylla*, *Ophthalmopsylla*, *Paradoxopsyllus* (tribe Paradoxopsyllini) are represented mostly in the Palearctic region. Here, the species of the monotypic tribe Amphipsyllini and of tribe Paradoxopsyllini are confined to the central and eastern parts, and the tribe Leptopsyllini, to the forest zone of the western and central parts of the Palearctic region.

Endemic species make up almost 94% of the fauna of the Palearctic. The share of endemic genera in the fauna of the Palearctic (compared to other regions) is relatively small, making up 45% of their total number. The monotypic family Coptopsyllidae (19 species) is the only family endemic to this region. The greatest number of endemic species in this region is confined to the East-Asian subregion. They make up 64% of the total number, or 72 species. There are 55 species in the fauna of the Central Asian subregion, and 68 species are known in the fauna of the European-Siberian subregion. In the Mediterranean subregion, 25 species are distributed, in the Sahara-Arabian subregion, 10 species. In the Palearctic region, the largest number of genera (18 genera, four of them are endemic) is also distributed in the East Asian subregion.

Family Hystrichopsyllidae (infraorder Hystrichopsyllomorpha) and families Ceratophyllidae, Leptopsyllidae, and Ischnopsyllidae (infraorder Ceratophyllomorpha) are mostly distributed within the Central-East Asian region. Two other families of the Palaearctic fauna (Pulicidae and Coptopsyllidae, belonging to infraorder Pulicomorpha) have a different type of distribution. The formation of the faunas of these two groups of families followed significantly different paths. The family Pulicidae is characteristic for the fauna of the tropical and subtropical zones. It is characterized by the absence of endemic species in the East Asian subregion and by their small number in the European-Siberian and Central Asian subregions. At the same time, the highest share of endemics of the family Pulicidae is noted in the Irano-Turanian subregion, followed by the representatives found in the Mediterranean and Saharo-Arabian subregion.

The families Vermipsyllidae and Coptopsyllidae are confined to the Northern Hemisphere. In particular, the family Coptopsyllidae is characterized by southern Palaearctic, or European-Western Mediterranean-Saharo-Arabian-Irano-Turanian ranges. In the Mediterranean and in the Saharo-Arabian subregions, all species of the family Coptopsyllidae are endemic. A significant number of endemics of this family are noted in the fauna of the Irano-Turanian subregion. In the Central Asian subregion, one non-endemic species is widespread. In the fauna of Russia, the family Coptopsyllidae is represented in the northwestern Caspian region by only one species (*Coptopsylla bairamaliensis*). This species is a winter parasite of gerbils; generally, it has the Western Palaearctic range. The family Vermipsyllidae (39 species, 3 genera) is characterized by a Holarctic range. Among its representatives, there are species with a “stationary” and “semi-stationary” type of parasitism. The hosts are predators and ungulates.

The ratio of the total number of species to endemic species is an interesting indicator for the Palearctic subregions. In the families Ceratophyllidae and Pulicidae, dynamics of this index is directly proportional in different subregions. However, there is a negative correlation between the total number of species and the percentage of endemic species in other families. Thus, the total number of species in the family Hystrichopsyllidae is less in the Irano-Turanian subregion than in the Central Asian and Mediterranean subregions, while the share of endemic species in the Irano-Turanian subregion is higher than in the Central Asian subregion, but lower than in the Mediterranean subregion. In the family Leptopsyllidae, the fauna of the Central Asian subregion may be an example of such a negative correlation, when the maximum number of species for this family is observed, but the share of endemic species among them (46%) is much lower than in the East Asian subregion (72%) and somewhat lower than in the Irano-Turanian one (48%). The family Ischnopsyllidae has such a negative correlation in the East Asian, Central Asian, and Irano-Turanian subregions. In one of these subregions (Central Asian), the highest share of endemic species is noted (57%), while the total number of species here is one of the lowest in the Palearctic.

Host-parasite relationships

The main hosts of fleas in the fauna of Russia and the entire Palearctic are various species of rodents (mice, voles, gerbils; to a lesser extent, hamsters). The other mammalian orders, serving as flea hosts, are Lagomorpha and Eulipotyphla. In Russia, a number of flea species parasitize on birds, and the most important hosts are the representatives of the family Passeriformes.

Family Muridae. This mammalian family has about 150 genera. Its range covers the steppes and semi-deserts of Africa, Central and Western Asia. Gerbils settle in burrows, which can be complex underground structures down to 3-m deep. In total, 243 species of fleas have been found on 53 Gerbillinae species out of 95 in total. The fleas of the monotypic family Coptopsyllidae are tied to Gerbillinae the most. Species of genus *Coptopsylla* parasitize on gerbil species of genera *Gerbillus*, *Meriones*, *Psammomys*, and *Rhombomys*. About 16 species of the large genus *Xenopsylla* and species *Synosternus cleopatrae* (Rothschild, 1903) (family Pulicidae) are also tied closely to the gerbils. In the Palearctic region, they parasitize on the gerbils of genera *Rhombomys* and *Meriones*. Nineteen species of the subgenus *Gerbillophilus* (genus *Nosopsyllus*, Ceratophyllidae), distributed from Algeria to Mongolia, are tied with gerbils of genera *Meriones*, *Rhombomys*, and *Gerbillus*. Flea genus *Stenoponia* (*S. tripectinata* (Tiraboschi, 1902), *S. vlasovi* Ioff et Tiflov, 1934, and *S. conspecta* Wagner, 1926) and genus *Rhadinopsylla* (*Rh. cedestis* Rothschild, 1913, *Rh. masculana* Jordan et Rothschild, 1912, and *Rh. ucrainica* Wagner et Argyropulo, 1934) are other representatives parasitizing on gerbils.

Family Murinae. There are 41 Muridae species recorded as flea hosts in the East Asian subregion of the Palearctic, 11 species of them are noted as primary hosts. In other subregions of the Palearctic, fleas are found on 25–29 Muridae species (4–23 species are their primary hosts), and in the Saharo-Arabian subregion, 19 Muridae species. The largest number of primary ties are noted between flea species and the species of widespread Muridae genera, such as *Rattus*, *Apodemus*, and *Mus*. In the Irano-Turanian and East Asian subregions, species of genera *Nesokia* and Millardia are noted as the main hosts, in the Mediterranean and Saharo-Arabian subregions, genus Acomys. The Palearctic genus *Apodemus* (wood mice and field mice) hosts seven flea species. Large Japanese field mouse (*A. speciosus* (Temminck, 1845)) is one of the main hosts of a number of Japanese flea species (*Rhadinopsylla attenuata* Jameson et Sakaguti, 1954, *Stenoponia tokudai* Sakaguti et Jameson, 1959, and *Atyphloceras shogakii* Jameson et Sakaguti, 1954). Wood mouse, *Apodemus sylvaticus* (L., 1758), has the most extensive parasitic fauna of fleas, among which the species of the genus *Ctenophthalmus* predominate. The wood mouse is a constant host for a number of flea species from genera *Rhadinopsylla*, *Nosopsyllus*, and *Leptopsylla*.

In the Palearctic, fleas *Nosopsyllus punjabensis* (Jordan et Rothschild, 1921) and *N. simla* (Jordan et Rothschild, 1921) must be also noted here as the parasites of Turkestan rat, *Rattus rattoidesi* (Hodgson, 1845), is the junior synonym of *R. pyctoris* (Hodgson, 1845).

Natural plague foci and vectors in the Palearctic region

Within the Palearctic region, natural foci of plague have been found in 25 countries. In most countries, over the past quarter of a century, human morbidity has not been observed, or it has manifested itself as isolated cases. Mongolia and China (PRC) are the only countries in the region, where infection and death of people are registered almost annually. In the Russian Federation, since the beginning of the new millennium, 3 cases of human plague have been registered, all in the Altai Republic in 2014–2016. It is noted that since 2012, there has been an abnormal activation of natural plague foci in the Central Asian region (the Great Lakes Depression of Mongolia and adjacent territories of Russia and China, where the hypothetical center of origin of the plague microbe is probably located), which can lead to the most serious epidemiological consequences (Verzhutsky, 2018; Balahonov et al., 2019).

In the Palearctic region, 129 separate natural foci of plague have been described (Akiev, 1974; Varshavsky, Kazakevich, 1984; Kozlov, Sultanov, 2000; The Atlas…, 2000; Karimova, Neronov, 2007; Bazanova, Verzhutsky, 2009; Kutyrev, Popova, 2016; Shahraki et al., 2016; Verzhutsky, Ad'yasuren, 2019; Popova, Kutyrev, 2022; Verzhutsky, 2022; Medvedev et al., 2023a, 2023b). Of these, two foci are located in northern India and Nepal, six foci, in North Africa, 11 foci, in the Middle East, 45 foci are located within the former USSR, 65 foci are found in Mongolia and the PRC (except the most southern areas). Among the presented foci, 63 foci belong to marmot type (including mix foci, with marmot and other main carriers), 46 foci, to gerbil type (also including mix foci), 11 foci, to vole type, 10 foci, to ground squirrel type and 2 foci are associated with pikas (Ochotona).

In these foci, natural plague infection was detected in 150 flea species, which is 57.0% of the 263 flea species found infected with this pathogen in the world. Of these, 49 species belong to the Leptopsyllidae family, 42 species, to the Hystrichopsyllidae family, 36 species, to the Ceratophillidae family. Fifteen species of plague-infected fleas were the representatives of the Pulicidae family. In addition, plague-infected fleas were found in the families Hystrichopsyllidae (5 species), Coptopsyllidae (4 species), and Vermipsyllidae (1 species). However, the representatives of the families Ischnopsyllidae, Stivaliidae, and Tungidae were not infected with the plague pathogen in the Palearctic region. The first family is entirely related to bats and, due to the ecological characteristics of their hosts, cannot have any significant contacts with the plague pathogen. The two remaining families are territorially localized, respectively, in the New World and the Indo-Malayan region, entering only a single species within the Palearctic.

