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Distribution and Specificity of Host-Parasite Associations of Fleas (Siphonaptera) in the Central Caucasus

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Abstract—In the territory of the Central Caucasus, which constitutes one-fifth of that of the Greater Caucasus, the order of fleas is represented by 87 species, 67 of which are associated with mammals and 20 species, with birds. The regional fauna includes 6 species endemic to the Greater Caucasus and 3 species endemic to its central part. Fleas of 72 species are distributed along the entire longitudinal extent of the Central Caucasus; 18 species are associated with the highlands and 2 species are found only in the steppe foothills and forest-steppe midlands. The flea distribution is determined by the presence of suitable hosts and by some other factors. Rodents of the family Cricetidae are the main hosts of more than one third of all the mammal flea species in the region. Passeriform birds of the families Hirundinidae, Motacillidae, and Muscicapidae are the main hosts of the greatest part of bird flea species. The flea fauna of the Central Caucasus is highly similar in species composition to the faunas of the West and East Caucasus, largely due to the wide distribution of many host species throughout the Greater Caucasus.

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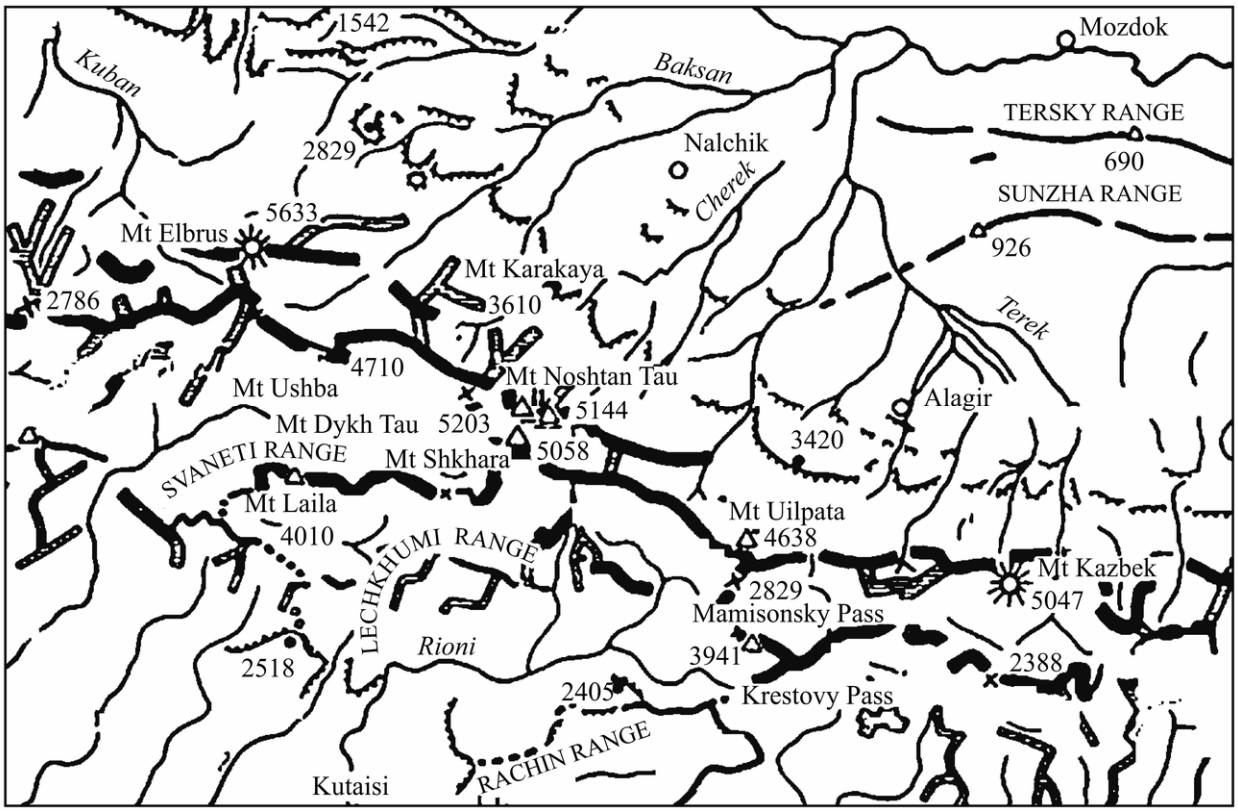
The characteristic of animal distribution and host-parasite relations within a natural region is important for understanding the history of its fauna. Earlier, we have analyzed the specific trends in species diversity and host associations of fleas in the Caucasus and also determined the main ways of migration of certain taxa into this territory (Medvedev and Kotti, 2011, 2012). Other works are devoted to the fleas of the Greater Caucasus (Kotti, 2015) and its western part (Kotti and Kotova, 2014a, 2014b). The available data allow one to consider the flea fauna of the central part of this mountain system, in particular, to reveal the host taxa which determine the regional flea fauna diversity and to clarify the species distribution within the region and the adjoining areas of the Greater Caucasus.