A somewhat different picture emerges if we take only those species of fleas for which the role of the main vectors of plague in certain foci of the Palearctic has been proven (or is assumed). Most species of fleas, which are found infected with the plague microbe in nature, receive the pathogen during bloodsucking, but since they are not able to preserve and transmit this microbe, they get rid of it quite quickly. On the contrary, the main vectors are characterized by a high degree of adaptation to interaction with the pathogen, allowing fleas to store the pathogen for a long time in their body and to transmit it effectively to warm-blooded animals, ensuring periodic circulation and survival of the microorganism in certain areas. In total, 37 species of fleas considered as the main vectors of plague in this area. Of these, 11 species belong to the family Ceratophillidae, 9 species, to the family Pulicidae, 8 species, to the family Leptopsyllidae, 7 species, to the family Hystrichopsyllidae, and one species, to the family Hystrichopsyllidae.

Among the 37 main vector species, 13 ones perform this function in only one or two foci out of 129 foci of the Palearctic. All these species are part of the multi-vector foci pools, so none of them is the only main vector of infection anywhere. The opposite pattern is observed at this territory with only one species, the marmot's flea *Oropsylla silantiewi* (Wagner, 1898). This species is among the main vectors of plague in 63 natural foci, while in 39 foci it is the only main vector, ensuring the circulation and storage of the infectious agent with no participation of other flea species. *Xenopsylla conformis* is the species closest in epizootic significance with respect to the plague pathogen in the Palearctic area (17 foci, all multi-vector), followed by *Xenopsylla skrjabini* Ioff, 1930 (15 foci, in 2 foci the species is the only main vector), *Nosopsyllus laeviceps* (15 multi-vector foci), and *Citellophilus tesquorum* (14 foci, 4 mono-vector).

This pattern reflects well the most probable genesis of the plague microbe, primarily associated with habitation in fleas *Oropsylla silantiewi*. In other foci of marmot type, mono-vector formations with any other main vector are not presented elsewhere. Such species as *Callopsylla dolabris* (Jordan et Rothschild, 1911) (7 foci), *Rhadinopsylla li* Argyropulo, 1941 (5 foci) or *Citellophilus lebedewi* (Wagner, 1933) (3 foci), which are presented in the pools of main vectors of marmot type, are not able to ensure the epizootic process and the preservation of the pathogen on their own.

NEARCTIC REGION

Flea fauna diversity

In the Nearctic region, there are 257 endemic species; 155 species (60%) of these have West American ranges. The other two subregions of the Nearctic have significantly less endemics: 25 species (10%) in the Canadian subregion and 19 species (7%) in the Caribbean subregion. The highest similarity is found between the Canadian and West American subregions (28 species in common). West and East American subregions have 14 species in common, Canadian and East American subregions, 9 species. So, the flea fauna of the West American (mainly mountainous) region dominates in the Nearctic. The greatest number of endemic genera and species is noted here. The flea fauna of the Canadian subregion has the signs of influence of the Palearctic fauna. The flea fauna of the East American subregion is the poorest. There is some similarity between the flea faunas of Canadian and East American subregions; it refers mostly to the distribution of the species belonging to the families Hystrichopsyllidae, Ceratophyllidae, and Leptopsyllidae. The similarity between the West and East American subregions is preconditioned by the distribution of species belonging to Hystrichopsyllidae and Ceratophyllidae.

Parasite-host relationships

The representatives of three orders Rodentia, Eulipotyphla (formerly, insectivores), and Lagomorpha, are the main host groups for endemic flea species of the Nearctic region. A significant number of flea species are also found on Carnivora. Rodents as hosts account for more than 72% of the total number of parasite-host pairs; specific and primary relationships in this group are even larger (91%). The representatives of Nearctic flea families Ceratophyllidae, Hystrichopsyllidae, and Leptopsyllidae are associated with rodents most closely. In turn, Cricetidae are the main hosts for these flea species, represented mainly by meadow voles (genus *Microtus*), deer mice (*Peromyscus*), and pack rat (*Neotoma*), common in North and Central America. Fleas of family Ceratophyllidae, which have the largest number of parasite-host relationships with Cricetidae, parasitize both rodent genera listed above and the species from genera *Baiomys*, *Onychomys*, *Sigmodon*, and *Clethrionomys*. Deer mice have tight relationships with the species of the family Ceratophyllidae, in particular, with American genera *Aetheca*, *Jellisonia*, *Kohlsia*, *Malaraeus*, *Opisodasys*, *Orchopeas*, *Pleochaetis*, and *Plusaetis*, which form the endemic core of the Nearctic flea fauna. Holarctic flea genera *Amalareus* and *Megabothris* are associated mainly with meadow voles in the Nearctic region.

Pack rats are the main hosts of Nearctic flea endemics from the family Hystrichopsyllidae (genera *Anomiopsyllus*, *Megathroglossus*, and *Stenistomera*) and Ceratophyllidae (genera *Amaradix*, *Orchopeas* (also known from the Caribbean subregion), and *Traubella*). In the Nearctic, Holarctic species of meadow voles are closely related to the Holarctic-Caribbean genera *Hystrichopsylla* and *Atyphloceras* (family Hystrichopsyllidae) and Holarctic genera *Peromyscopsylla* and *Amphipsylla* (family Leptopsyllidae).

Sciuridae are the second most important host group for Nearctic flea species after Cricetidae. Among Sciuridae, the greatest number of parasite-host relationships are registered between ground squirrels of the North Holarctic genus *Spermophilus* and the fleas of the families Ceratophyllidae and Hystrichopsyllidae. Ceratophyllidae family is represented by the Nearctic genus *Thrassis* and the Holarctic genus *Oropsylla*, Hystrichopsyllidae family, by the Holarctic-Indo-Malayan genus *Neopsylla* and the Holarctic genus *Rhadinopsylla*. In the Nearctic, tree squirrels (genus *Sciurus*) are the primary hosts of fleas of the North American genus *Opisodasys* and the Nearctic-Caribbean genus *Orchopeas*. Marmots (genus *Marmota*) are the primary hosts of fleas of the North American genus *Thrassis* and the Holarctic genus *Oropsylla*. The North Holarctic chipmunks (genus *Tamias*) are closely related to fleas of the Nearctic genus *Eumolpianus* and the widespread genus *Ceratophyllus*.

Eulipotyphla are related most closely to the flea species belonging to the family Hystrichopsyllidae. Widespread in Eurasia and Africa, shrews (*Sorex*) are the main hosts of the Asian-Nearctic genus *Nearctopsylla* and the Holarctic-Caribbean genus *Corrodopsylla* in the Nearctic. Fleas of genus *Nearctopsylla* are also known for the West American moles (*Scapanus*), fleas of genus *Corrodopsylla*, for the Nearctic species of American short-tailed shrews (*Blarina*) and small-eared shrews (*Cryptotis*), distributed mainly in the Caribbean subregion. Both the fleas of the genus *Corypsylla* and their main hosts, moles of the genera *Scapanus* and *Neurotrichus*, are Western American species.

South American grass mice (genus *Akodon*), groove-toothed New World harvest mice (genus *Reithrodontomys*), hamsters of the tribe Oryzomyini, and some other hamster species are hosts to the fleas of the Neotropical genera *Agastopsylla*, *Chiliopsylla*, *Neotyphloceras*, *Ctenoparia*, and *Adoratopsylla* (Hystrichopsyllidae). Other genera of fleas from the same family, but with wider ranges, are associated with other groups of Cricetidae. The South American flea species of the genera *Ctenophthalmus* and *Hystrichopsylla* are known for meadow voles, widespread in other areas. These two flea genera are found on the New World species of Cricetidae: deer mice (*Peromyscus*) and groove-toothed New World harvest mice (*Reithrodontomys*), which have Nearctic-Neotropical ranges.

Natural plague foci and vectors of infection in the Nearctic

In the Nearctic region, enzootic plague areas are found within the borders of all three countries located there: the United States of America, Canada, and Mexico. In Canada, areas dangerous for plague outbreaks are located in the south of the country; however, no incidence has been recorded since 1939. On the contrary, natural foci in Mexico are localized near the northern borders of the state; there have also been no reports of plague there since the middle of the XX century. In the USA, annual outbreaks of plague in humans are observed; on average, seven cases are registered annually since the year of 2000. Most cases are reported in the southern states of New Mexico, Colorado, Utah, Arizona, and California (Dubyanskiy, Yeszhanov, 2016; Rasprostranenie…, 2022; Plague..., 2024).

They assume there are approximately 36 separate natural plague foci on the North American continent: 3 foci each in Mexico and Canada and about 30 foci in the USA (Medvedev et al., 2023b). A more in-depth analysis of epizootic and epidemic manifestations in the USA (Maher et al., 2010; Abbot, Rock, 2012; Walsh, Haseeb, 2015; Richgels et al., 2016; Bevins et al., 2021) allows us to identify 71 areas with stable autonomous circulation of the plague pathogen in 17 states, which can be conditionally considered independent natural foci of this infection.

The spread of natural plague foci in the United States was limited to the 103rd meridian to the east. Recently, as serological and molecular genetic methods are given wide use, new areas with the presence of the plague pathogen are sporadically discovered at the territories located to the east of previously known (Walsh, Haseeb, 2015; Mize, Britten, 2016; Bevins et al., 2021).

Most of the natural foci in North America are associated with various species of ground squirrels, often in combination with prairie dogs (*Cynomys*). In the south, prairie dogs and pack rats *Neotoma* act as the main hosts in a significant number of foci. Marmots, voles, steppe lemmings (genus *Lagurus*), chipmunks (subtribe Tamiina), kangaroo rats, kangaroo mice, pocket mice, and spiny pocket mice (Heteromyidae), are involved in the epizootic process; quite often, representatives of cats (Felidae) are also participated in epizooties.

In North America, 59 species of fleas are registered to be infected naturally with plague microbe. Among them, absolute dominants are representatives of the Ceratophillidae family (36 species), followed by the families Hystrichopsyllidae (15 species) and Pulicidae (7 species). In addition to listed above, infection with the plague pathogen has been noted in only one species *Peromyscopsylla hesperomys* (Baker, 1904) from the family Leptopsyllidae. Although Palearctic and Nearctic regions are generally close in regard to their faunas, the differences in the quantity and qualitative composition of flea species involved in plague epizootics are quite pronounced. In the Palearctic, Leptopsyllidae is the dominant family (49 species are noted to be infected), followed by family Hystrichopsyllidae (42 species). Family Ceratophillidae (36 species), which occupies the first place in the New World, has only the third one in the Palearctic.

Only 15 flea species out of the 59 ones, found infected with plague in North America, can be considered as the main hosts of plague. Among them, representatives of the family Ceratophillidae dominate absolutely (13 species) with a small contribution from the family Pulicidae (2 species).

The flea *Oropsylla hirsuta* (Baker, 1895) is the most active primary vector in North America. This species is the main vector in the plague pathogen circulation in 36 natural foci located in 12 states: Montana, North Dakota, South Dakota, Wyoming, Nebraska, Utah, Colorado, Kansas, Oklahoma, Arizona, New Mexico, and Texas. It should be noted that *O. hirsuta* acts as one of the main hosts in all these foci, but in none of them it ensures the plague outbreak by its own. This phenomenon is due to the fact that all specific hosts of this flea, prairie dogs of genus *Cynomys*, are species highly susceptible to plague infection. When exposed to the pathogen, nearly all prairie dogs in the settlements die, and the subsequent pathogen “survival” is ensured by the species that are less sensitive to the plague microbe, or having a highly expressed polymorphism in sensitivity. In this region, the main carriers are ground squirrels, as the most common species in this area.

The flea *Oropsylla montana* (Baker, 1895) (invalid name *Diamanus montanus*) is the second most important species for ensuring the stability of plague enzootics in the northern part of the Western Hemisphere. It is involved in the circulation and storage of the plague pathogen in 33 foci, including 8 foci where it performs this role by its own, i.e., without significant participation of other flea species. *O. montana* serves as the main plague vector in 10 states of the country: Washington, Oregon, Idaho, California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas. As found experimentally by Valentin Vashchenok (1984), this species belongs to the group of active plague vectors only at the air temperature of 18–23°C; at 8°C, no transmission of infection is observed. Later, on the contrary, vast study proved that the effectiveness of *O. montana* as a plague vector was much higher at low temperatures (6°C), than at 10, 15 and 23°C (Williams et al., 2013).

The flea *Oropsylla idahoensis* (Baker, 1904) is the third most common plague vector in the region (21 natural foci; it is the only main host in two of them). Geographically, this applies to seven states: Washington, Oregon, Idaho, Montana, Nevada, Colorado, and New Mexico. Here, Columbian ground squirrel *Spermophilus columbianus* (Ord, 1815), Belding's ground squirrel *S. beldingi* Merriam, 1888, and golden-mantled ground squirrel Callospermophilus lateralis (Say, 1823) are the main hosts for *O. idahoensis* (Baker, 1904).

In the United States, the fourth most important plague vector is *Oropsylla tuberculata* (Baker, 1904), considered the main infection vector in 19 foci. These foci are located within seven states: Idaho, Montana, Nevada, Utah, Colorado, Arizona, and New Mexico. The Belding's ground squirrel *Spermophilus belding*i, Richardson's ground squirrel *Urocitellus richardsonii* (Sabine, 1822), thirteen-lined ground squirrel *Ictidomys tridecimlineatus* (Mitchill, 1821), and Gunnison's prairie dog *Cynomys gunnisoni* (Baird, 1855) are the main hosts for this flea species.

The flea *Oropsylla bruneri* (Baker, 1895) is the next most important flea species providing plague circulation in the United States. It parasitizes on thirteen-lined ground squirrel *Ictidomys tridecimlineatus* in the northern part of its range (North and South Dakotas, Wyoming, Nebraska) within 12 natural plague foci, where this species is one of the main vectors. In all these foci, thirteen-lined ground squirrel is one of the main hosts, in six foci, it is the only one.

The next important flea species is *Thrassis acamantis* (Rothschild, 1905), a parasite of yellow-bellied marmot (*Marmota flaviventris* (Audubon et Bachman, 1841)), found in seven natural foci in three states of the USA (Idaho, Montana, Wyoming) and in Canada (British Columbia). Some researchers believe that the participation of marmots in the plague enzootic in North America is insignificant, so they can be considered at best only secondary hosts (Rall', 1958; Popova, Kutyrev, 2022). However, it should be taken into account that the local population density of yellow-bellied marmot is quite large in some areas of the northwestern United States and southwestern Canada. Active natural foci of plague are located there, according to available data. Taking into account Th. acamanthis is considered an active host of the infection (Vashchenok, 1984), we tentatively leave this flea species in the list of the main plague vectors in North America.

It is necessary to mention also several flea species that participate in the circulation of the plague pathogen in 5 or 6 natural foci of this continent. *Thrassis fotos* (Jordan, 1925) and *Th. bacchi* (Rothschild, 1905) are known as active plague vectors, parasitizing thirteen-lined ground squirrel *Ictidomys tridecimlineatus* in the central (Kansas, Oklahoma) and southern (Arizona, New Mexico, Texas) parts of its range, respectively. This group also includes *Oropsylla labis* (Jordan et Rothschild, 1922) parasitizing mainly on Richardson's ground squirrel *Urocitellus richardsonii* (Montana, Nevada, Utah); two flea species *Orchopeas neotomae* (Augustson, 1943) and *O. sexdentatus* (Baker, 1904), associated with pack rats *Neotoma* (Arizona, New Mexico, Texas, Northern Mexico); and *Hoplopsyllus anomalus*

(Baker, 1904), a parasite of California ground squirrel *Otospermophilus beecheyi* (Richardson, 1829) in the northern part of its range (Oregon). Also, Thrassis pandorae Jellison, 1937 and Th. francisi (C.Fox, 1927) have been reported as the primary vectors of plague parasitizing on the Uinta ground squirrel *Urocitellus armatus* (Kennicott, 1863) in two natural foci in the mountains of Idaho and Wyoming.

Regard must be also paid to possible existence of natural foci of plague associated with voles, hamsters, and steppe lemmings in North America, included in a recent summary of plague foci around the world as the main hosts of infection in this region (Popova, Kutyrev, 2022). Thus, a special study, performed in northeastern California between 1970 and 1997 at 10 stationary points, has showed that California vole (*Microtus californicus* (Peale, 1848)), chipmunks, tree squirrels, hamsters, and other small mammal species are involved actively in plague epizootics (Smith et al., 2010). However, according to the data presented, widespread California ground squirrel plays the main role in maintaining the enzootic on this territory. Possible existence of an independent plague focus / foci associated with any Muridae and / or Cricetidae in California, look dubious. For example, California vole is infected very rarely with plague in experiments (Nelson, 1980). Even given the flea *Malaraeus telchinus* (Rothschild, 1905) is its mass parasite, it is still ineffective vector (Vashchenok, 1984). We assume that this parasite-host pair cannot participate significantly in maintaining the epizootic process here. Similar pattern is true for the other species of small Muridae and / or Cricetidae of this region.

In Canada, known plague enzootic areas are located in the southern provinces (British Columbia and Saskatchewan) near the border with the United States of America. In Alberta, the plague focus is located at a considerable distance from both other plague foci in Canada and from the areas with recorded epizootic activity in the adjacent USA. The main hosts and transmitters of plague are Richardson's ground squirrel (*Urocitellus richardsonii* (Sabine, 1822)) and the flea *Oropsylla idahoensis* (Baker, 1904) in Alberta, Richardson's ground squirrel and black-tailed prairie dog *Cynomys ludovicanus* (Ord, 1815) and fleas *Oropsylla tuberculata* and *O. hirsuta* in Saskatchewan, yellow-bellied marmot (*Marmota flaviventris* (Audubon et Bachman, 1841)) and the flea *Thrassis acamantis* (Rothschild, 1905) in British Columbia (Gibbons, Humphreys, 1941; Plague..., 1963; Antonation et al., 2014; Liccioli et al., 2020; Popova, Kutyrev, 2022).

The plague enzootic territory is also known in the northern part of Mexico (the vicinity of the Sonara and Northern Mesa deserts). There are at least three separate natural plague foci, and Mexican prairie dog (*Cynomys mexicanus* Merriam, 1892) is the main host in all of them. In some areas, pack rats *Neotoma* and some other representatives of the local fauna of small mammals takes part in the epizootic process as secondary hosts. In Mexico, prairie dogs are considered to be the main vectors of flea *Oropsylla hirsuta* (Baker, 1895) and of the common multi-host species *Pulex simulans* Baker, 1895 (Eskey, Haas, 1940; Varela, Vasquez, 1954; Gage, Kosoy, 2005; Popova, Kutyrev, 2022). Attempts to identify plague epizootics among the penetrating black-tailed prairie dog were yet unsuccessful (Zapata-Waldes et al., 2018).

NEOTROPICAL REGION

Flea fauna diversity

In the Neotropical region, most of flea species are characterized by the ranges confined to a certain degree to the Central and South American Andes. A total of 105 species are known from the Patagonian subregion (including 82 endemic species), 102 species (71) from the Caribbean subregion, 84 species (56) from the Andean subregion, 36 species (14) from the Brazilian subregion, and 27 species (8) from the Amazon subregion. Low flea diversity of the Antilles subregion is noteworthy, with only 3 species of fleas known in its fauna. The faunas of the Amazon and Brazilian subregions are related most closely, having 12 species in common that are characterized by seven range types. The faunas of the Andean and Patagonian subregions are also related quite closely (13 species in common; 5 range types). The flea faunas of other subregions are characterized by 3 to 5 range types in common.