The Central Caucasus stretches over an area of about 30 thousand km^2 from Elbrus to Kazbek and forms the highest part of the Greater Caucasus. Its environmental conditions determine the species richness and heterogeneous spatial distribution of various animal taxa. It should be noted that the Central Caucasian alpine plague focus lies within the study region while the Terek-Sunzha lowland focus and the East Caucasian alpine focus adjoin it (Kutyrev and Popova, 2016).

The study of fleas in the central part of the Greater Caucasus was initiated early in the past century, when new species were described from the environs of Nalchik (Dampf, 1912) and from Gudauri in Georgia (Wagner, 1916).

Subsequently, I.G. Ioff, his colleagues and successors described nine species from different parts of the region: the valleys of the rivers Armkhi (west of Ingushetia), Tsey (North Ossetia), and Baksan (Kabardino-Balkaria), the Krestovy Pass, and environs of Shovi, Kazbegi, and Suatisi in Georgia (Ioff, 1940; Ioff et al., 1946, 1953; Rostigaev, 1948; Savenko, 1949; Darskaya, 1950). Much later, one more species was described from Kobi in Georgia (Goncharov, 1980).

Records of 15 flea species collected off rodents, carnivores, insectivores, and also passerine birds on the southern slope of the Central Caucasus were published by Savenko (1950). Data on 17 species of Siphonaptera were provided in the dissertation on rodent parasites collected in the environs of Vladikavkaz, highlands of North Ossetia, and the adjoining territory of Georgia (Razumova, 1954). In her review of fleas from Kabardino-Balkaria, Syrvacheva (1964) described localization and distribution over mammal hosts for 37 flea species based on her own collections and the material of I.G. Ioff and other researchers. The literature and original data on the central part of the Greater Caucasus are to be found in the *Key to the Fleas of the Caucasus* (Tiflov et al., 1977).



Territory of the Central Caucasus

An important stage was the study of the fleas associated with the Caucasian mountain ground squirrel and some other mammals and birds in the Mount Elbrus area (Devkin, 1966; Labunets et al., 1974, 1983; Goncharov et al., 1982; Kotti et al., 2001; Belyavtseva et al., 2007). During search for enzootic plague regions, some research was focused on the species composition of vole parasites on the northern (Labunets et al., 1984, 1988) and southern (Tsikhistavi, 1983, 1987; Tsikhistavi et al., 1987, 1988) macroslopes of the Central Caucasus. Collections of fleas, mainly off birds and bats in North Ossetia, were also carried out by Yu.E. Komarov (Komarov and Labunets, 1983, 1988; Labunets and Komarov, 1987; Komarov et al., 2000).

NATURAL CONDITIONS

The Central Caucasus is a part of the Greater Caucasus located between Elbrus and Kazbek (figure). Climate continentality increases from west to east over a distance of 180 km. The annual precipitation on the Kluchor Pass is 1990 mm, and that on the Krestovy Pass is noticeably lower, only 1500 mm. The region is traversed by numerous rivers and tributaries: the upper reaches of the Kuban and Terek on the northern macroslope and the Enguri and Rioni on the southern one.

The foothills and mid-mountain territories are occupied by forest-steppes and forests, the highlands, by subalpine and alpine vegetation. Upland steppes are common in the Mount Elbrus area (Gulisashvili et al., 1975).

Data on the bird and mammal faunas of the Central Caucasus are to be found in a number of publications (Chunikhin, 1962; Shidlovsky, 1964; Isakov et al., 1966; Tembotov, 1972; Tembotov and Kazakov, 1982; Tarasov, 1983, 2002; Beme et al., 1987; Korzhov and Labunets, 1987; Sokolov and Tembotov, 1989; Dyatlov and Grigoriev, 1990; Komarov, 1995; Komarov and Khokhlov, 2003; Belik, 2013).