The fauna of the Neotropical region is represented by 9 families of fleas, which are distributed differently in subregions. Fleas of the families Ceratophyllidae and Hystrichopsylldae have the most diverse fauna in the Palearctic and Nearctic; they are also the most numerous in the Caribbean subregion. In the faunas of other subregions of the Neotropical region, the number of species and genera of these two families decreases southwards. However, at the same time, the family Hystrichopsyllidae is represented in the Patagonian subregion by two endemic genera. The most characteristic species of the Neotropical region are the families Rhopalopsyllidae and Stephanocircidae. In the family Rhopalopsyllidae, the number of species and genera increases noticeably to the south, reaching its maximum in the Patagonian subregion. In general, most species of this family relate to the Andean and Patagonian subregions. The family Tungidae has a similar distribution; it is also represented most widely in the Brazilian subregion. Finally, flea species of the family Malacopsyllidae are distributed in Patagonia only. It can be concluded that the number of taxa, which are characteristic of the Neotropical region, increases generally to the south.

In the fauna of the Neotropical region, the greatest number of species (23) are found in the Caribbean subregion, while in other subregions their number is 3-4 times smaller. This probably indicates a late penetration of most genera of the family into this region. This was probably associated with the migration of hamsters of the subfamily Hesperomiinae, which penetrated there in the Pliocene (Simpson, 1980).

Flea fauna of the family Hystrichopsyllidae is unique in the Neotropical region. It is characterized by a significant number of small endemic tribes. The distribution of species-rich genera of the family in this region is limited to the northern part. It can be assumed that the long isolation of the Neotropical and Australian regions contributed to the preservation of representatives of the ancient flea fauna here. Phylogenetic relationships of these taxa with the main taxa of the family Hystrichopsyllidae are unclear. Monotypic tribes of the family Hystrichopsyllidae may represent the remains of largely extinct taxa of subfamily or family rank that were once widespread in South America and Australia. If these groups had actually existed and were known to us, the features of their structure would probably have allowed us to reconstruct the missing links that confirm the integrity of the family Hystrichopsyllidae s.l. or, on the contrary, allowing us to conclude on its paraphyletic nature.

Parasite-host relationships

Similar to the Nearctic, rodents are the dominant host group for fleas in the Neotropical region, providing 79% of all types of relationships and 95% of the total number of specific and basic relationships. Marsupials account for 7% of the types of parasite-host relationships with fleas in the Neotropical region. Among rodents, the greatest number of parasite-host relationships with fleas is found in Cricetidae (72% of the total number). The New World hystricognaths (Caviomorpha) are another main group of flea hosts in this region (18%). Flea species from 9 families have been found on them.

In the Neotropical region, Cricetidae are represented mainly by the subfamily Sigmodontinae. The species of this subfamily are closely related to the flea family Rhopalopsyllidae, including such large genera as *Polygenis*, *Tetrapsyllus*, and *Ectinorus*.

Various species of akodons (genus *Akodon*) serve as the host for these flea genera. Among the other 24 genera of Cricetidae of the New World, rice rats (*Oryzomys*), Andean mice (*Thomasomys*), and some others are the hosts for the fleas of the family Rhopalopsyllidae.

Akodons, rice rats, and other cricetids are hosts for the Neotropical flea genera *Agastopsylla*, *Chiliopsylla*, *Neotyphloceras*, *Ctenoparia*, and *Adoratopsylla* (Hystrichopsyllidae). Other flea genera from the same family, but with wider ranges, are associated with other groups of Cricetidae. For example, South American species of the genera *Ctenophthalmus* and *Hystrichopsylla* are known from meadow voles that are widespread in other areas. These flea genera are found also on the New World Cricetidae, such as deer mice (*Peromyscus*) and groove-toothed New World harvest mice (*Reithrodontomys*), which have Nearctic-Neotropical ranges.

The Neotropical flea family Ceratophyllidae has a relatively small number of types of relationships with Cricetidae. However, among these types, the highest percentage (57%) of basic and specific relationships are due to the fleas of the Caribbean genus *Baculomeris* parasitizing on Cricetidae. In addition, these are flea species of the West American-Neotropical genera *Jellisonia*, *Kohlsia*, *Pleochaetis*, and *Plusaetis*, parasitizing on rice mice (*Oryzomys*), deer mice (*Peromyscus*), groove-toothed New World harvest mice (*Reithrodontomys*), and singing mice (*Scotinomys*).

Neotropical flea species of the family Stephanocircidae also parasitize on the New World cricetids, in particular, on akodons (*Akodon*), as well as on mice, rats, and hamsters of genera *Thomasomys*, *Bolomys*, *Oxymycterus*, *Microryzomys*, *Irenomys*, etc. (35 genera in total).

Among the New World hystricognaths (Caviomorpha), cavies (Caviidae), tuco-tuco (Ctenomyidae), and octodontids (Octodontidae) have the largest number of relationships with flea species. Cavies are closely related to four flea genera of the family Rhopalopsyllidae (*Tiamastus*, *Delostichus*, *Eritranius*, and *Polygenis*). The main hosts of these fleas are cavies (*Galea*), mountain cavies (*Microcavia*), rock cavies (*Kerodon*), and true guinea pigs (*Cavia*). Similar genera serve as the hosts for the fleas of the genus *Hectopsylla* (family Tungidae).

The family Ctenomyidae is represented by the single genus tuco-tuco (*Ctenomys*), the fleas of the genera Tetrapsyllus, Polygenis and Ectinorus are parasites of this mammalian genus. Degu (*Octodon*) and mountain viscacha rat (*Octomys*) are the hosts for the fleas of the South American genera *Ectinorus*, *Delostichus*, и *Tetrapsyllus* (Rhopalopsyllidae). Fleas of the genera *Neotyphloceras* and *Ctenoparia* (Hystrichopsyllidae) also parasitize on *Octodon* and *Octomys*, and on a number of other genera, mostly *Octodontomys*, *Spalacopus*, and *Aconaemys*.

Opossums (Didelphidae) of the genera *Marmosops*, *Monodelphis*, *Metachirus*, and *Didelphis* are the main marsupial hosts for the fleas of the genus *Neotyphloceras* (Hystrichopsyllidae), fleas of the genera *Polygenis* (Rhopalopsyllidae), *Cleopsylla* and *Craneopsylla* (Stephanocircidae) have also been noted on opossums. A significant number of relationships with fleas are also found in shrew opossums (*Caenolestidae*). Common shrew opossums (*Caenolestes*) and Chilean shrew opossums (*Rhyncholestes*) have been recorded as hosts of fleas of the South American genera *Ctenidiosomus* (Pygiopsyllidae), *Barreropsylla*, *Cleopsylla*, *Plocopsylla*, and *Sphinctopsylla* (Stephanocircidae), as well as the widespread genus *Hystrichopsylla* (Hystrichopsyllidae).

Natural plague foci and vectors in the Neotropical region

There are nineteen officially recognized countries and six dependent territories within the Neotropical region, including the Caribbean Islands. Enzootic plague is known only for six countries in this region, located on the South American continent: Argentina, Bolivia, Peru, Ecuador, Brazil, and Venezuela. At present, no natural plague foci are found in Chile, Paraguay, Uruguay, Colombia, and Guyana. Sporadic plague cases in the first quarter of the XXI century were recorded only in Peru, Ecuador, and Bolivia (Schneider et al., 2014; Dubyanskiy, Yeszhanov, 2016, Rasprostranenie…, 2022;).

In South America, there are at least 37 independent natural plague foci, according to the available literature (Rall', 1958; Kucheruk, 1965; Plague…, 1963; Kozakevich et al., 1970; Tavares et al., 2012; Popova, Kutyrev, 2022). It is assumed that there are at least 10 natural plague foci in Argentina. At least four autonomous plague foci are identified in Bolivia. In Brazil, 14 areas with independent circulation of the plague pathogen are known (Fernandes et al., 2020). There are probably at least four natural plague foci in Peru. There are also at least four plague foci in Ecuador, and one in Venezuela.

In total, in the Neotropical region, 61 species of mammals are known, from which the plague pathogen has been isolated in natural conditions, and 43 species of which belong to the cricetids (Cricetidae). Cricetids, cavies, agouti (*Dasyprocta*), and Sciuridae (Guayaquil squirrel *Sciurus stramineus* Eydoux et Souleyet, 1841) are considered the main plague hosts in South America.

In the Neotropical region, 30 flea species have been found infected with plague in nature, twelve of them are the representatives of the South American family Rhapalopsyllidae, followed by family Pulicidae (8 species), comprising such well-known cosmopolitan species as *Pulex irritans* Linnaeus, 1758 and *Xenopsylla cheopis*. Another four flea species found infected with the plague microbe in nature belong to the family Ceratophillidae (including cosmopolitan species *Nosopsyllus fasciatus* (Bosc, 1800)). Only three species from the South America endemic family Stephanocircidae are the natural vectors of plague pathogen in this region. Two species from family Hystrichopsyllidae, parasitizing marsupials (opossums) and the species from the family Leptopsyllidae, related to rabbits, have also been found infected.

In South America, the up-to-date state of knowledge about the plague vectors is relatively scarce, so almost all publications indicate the issue complexity and lack of its development. Nevertheless, focusing on the distribution of the fleas found infected and their connection with the main hosts in certain territories, it is possible to give a rough estimate of the flea species that could be main plague vectors. Undoubtedly, the leading role belongs to fleas of the genus *Polygenis*, endemic to this continent, as the plague vector in almost all plague foci of the Neotropical region.

Three species of the flea genus *Polygenis* are the most important in the plague enzootic. *P. bohlsi* (Wagner, 1901) has been noted as an active vector in 19 plague foci in Bolivia, Brazil, and Venezuela; *P. byturus* (Jordan et Rothschild, 1923) appears to be the main vector in 16 foci in Argentina, Bolivia, and Brazil; and *P. litargus* (Jordan et Rothschild, 1923) is associated with at least six plague foci in Peru and Ecuador. Another species of this genus, *Polygenis brachinus* Jordan, 1950, which parasitizes mainly on yellowish rice rat *Aegialomys xanthaeolus* (Thomas, 1894), can probably be considered as the main vector in two foci of Ecuador. Cavies are of significant importance in the plague enzootic in 18 foci (Argentina, Bolivia, Brazil, and Peru), where the main vector is the flea *Ectinorus galeanus* (Jordan, 1939). In the highlands of Peru, the main vector is the flea *Plusaetis dolens* (Jordan et Rothschild, 1914) (at least one focus). Therefore, only 7 out of 30 flea species, found naturally infected with the plague microbe in South America, can be considered the main vectors.

Flea fauna diversity

The East African subregion has the largest number of species (145, including 112 endemic). The Cape subregion has the second largest number of species (77 and 65, respectively), followed by the West African subregion (57 and 39). The least diverse, but at the same time the most isolated fauna belongs to the Madagascar subregion, which has only 24 flea species. The faunas of the East and West African subregions are most closely related. They have 14 species in common, divided into two groups by the type of habitat. The fauna of the East African and Cape subregions includes 8 species in common with two types of habitats, the Cape and West African subregions have 2 species, each of which has a special type of habitat.

The largest number of endemic genera (9), as well as one endemic family Xiphiopsyllidae are represented in the fauna of the East African subregion. Most of these genera (5) belong to the family Pulicidae. There are seven endemic genera in the fauna of the Cape subregion, five of them belong to the Afrotropical family Chimaeropsyllidae. There are no endemic genera or families in the West African subregion, which is probably explained by the fact that tropical and equatorial forests are unsuitable for fleas to live in.

Parasite-host relationships

In the African region, similarly to the Neotropics, rodents are the dominant host group for fleas. However, the largest number of host species belong to the family Muridae, accounting for 70% of all parasite-host relationships here. In the Afrotropical region, family Muridae is represented by four subfamilies: the widespread subfamily Murinae, as well as the endemic subfamilies Cricetomyinae, Dendromurinae, and Otomyinae. The Muridae are most closely related to the flea genera *Ctenophthlamus*, *Dinopsyllus*, and *Listropsylla*, the last two of which are endemic to the Afrotropical fauna. Fleas of these genera, as well as those of family Chimaeropsyllidae, are closely related to the African vlei rats and whistling rats (Otomyinae); flea genus *Dinopsillus*, to African climbing mice, fat mice, and tree mice (Dendromurinae); a number of species of the flea genus *Xenopsylla*, to pouched rats (Cricetomyinae). African mole-rats (Rhizomyidae) host the fleas of the endemic subgenera *Geoctenophthalmus* and *Ethioctenophthalmus* of the genus *Ctenophthalmus*. A number of species of the flea genus *Dinopsyllus* are closely related to blesmoles (Bathyergidae). In the Afrotropical region, gerbils of the genera *Gerbillus*, *Meriones*, and *Tatera* (Gerbillinae, Cricetidae) have extensive relationships with fleas, serving as hosts to fleas of the genera *Xenopsylla* and *Synosternus*, which are widespread in the Eastern Hemisphere.

Three families of Eulipotyphla are hosts of fleas in the Afrotropical region: shrews (Soricidae), golden moles (Chrysochloridae), and tenrecs (Tenrecidae). Shrews of the Afrotropical genus *Scutisorex* and the Eurasian-African genus *Crocidura* serve as hosts for flea species *Afristivalius vancanneyti* (Berteaux, 1947), *A. nigeriensis* (Jordan, 1938), and *A. torvus* (Rothschild, 1908), as well as for some species from the genera *Ctenophthalmus* and *Dinopsyllus*. The South Eurasian-African shrew genus Suncus hosts the fleas of the genera Dinopsyllus and Listropsylla; golden mole (*Chrysochloris stuhlmani* Matschie, 1894), fleas of the genus *Ctenophthalmus*. Tailless tenrec (*Tenrec ecaudatus* (Schreber, 1778)) and Dobson's shrew tenrec (*Microgale dobsoni* Thomas, 1884) are the hosts for the Madagascar flea genus *Paractenopsyllus*.

Hyraxes (Hyracoidea) have their own specific flea fauna. In particular, rock hyrax (*Procavia capensis* (Pallas, 1766)) and yellow-spotted rock hyrax (*Heteroxyrax brucei* (Gray, 1868)) are the main hosts for fleas of the genus *Procaviopsylla*; southern tree hyrax (*Dendrohyrax arboreus* (A. Smith, 1827)), for *Ctenocephalides craterus* (Jordan et Rothschild, 1913).

Flea *Neotunga euloidea* Smit, 1962 may parasitize on Asiatic pangolins of genus *Manis* (Pholodota). However, another species of the genus, *N. inexpectata* (Smit, 1950), is noted as a specific parasite of common warthog (*Phacochoerus africanus* (Gmelin, 1788)). Artiodactyls are the main hosts of a number of flea species from family Pulicidae. In particular, desert warthog (*Phacochoerus aethiopicus* (Pallas, 1766)) is the host for *Echidnophaga larina* Jordan et Rothschild, 1906 and the monotypic flea genera *Delopsylla* and *Moeopsylla*. Elephant shrews (Macroscelidea) relate to the fleas from the family Chimaeropsyllidae, in particular, genus *Chimaeropsylla*.

Natural plague foci and vectors of infection in the Afrotropical region

The United Nations recognizes officially 48 states in Africa (Africa, 2024), in the part related to the Afrotropical region. Apparently, there are natural foci of plague on the territory of all these states. In the first quarter of the XXI century, this area ranks first in terms of human incidence of plague. The most active plague foci are located in Madagascar, Congo, Uganda, and Tanzania (Moore et al., 2015; Dubyanskiy, Yeszhanov, 2016; Popov et al., 2024).

On the African continent, south of the Sahara Desert, 44 separate natural plague foci are believed to exist; among them four foci are located in West Africa (Ghana, Nigeria, Senegal), four in Central Africa (Angola), 20 in East Africa (Congo (Zaire), Zambia, Kenya, Malawi, Somalia, Tanzania, and Uganda), and 16 in Southern Africa (Botswana, Zimbabwe, Lesotho, Mozambique, Namibia, South Africa, and Madagascar) (Kozakevich et al., 1971, 1972; Shangula, 1998; Dubyanskiy, Yeszhanov, 2016; Popova, Kutyrev, 2022; Medvedev et al., 2023b).

The Afrotropical region is characterized by a much richer diversity of foci with different hosts and vectors, compared to the Indo-Malayan region, located at similar latitudes. Plague foci here are associated with two groups of main hosts: gerbils (Cricetidae) and Muridae. The species richness of both groups in Africa is quite pronounced, which also affects the number of flea species that parasitize them.

In total, 30 species of fleas are reported to be the natural plague vectors in this zoogeographic region. The family Pulicidae (17 species) is involved the most in contacts with the plague microbe. Apparently, this relates greatly to the genesis of this family, since it has been probably originated on this continent (Medvedev, 1998b). The degree of natural infection with the plague microbe in the flea family Hystrichopsyllidae (6 species) is also quite high. In the family Chimeropsyllidae, these are two species spontaneously infected with the plague pathogen, and one species each from the families Ceratophillidae, Leptopsyllidae, Tungidae, and Xiphiopsyllidae.

Accordingly, the main hosts of plague in the region are also representatives of two families: Pulicidae (6 species) and Hystrichopsyllidae (2 species). Three species from the family Pulicidae are actively involved in epizootics practically throughout the entire region. *Xenopsylla cheopis*, a parasite of Muridae species in addition to its main host, black rat (*Rattus rattus*), is known as the main vector in 22 natural plague foci; in four of them, it is the only species that ensures the epizootic process without significant influence of other flea species. Flea *Xenopsylla brasiliensis*, associated in the region predominantly with multimammate mice *Mastomys*, manifests itself as the main vector in 26 plague foci, but everywhere as part of a pool of two or more flea species. *Xenopsylla philoxera* is the third most important plague vector in the Afrotropical foci, parasitizing mainly on gerbils and other species (17 plague foci; the only vector in six foci).

Xenopsylla piriei plays an important role in maintaining the plague enzootic, being the parasite of gerbils and other representatives of Cricetidae (7 foci; in each, in the pool of 2–3 main vectors). In addition to the listed species, *Xenopsylla hipponax* should be mentioned (4 foci in Angola, everywhere in the pools of main vectors) and *Synopsyllus fonquerniei*, a multi-host and a narrow-range parasite of small mammals (3 foci in Madagascar; in all of them, together with *Xenopsylla cheopis* (Rothschild, 1903)).

The species of the family Hystrichopsyllidae are also involved in the plague epizootic process in the region. Two flea species of this family are considered as the main vectors: *Dinopsyllus lypusus* Jordan et Rothschild, 1913 parasitizing on unstriped grass mice of genus *Arvacanthis* (10 foci; in all of them, together with other flea species) and multi-host flea *Ctenophthalmus nyikensis* Smit, 1962 parasitizing on various species of the family Muridae (3 foci in Tanzania, together with *Dinopsyllus lypusus* and *X. brasiliensis* (Baker, 1904)).

Therefore, a fairly low number of the flea families (Pulicidae and Hystrichopsyllidae) is involved in the epizootic process in the Afrotropical region. However, a significant diversity of hosts and number of natural plague foci are observed. These facts undoubtedly indicate that the colonization of this continent by the plague microbe occurred at a fairly late time, compared to that in the Palaearctic region.