MATERIALS AND METHODS

Data on the fleas were collected by the author during expeditions to different parts of the Central Caucasus: Karachay-Cherkessia (Daut, Karachaevsky District, 1984; Khasaut, Malokarachaevsky District, 1993; Dzhalpakol River, Karachaevsky District, 2008), Ka-

bardino-Balkaria (Elbrus Village on the Baksan River, 2007), North Ossetia (Tsey, Alagirsky District, 2009; Dzinaga, Irafsky District, 2011). The specimens collected there earlier by other researchers (L.E. Arens, L.V. Degtyareva, N.L. Gershkovich, M.P. Grigoriev, K.V. Kharin, T.A. Ivanova, Yu.E. Komarov, M.P. Tarasov, V.S. Tkachenko, G.V. Trufanov, and K.Yu. Shkarlet) were identified. The flea collection sites lie at altitudes from 1300 to 3100 m above sea level. Data from the above publications on the fleas of the Central Caucasus were also used.

Some data were obtained when working with collections and archive material of the Stavropol Anti-Plague Research Institute and also the Georgian, Dagestan, and Black Sea anti-plague stations.

Altogether, the analyzed material included the collections of fleas from 3700 specimens of mammals and 300 nests of mammals and birds from 25 geographic localities. Data on findings of over 40 thousand specimens of fleas were taken into account.

The names of birds are given according to Stepanov (2003), those of mammals, according to Pavlinov and Lisovsky (2012).

According to the degree of host specificity, fleas were classified into monoxenous or ultraspecific (associated with only one host species), oligoxenous (with several congeneric host species), pleioxenous (with hosts from different genera within one family), and polyxenous (with hosts belonging to different families, orders, or classes) (Balashov, 2009).

The distribution of fleas was characterized using additional faunistic data for the western and eastern parts of the Greater Caucasus (Kotti, 2015) and records from other territories (Kotti, 2013, 2014, 2016).

RESULTS AND DISCUSSION

Although the Central Caucasus occupies only one fifth of the Greater Caucasus area, its flea fauna is rather diverse, comprising 87 species, or over 75% of the total species number in the Greater Caucasus.

The Central Caucasus is inhabited by 60 species of mammals but only 35 species from the orders Eulipotyphla, Chiroptera, Carnivora, and Rodentia are known as the main hosts of 67 species of fleas (Table 1). There are 83 bird species nesting in the region. The bird fleas are represented by 20 species from 4 genera, and 26 bird species from 5 orders are known as the main hosts of fleas (Table 2).

Three groups of flea species can be distinguished by the patterns of their distribution in the region.

1. Fleas widely distributed along the whole longitudinal stretch of the Central Caucasus, from Elbrus (the Daut River in the Kuban basin and the upper reaches of the Kodori River) in the west to Kazbek (the Armkhi River in the Terek basin and the upper reaches of the Aragvi River) in the east.

This group comprises the great majority of flea species. It includes all the parasites of insectivores (Eulipotyphla), in particular the fleas of moles (Talpidae): *Palaeopsylla alpestris* Argyropulo, 1946, *P. osetica* Ioff, 1953, *Hystrichopsylla talpae* Curtis, 1826, and *H. satunini* Wagner, 1916, and also parasites of shrews (Soricidae): *Doratopsyla dampfi* Argyropulo, 1935 and *Palaeopsylla gromovi* Argyropulo, 1934.

The records of fleas associated with bats (Chiroptera) in the Central Caucasus are scanty but, judging by the wide distribution of their hosts, the recorded flea species inhabit the foothills and mid-mountains over the whole study region. *Rhinolophopsylla unipectinata* (Taschenberg, 1880) occurs on horseshoe bats (Rhinolophidae). The rest of the flea species parasitize vesper bats (Vespertilionidae): *Ischnopsyllus obscurus* (Wagner, 1898), *I. elongatus* (Curtis, 1832), *I. intermedius* (Rothschild, 1898), *I. octactenus* (Kolenati, 1856), *I. variabilis* (Wagner, 1898), *I. dolosus* Dampf, 1912, *I. hexactenus* (Kolenati, 1856), *I. transcaucasicus* Scalon, 1979, and *Nycteridopsylla eusarca* Dampf, 1909.