INDO-MALAYAN REGION

Flea fauna diversity

The fauna of the Indo-Malayan region includes 191 flea species of 52 genera, of which 162 species of 22 genera are endemic. Most endemics (82 species of 17 genera) belong to the family Stivallidae. There are seven more families: family Pulicidae, 5 genera (*Ctenocephalides* (2 species), *Nesolagobius* (1), *Pariodontis* (1), *Synosternus* (1), and *Xenopsylla* (5)); family Ancistropsyllidae, 1 genus (*Ancistropsylla* (2)); family Hystrichopsyllidae, 3 genera (*Neopsylla* (7), *Rothschildiana* (2), and *Palaeopsylla* (5)); family Ceratophyllidae, 7 genera (*Dasypsyllus* (3), *Hollandipsylla* (1), *Macrostylophora* (10), *Nosopsyllus* (11), *Paraceras* (3), *Smitipsylla* (3), and *Syngenopsyllus* (1)); family Ischnopsyllidae, 5 genera (*Araeopsylla* (5), *Ischnopsyllus* (2), *Lagaropsylla* (7), *Nycteridopsylla* (1), and *Thaumapsylla* (1)); family Leptopsyllidae, 3 genera (*Acanthopsylla* (1), *Cratynius* (3), and *Sigmactenus* (5)); and family Pygiopsyllidae, 4 genera (*Acanthopsylla* (7), *Bibikovana* (4), *Hoogstraalia* (2), and *Pygiopsylla* (1 species)).

In the Indo-Malayan region, both the total number of species and the number of endemic species increase within each of the subregions from west to east and from north to south. This indicator is the lowest in the Indian and Indo-China subregions and the highest in the Malayan and Papuan ones, i.e., in the subregions located in the equatorial climatic zone. Low similarity of the faunas of the subregions with each other is noteworthy. The faunas of the Indo-China and Malayan subregions have the highest similarity, but these are only four species in common and two types of habitats. The flea faunas of the Indian and Indo-China subregions, as well as the Malayan and Papuan subregions have each two species in common and two types of habitats. It should be noted that this assessment is preliminary due to the poor study of the flea fauna of the region in general and, in particular, of the Indian and Indo-China subregions.

Parasite-host relationships

Similar to other zoogeographic regions, rodents are the dominant host group in the Indo-Malayan region, where all parasite-host relationships with fleas account for 57%. The second dominant host group in this region are marsupials (23%), followed by bats (8%), and Eulipotyphla and treeshrews (Scandentia), 3% each. Among rodents, the main hosts are Muridae (38% of all parasite-host relationships with rodents) and Sciuridae (16%). In the

Indo-Malayan region, fleas are associated to a lesser extent with Cricetidae, flying squirrels Pteromyidae, and the Old World porcupines (Hystricidae).

Muridae hosts of fleas belong mainly to the subfamily Murinae in the Indo-Malayan region. Flea species of the Palearctic-Indo-Malayan genera *Stivalius* and *Aviostivalius*, as well as the Indo-Malayan-Australian genus *Metastivalius* (Stivaliidae) are most closely related to the widespread genus *Rattus*. Fleas of the first two genera also parasitize on spiny rats (*Maxomys*), common in Southeast Asia. Fleas of the Indo-Malayan genera *Papuapsylla* and Smitella parasitize on mosaic-tailed rats (*Melomys*).

The flea species of the Indo-China-Malayan genus Medwayella parasitize on Sciuridae (genera *Sciurus*, *Callosciurus*, *Menetes*, and *Rhinosciurus*). Flea species of the large Palaearctic-Indo-Malayan genus Macrostylophora are parasites of mammalian genera *Callosciurus*, *Tamiops*, *Sundasciurus*, *Dremomys*, and *Sciurotamias*; widespread genus *Nosopsyllus*, of the genus *Funambulus*; and the Malayan monotypic genus *Syngenopsyllus*, of the genus *Callosciurus*. Gerbils of the genera *Tatera*, *Meriones* and *Gerbillus* (Cricetidae) serve as the hosts of the fleas *Xenopsylla astia* Rothschild, 1911 and *Synosternus pallidus* (Taschenberg, 1880) in the Indo-Malayan region. The fleas of the West Palaearctic-Indo-Malayan genus *Smitipsylla* parasitize on flying squirrels (genus Petaurista), fleas of the genus *Macrostylophora* — on the Indo-China genus *Belomys*. African-South Eurasian porcupines (*Hystrix*) are hosts to fleas of the genus *Pariodontis*, which has similarities with porcupines' distribution.

Among the marsupials of the Indo-Malayan region, carnivorous marsupials (Dasyuridae), possums (Petauridae), rainforest bandicoots (Peroryctidae), and ringtail possums (Pseudocheridae) are characterized by the closest links with fleas (mainly of the families Pygiosyllidae and Stivaliidae). Fleas *Xenopsylla vexabilis* Jordan, 1925 (Pulicidae) and *Sigmactenus toxopeusi* Smit, 1953 (Leptopsyllidae) are found on carnivorous marsupials and ringtail possums. Quolls (*Dasyurus*) and broad-footed marsupial ʽmice' (*Antechinus*) (both from Dasyuridae family), flying phalangers (*Petaurus*; Petauridae), New Guinean long-nosed bandicoots (*Peroryctes*; Peroryctidae), and ringtail possums (*Pseudocheirus*; Pseudocheridae) are listed most frequently as the hosts for the fleas of the family Stivaliidae (mostly, genera *Metastivalius* and *Papuapsylla*). Fleas of the genus *Parastivalius* are known from dasyurids and New Guinean long-nosed bandicoots; flea genus *Rectidigitus*, from ringtail possums and flying phalangers; and genus Muesebeckella, from ringtail possums.

Fleas of the genus *Acanthopsylla* (family Pygiosyllidae) have the closest links with all four marsupial families in the Indo-Malayan region. Fleas of the genera *Bibikovana* and *Pygiopsylla* parasitize also on quolls.

Natural plague foci and vectors of infection in the Indo-Malayan region

Plague enzootic is known in most countries of the Indo-Malayan zoogeographic region (Ioff, 1941; Rall', 1958; Kucheruk, 1965; Velimirovic, 1972; Akiev et al., 1983; Ramalingaswami, 1995; Plague manual, 1999; Kozlov, Sultanov, 2000; Dubyianskiy, Eszhanov, 2016; Meerwijk, 2022; Popova, Kutyrev, 2022; Medvedev et al., 2023b). However, given the lack of information on the manifestations of infection in many of these countries, the presence of natural foci has been recognized in 12 countries of the region in recent decades. In the 1980s–1990s, there was incidence of plague in humans in Vietnam. During the period of 1980–1997, 3,973 cases of human disease were registered in this country, and 197 people have died (mortality rate of 5.0%). This accounted for more than half of the human cases in Asia (Plague manual, 1999). Since 2002, WHO did not received information on plague incedences.

In the countries of South and Southeast Asia, including the adjacent part of Oceania, 31 separate plague foci have been described so far (Velmirovic, 1972; Ramalingaswami, 1995; Kozlov, Sultanov, 2000; Meerwijk, 2022; Popova, Kutyrev, 2022; Medvedev et al., 2023b). Of these, two foci are located in the northern India and in Nepal, so they locate on the border with the Palearctic region and are described in the corresponding section of the present manuscript. Information on 29 plague foci is considered below. All these foci are secondary; they are characterized by their proximity to varying degrees to human settlements. Therefore, these foci cannot be considered as natural focal type of plague enzootic here, but as of the mixed, anthropogenic-natural foci. In the region, 7 foci are described in India; at least one focus exists in Bangladesh and in Sri Lanka each; two in Burma (Myanmar); three in Thailand; two in Laos, Cambodia (Kampuchea) and Indonesia (Java) each; three in southern China; four in Vietnam; and two foci in Oceania. All 29 foci are of the rat type, with only strains of one oceanic phylogenetic lineage, ORI, circulating everywhere (Medvedev et al., 2023b).

In terms of the number of flea species found infected with the plague, this region is distinguished by its extreme minimalism. Here, in natural conditions, only 17 flea species have been found infected with the plague pathogen (6.3% of the number of infected flea species registered worldwide), which is extremely low compared to any other zoogeographic regions enzootic for plague. Of these, seven flea species belong to the family Pulicidae, four to Stivaliidae, three to Ceratophillidae, two species to Hystrichopsyllidae, and only one species was found infected with plague in the family Leptopsyllidae, although it is the dominant family in terms of the number of fleas in contact with plague in the Palearctic.

Within 17 species of fleas that have been found infected spontaneously with the plague microbe in the region, the main vectors are three species: (1) *Xenopsylla cheopis* (75%; in 21 foci it is the only main host), (2) *X. astia* (7 foci in India and one foci each in Sri Lanka and Hawaii, in all these foci *X. astia* is one of the two main vectors, together with *X. cheopis*), and (3) *X. vexabilis* (main host in one Hawaii foci, now the outbreak is apparently stopped). Therefore, in the Indo-Malayan region, fleas of the genus *Xenopsylla* (mostly *Xenopsylla cheopis*) are the main plague vectors found nearly everywhere, although a total number of flea species, found infected with plague in natural conditions, is small.

This picture clearly evidences on both the secondary nature of the current plague foci in the region and on the much later contact of *Xenopsylla* fleas with the plague microbe here.

AUSTRALIAN REGION

Flea fauna diversity

In total, 64 flea species from 9 families are registered in the Australian region. Two of these families (Lycopsyllidae and Macropsyllidae) are endemic to the Australian fauna. The largest number of endemic species belong to the families Pygiopsyllidae (23 endemic species) and Pulicidae (11 endemic species).

When analyzing the distribution of Australian species by subregions, there are several distinctive features of the flea fauna. Firstly, the East Australian subregion is characterized by a significantly higher diversity at both the species and genus levels. Secondly, in the West and East Australian subregions, there is a large number of species in common (7 species); at the same time, they are unknown for the Central Australian subregion. Thirdly, there are five trans-Australian species, which form a significant group.

Parasite-host relationships

Marsupials are the dominant host group in the Australian region, accounting for 52% of all types of relationships, followed by rodents (33%), and bats (6%). Monotremes (order Monotremata) have a specific associated flea fauna.

Fleas are found on marsupials belonging to 14 families. The largest number of parasite-host relationships (49) of flea species is recorded with dasyurids (Dasyuridae). This group is also characterized by the largest number of flea species (26). Extant bandicoots (Peramelidae) are the second largest family of marsupials in terms of the number of all types of relationships with fleas (26); in total, 16 species of fleas are found for this family. Marsupial families Phalangeridae, Pseudocheiridae, Vombatidae, and Burramyidae have approximately the same number of types of relationships (from 5 to 9) and the number of flea species (7–8). The family Pygiopsyllidae has the greatest number of flea species parasitizing marsupials, in particular, these are genera *Acanthopsylla* and *Pygiopsylla*. Fleas of the first genus are most often found on carnivorous marsupials, mostly the broad-footed marsupial ʻmice’ (*Antechinus*) and wambengers (*Phascogale*), the second genus is found on the long-nosed bandicoots (*Peramelis*) and short-nosed bandicoots (*Isoodon*) from the family Peramelidae. “Helmet fleas” (family Stephanocircidae) are known for carnivorous marsupials (Dasyuromorphia), bandicoots and bilbies (Peramelemorphia), fleas of the family Lycopsyllidae, on wombats and flying phalangers.

Australian species of Muridae family has a significant number of types of relationships with a large number of flea species. Rats of the widespread genus *Rattus* are characterized by the largest number of relationships (54) with fleas. Fleas have also been found on Australian native mice (*Pseudomys*), Australian hopping mice (*Notomys*), and giant naked-tailed rats (*Uromys*).

The representatives of six flea families are found on rats (*Rattus*), most of them belong to the family Pulicidae. In particular, three species of the genus *Echidnophaga* are known from three rat species, and two species of the genus *Xenopsylla*, from nine rat species. Flea *X. vexabilis* is represented most widely on rats (8 species); this flea species is found in the Malayan, Papuan and Central Australian subregions. The flea genera *Pygiopsylla*, *Bibikovana*, *Acanthopsylla*, and *Geohollandia* (family Pygiopsyllidae) have been found on rats also. Flea *Macropsylla hercules* Rothschild, 1905 (Australian family Macropsyllidae, two species in total) parasitizes on rats as well. The flea genus *Stephanocircus* (Stephanocircidae) is also widely represented on rats: five out of seven species in total were found on six species of rats. Flea family Stivaliidae is represented as rat parasites by two species of the genus *Metastivalius*, family Rhopalopsyllidae, by two species of the genus *Parapsyllus*.

Australian native mice (*Pseudomys*) are the hosts for the fleas from family Macropsyllidae (flea species of both genera), for three species of the genus *Stephanocircus* (out of seven in total), and for the flea genera *Pygiopsylla*, *Acanthopsylla*, and *Bibikovana*. Fleas *X. australiaca* Mardon et Dunnet, 1971 (family Pulicidae) are also their parasites. Australian hopping mice (*Notomys*) are known as the hosts of the fleas *Echidnophaga myrmecobii* and *Xenopsylla australiaca* only. Giant naked-tailed rats (*Uromys*) are hosts for the flea genera *Acanthopsylla*, *Bibikovana*, *Pygiopsylla*, and *Stephanocircus*.

Natural plague foci and vectors of infection in the Australian region

There are no natural foci of plague in the Australian region. Although there were numerous introductions of plague infection into Australian ports during the third plague pandemic (Popova, Kutyrev, 2022), marsupial burrowing animals (wombats) are widespread, the abundance of rats in coastal settlements is high and the fauna of the Muridae family is generally diverse, represented by 13 genera and 67 species (Kucheruk, 1965), the penetration of the pathogen into natural biotopes and its subsequent circulation did not occur by now.

DISCUSSION

Each natural plague focus has undergone a long evolutionary process. During the interaction between the epizootic triad components, a specific number of vector species has evolved. These flea vectors ensure the preservation of the pathogen in the focus area. In our opinion, mono-vector foci of the marmot type with the main vector *Oropsylla silantiewi* should be considered the most ancient ones.

According to recently published summary of natural plague foci in the world, 303 species and subspecies have been found naturally infected with the plague pathogen to date, of which 280 species and subspecies are fleas (Popova, Kutyrev, 2022).

According to our data, plague infection has been recorded in 263 flea species, or 12.2% of the 2,162 known species. They belong to 76 genera (240 in total) and 12 (19) families of fleas, which is 31.5% of the number of flea genera known in the world fauna by now.

The widespread belief that all these insects play a similar role in the circulation of the plague pathogen in nature is erroneous. Most of flea species, out of 263 found infected with the plague pathogen, are secondary or accidental vectors in nature. In general, a blood-sucking arthropod of any species, having drunk the infected blood of a sick animal, may retain the plague pathogen in its body for some time. However, this does not mean that this species can retain the plague microbe in itself for a long time and to transmit it to a new warm-blooded host. Only a relatively small number of species from this list are main plague vectors. This is due to the evolutionary history of the interaction of the pathogen with certain flea species, which are characterized by both the population and physiological characteristics that ensure the survival, accumulation, and transmission of the plague microbe in specific natural foci. We have analyzed the distribution characteristics, parasite-host relationships, and vector characteristics of 66 flea species that carry plague pathogens. These are flea genera *Citellophilus* and *Oropsylla* (Ceratophyllidae), *Frontopsylla* (Leptopsyllidae), *Rhadinopsylla* and *Neopsylla* (Hystrichopsyllidae), represented in 45 plague foci of Russia and neighboring countries. According to this analysis, gopher-related and marmot-related fleas *Citellophilus tesquorum* and *Oropsylla silantiewi* are highly active plague vectors characterized by: (1) high feeding activity; (2) the ability to develop rapidly the “block formation” of the forestomach during the period of epizootic activation, (3) long-term preservation of the pathogen, (4) survival in the cold season as imago, (5) forming a high-number population in a local area. Species of the genera *Rhadinopsylla*, *Frontopsylla*, and *Neopsylla* are additional natural depots for the plague pathogen during the cold period of the year, when the plague microbe is most vulnerable, or when main warm-blooded hosts are eliminated.

Based on the available information, there are at least 129 separate natural plague foci in Palearctic (Karimova, Neronov, 2007; Popova, Kutyrev, 2022; Medvedev et al., 2023a, 2023b). Here, 156 species of fleas naturally infected with the plague pathogen are found. For comparison, spontaneous carriage of the plague microbe was found in 58 flea species in North America, 35 in Africa, 30 in South America, and 6 in Indo-Malayan region. Such a wide representation of fleas that have ever encountered the plague in the Old World is associated with the center of origin of the plague. We believe that this center is undoubtedly located within the Eurasian continent. Only 37 flea species out of 156 found infected in Palearctic (23.7%) are considered to be the main vectors of the plague pathogen in at least one of the natural plague foci in the world. At the same time, 8 flea species act as the main vectors in ten or more separate foci. These are *Oropsylla silantiewi* (63 of 129 known natural foci), *Xenopsylla cheopis* (19 foci), *Citellophilus tesquorum* (15), *Nosopsyllus laeviceps* (14), *Xenopsylla skrjabini* (14), *Xenopsylla conformis* (13), *Neopsylla pleskei* Ioff, 1928 (12), and *Xenopsylla gerbilli* (Wagner, 1903) (11 foci).

According to experimental work with representative samples of these insects, almost all of the listed flea species are able to persist the plague pathogen for a long time in their bodies and to transmit it to healthy warm-blood hosts (Ioff, 1941; Burroughs, 1947; Pollitzer, 1952; Kartman, Prince, 1956; Bibikova, Alekseev, 1969; Novokreshchenova, 1970; Bibikova, Klassovsky, 1974; Voronova, Feoktistov, 1979; Vashchenok, 1984; Hinnebusch, 2005, Hinnebusch et al., 2017; Bazanova, 2009). However, a significant number of the flea species cannot transmit this infection, or this ability is expressed weakly. When considering the duration of retaining the plague microbes, most flea species also cannot keep it for any period and so get rid of it quite quickly (Wheeler, Douglas, 1941, 1945; Bibikova, Klassovsky, 1974; Vashchenok, 1988; Bazanova, 2009). Among the 129 described natural plague foci in Palearctic, 70 foci (54.3%) have one main vector. In 41 natural foci (31.8%), the flea *Oropsylla silantiewi* is the only main vector. All these foci are confined to the mountain systems of Central Asia, from Manchuria in the east to the Pamirs in the west, from Transbaikalia and Mongolia in the north to the foothills of the Himalayas in the south. Probably, the evolution of the plague pathogen as a species is primarily associated with the development of a new ecological niche by settling the ancestral microorganism of the gastrointestinal tract of fleas of this species. *Oropsylla silantiewi* is a specific parasite of marmots, whose origin is associated with the mountain steppes of Central Asia. In 14 plague foci, the flea *Xenopsylla cheopis* is considered the only vector. These foci undoubtedly have a later origin and are associated with rats of several species that primarily inhabited tropical biocenoses of South and Southeast Asia (Medvedev et al., 2023a, 2023b). In five plague foci in Eurasia (Middle East region), the circulation of the pathogen is supported by the species *Xenopsylla buxtoni* Jordan, 1949, associated with several species of gerbils. In four other plague foci, there are two flea vectors: (1) *Citellophilus tesquorum*, parasitizing on ground squirrels, acts as the sole vector (here foci are scattered from the Caucasus in the west to Manchuria in the east), and (2) *Xenopsylla astia* associated with Indian gerbil *Tatera indica* (Hardwicke, 1807) (foci are located in Western India and Pakistan). In addition, two more foci of the gerbil type, which have one main vector, are located on the Arabian Peninsula (*Xenopsylla nubica* (Rothschild, 1903)) and in the Dzungarian Basin of the Xinjiang Uyghur region of China (*Xenopsylla skrjabini*). Among the plague foci of the Old World, 43 foci (30.1%) have two main vectors of infection. The most representative are the flea pairs *Xenopsylla conformis – Nosopsyllus laeviceps* (7 foci of gerbil type), *Oropsylla silantiewi – Callopsylla dolabris* (6 marmot foci), *Citellophilus tesquorum – Neopsylla setosa* (Wagner, 1898) (5 foci, ground squirrels), *Callopsylla caspia* (Ioff et Argyropulo, 1934) – *Nosopsyllus consimilis* (3 natural foci of vole type), and *Xenopsylla astia – Xenopsylla cheopis* (3 foci, rat type). Other variants of co-dominance of the main vectors are found in one or two cases. In Palearctic, 24 natural plague foci have three main vectors, most of them (14) are associated with gerbils, more often with great gerbil Rhombomys opimus (Lichtenstein, 1823). Another four foci are associated with voles. Only two natural foci of plague in Palearctic are characterized by four main vectors at once; these are foci of a combined type involving marmots and voles and, accordingly, the related fleas and pathogen strains. Since these foci contain independent "host-vector-pathogen" systems, often separated biotopically, it is more correct to consider such formations as independent foci in one common territory. Finally, six or more main vectors are found in

4 foci, all of them are associated with the main host, Pallas's pika (*Ochotona pallasi* (Gray, 1867)). The circulation of the plague pathogen in such foci is characterized by the process when individual species of fleas is the main vector at different phases of the epizootic cycle.

CONCLUSIONS

Currently, the flea fauna of the world comprises 2,162 species belonging to 241 genera and 19 families. Among them, 263 species (76 genera, 12 families) were found infected with plague in nature, i.e., 12.2% in terms of the species richness (31.5% and 63.2%, respectively).

The flea families Hystrichopsyllidae and Ceratophillidae are most involved in epizootic processes worldwide. The family Hystrichopsyllidae is the most diverse in the world and the most widespread in the Palearctic; it comprises 647 species and 46 genera, of which 74 (11%) and 19 (41.2%), respectively, are found infected with the plague microbe in nature. The family Ceratophillidae has lower global faunistic diversity, comprising more than 443 species and 46 genera described to date, of which 69 species (16%) and 20 genera (43%) have been found infected with the plague pathogen in natural plague foci around the world.

The flea family Leptopsyllidae includes 258 species from 30 genera; 50 species (20.8%) and 11 genera (37%) are infected with plague. The family Pulicidae includes 164 species from 23 genera; 41 species (25%) and 10 genera (43%) are infected with plague. The role of the remaining flea families in the plague enzootic is significantly lower than of those listed above.

If one considers only the flea species that are the main vectors in natural plague foci in the world, the pattern becomes more obvious. Only 63 flea species out of 263 (24%) found infected with the plague pathogen are considered the main hosts. When looking at the family level, there are 24 species from 8 genera in family Ceratophillidae, 18 species and 4 genera in family Pulicidae, 10 species and 5 genera in family Hystrichopsyllidae, 8 species and 4 genera in family Leptopsyllidae, 5 species and 2 genera in family Rhopalopsyllidae. Therefore, the species of only 5 families are the main plague vectors, out of 12 families of fleas found infected with the plague microbe in nature. Among them, family Ceratophillidae has the largest number of both species and genera serving as main vectors.

According to the experimental work with representative samples, a significant number of flea species are shown to be main plague vectors able to retain these microbes in their bodies for a long time and to transmit them effectively to healthy warm-blooded animals (Ioff, 1941; Burroughs, 1947; Kartman, 1957; Bibikova, Alekseev, 1969; Novokreshchenova, 1970; Bibikova, Klassovsky, 1974; Voronova, Feoktistov, 1979; Vashchenok, 1984; Lorange et al., 2005; Bazanova, 2009; Bazanova, Verzhutsky, 2009; Hinnebusch et al., 2017). On the other hand, most species of fleas, which are not the main plague vectors, cannot transmit this infection to intact animals or their ability to do this is very low. Also, most flea species get rid of the plague microbe fairly quickly and are not able to retain it for any period (Bibikova, Klassovsky, 1974; Vashchenok, 1988; Bazanova, 2009).

The flea *Oropsylla silantiewi* plays a leading role in maintaining the plague enzootic among all the main vectors considered. The approximate number of natural plague foci in the world is at least 316: 129 foci in Palaearctic region, 77 in Nearctic, 44 in Afrotropical, 37 in Neotropical, and 29 foci in Indo-Malayan regions. In 63 natural plague foci, *O. silantiewi* acts as the main vector; in 41 natural foci, this species is the only main vector, i.e. it ensures the circulation of the pathogen without significant influence of other flea species. All these foci are confined to the mountain systems of Central Asia, from Manchuria in the east to the Pamirs in the west, and from Transbaikalia and Mongolia in the north to the foothills of the Himalayas in the south. No other species of flea is involved in the circulation of the plague pathogen in a comparable number of natural plague foci in any region of the world. Probably, the evolution of the plague microbe is primarily associated with the development of a new ecological niche by colonizing the gastrointestinal tract of fleas of this species with an ancestor microorganism.

O. silantiewi is a specific parasite of marmots. Its origin is associated with the mountain steppes of Central Asia, where the center of origin of the plague microbe is probably located. Apparently, further spreading of the plague pathogen to new territories was associated with the mastering of a new ecological niche by its vectors, gerbil-related fleas (primarily, *Xenopsylla skrjabini*, parasitizing mainly on great gerbil widespread in the Central Asian steppes). This allowed the transfer of the plague microbe to the western direction and further emergence of the plague foci in Kazakhstan, Central and Western Asia. Here, fleas parasitize on the Indian gerbil, so the plague pathogen was then transferred to *Xenopsylla cheopis*. This flea species is functionally most adapted to interact with the plague pathogen: it has susceptibility to infection, as the ability to store, to accumulate and to transmit effectively the pathogen via a bacterial "block", and the ability to feed on a wide range of hosts. Apparently, the penetration of the plague microbe into *Xenopsylla cheopis* populations allowed the plague infection to spread widely across many regions of the planet, forming new foci, where both local hosts and vectors were involved. However, natural plague foci in central Africa, North and South America are undeniably old, so the plague pathogen spreading across our planet during the 3rd pandemic was not the first, but it was preceded by the plague outbreaks occurred no earlier than the Sartan glaciation and associated with ground-living Sciuridae and their fleas.

Worldwide, natural plague foci of the vole type are quite rare and most often dispersed, not compact. As a rule, such foci are of multi-vector type, i.e., the circulation and preservation of the pathogen is ensured by several flea species. Among them, *Callopsylla caspia* is the only species able to retain the plague pathogen for a long time, so it can be considered an active pathogen vector (Vashchenok, 1984). However, this result has been obtained only in one experiment out of eight in total. As a rule, in the foci of the vole type, other flea species considered the main vectors have either a weak ability to transmit the pathogen or are not able to transmit these microbes at all. They form a forestomach block rarely or do not form it at all; they also free themselves fairly quickly from this pathogen (Vashchenok, 1984). Such data do not provide grounds to consider the plague microbe strains in the vole type foci as the ancestor for the entire diversity of this pathogen in the world. The ecological features of voles and their fleas, against the background of the peculiarities of plague pathogen spread in the world, allow us to assume that foci of this type were formed independently of each other during irradiation of the plague pathogen and its mastering of the new ecological niches.

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COMPLIANCE WITH ETHICAL STANDARDS

This work does not contain any studies on humans or animals that meet the criteria of Directive 2010/63/EU.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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БЛОХИ (SIPHONAPTERA) КАК ПЕРЕНОСЧИКИ В ПРИРОДНЫХ ОЧАГАХ ЧУМЫ МИРА: ПАРАЗИТО-ХОЗЯИННЫЕ СВЯЗИ, ФАУНИСТИЧЕСКИЙ И ГЕОГРАФИЧЕСКИЙ АНАЛИЗ, ЭПИЗООТОЛОГИЧЕСКОЕ ЗНАЧЕНИЕ

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Ключевые слова: блохи, Siphonaptera, переносчики, патоген чумы, паразито-хозяинные отношения, зоогеографическое разнообразие, эпизоотия

РЕЗЮМЕ

В фауне блох мира к настоящему времени известно 2162 вида, из них 263 (12.1%) видов из шести семейств обнаружены инфицированными чумой в природе. В наибольшей степени в эпизоотии вовлечены блохи семейств Hystrichopsyllidae (74 вида), Ceratophillidae (69 видов) и Leptopsyllidae (40 видов). Среди всех найденных инфицированными чумным патогеном видов блох только 64 (24%) считаются основными переносчиками. По семействам они распределяются следующим образом: Ceratophillidae – 24 вида, Pulicidae – 18 видов, Hystrichopsyllidae – 10 видов, Leptopsyllidae – 8 видов, Rhopalopsyllidae – 4 вида. Лидирующее положение по выполняемой роли в поддержании энзоотии чумы занимает блоха *Oropsylla silantiewi*. Примерное число природных очагов чумы в мире составляет не менее 316. *Oropsylla silantiewi* выступает как основной переносчик инфекции в 59 природных очагах чумы, причем из них в 41 природном очаге этот вид является единственным основным переносчиком, обеспечивая циркуляцию возбудителя без существенного влияния других видов блох. Ни один другой вид блох ни в одном регионе мира не вовлечен настолько сильно в циркуляцию возбудителя чумы. *Oropsylla silantiewi* является специфическим паразитом сурков, чье происхождение связывают с горными степями Центральной Азии, где, вероятно, и расположен центр происхождения чумного микроба. Отсюда произошла дальнейшая иррадиация возбудителя чумы и началось освоение им новых экологических ниш для жизнедеятельности в популяциях сусликов, песчанок, мышей, полевок и других мелких млекопитающих.