Among the parasites of squirrels (Sciuridae, Rodentia), the flea *Ceratophyllus sciurorum* (Schrank, 1803) is widespread on the red squirrel *Sciurus vulgaris* L., 1758. This flea also parasitizes members of a different rodent family, dormice (Gliridae). One more flea species, *Myoxopsylla jordani* Ioff et Argyropulo, 1934, is a specific parasite of dormice.

Within the rodent family Cricetidae, most of the known flea species are associated with voles (Arvicolinae). These are 6 species of the family Ceratophyllidae: *Nosopsyllus consimilis* (Wagner, 1898), *Callopsylla caspia* (Ioff et Argyropulo, 1934), *Megabothris turbidus* (Rothschild, 1909), *M. walkeri* (Rothschild, 1902), *Amalaraeus improvisus* (Ioff, 1946), and *A. arvicolae* (Ioff, 1948); 5 species of the family Leptopsyllidae: *Frontopsylla caucasica* Ioff et Argyropulo, 1934, *Amphipsylla rossica* Wagner, 1912, *A. kuznetzovi* Wagner, 1912, *Paradoxopsyllus hesperius* Ioff, 1946, and

Table 1. Distribution of fleas by orders and families of mammals in the Central Caucasus

Flea families	Eulipotyphla (6)			Chiroptera (9)			Rodentia (14)					Carnivora (8)				Total (37)
	Talpidae (2)	Soricidae (4)	Total for order	Rhinolophidae (1)	Vespertilionidae (8)	Total for order	Sciuridae (3)	Gliridae (2)	Cricetidae (7)	Muridae (3)	Total for order	Canidae (3)	Mustelidae (4)	Felidae (1)	Total for order	
Pulicidae	0	0	0	0	0	0	0	0	0	0	0	2*	1*	1	3	3
Vermipsyllidae	0	0	0	0	0	0	0	0	0	0	0	2*	5*	0	5	5
Ceratophyllidae	0	0	0	0	0	0	3	2	6	2	14	0	1	0	1	15
Leptopsyllidae	0	0	0	0	0	0	1	0	6	2	9	0	0	0	0	9
Ischnopsyllidae	0	0	0	1	9	10	0	0	0	0	0	0	0	0	0	10
Hystrichopsyllidae	4	2*	6	0	0	0	4*	0	17*	1	21	0	0	0	0	25
Total	4	2	6	1	9	10	8	3	26	5	44	4	6	1	9	67

The number of species recorded as flea hosts is given in parentheses. * Including species parasitizing hosts from two different families or orders. For explanation, see text.

Peromyscopsylla bidentata (Kolenati, 1863); 8 species of the family Hystrichopsyllidae: *Ctenophthalmus inornatus* Wagner, 1916, *C. chionomydis* Ioff et Rostigayev, 1950, *C. wagneri* Tiflov, 1928, *Rhadinopsylla caucasica* Argyropulo, 1946, *Stenoponia ivanovi* Ioff et Tiflov, 1934, *Paraneopsylla dampfi* Ioff, 1946, *Hystrichopsylla satunini* Wagner, 1916, and *H. talpae* Curtis, 1826. Many of them also parasitize hamsters (Cricetinae).

Rodents of the family Muridae are the main hosts of *N. mokrzeck*yi (Wagner, 1916), *Leptopsylla taschenbergi* (Wagner, 1898), *L. segnis* (Schönherr, 1811), and *C. proximus* (Wagner, 1903).

Mammals of the order Carnivora are hosts of the fleas *Pulex irritans* L., 1758, *Ctenocephalides felis* (Bouche, 1835), *C. canis* (Curtis, 1826), *Chaetopsylla globiceps* (Taschenberg, 1880), *C. trichosa* Kohaut, 1903, *C. caucasica* Smit, 1953, *C. rothschildi* Kohaut, 1903, *C. homoea* Rothschild, 1906, and *Paraceras melis* (Walker, 1856).

All the bird fleas are widely distributed over the Central Caucasus. There are a few cases of flea species associated with bird hosts from different orders. For example, *Callopsylla gemina* (Ioff, 1946) mainly parasitizes cliff-nesting birds of the orders Columbiformes and Passeriformes. *Callopsylla gypaetina* Peus, 1978 is a monoxenous parasite that inhabits complex nests of the bearded vulture *Gypaetus barbatus* (L.) (Falconiformes) built in rock crevices. Such nests protect adults and fledglings from bad weather to an extent unparalleled among birds of prey, and also provide suitable conditions for metamorphosis and development of fleas (Komarov, 2017).

Passerine birds form the great majority of the avifauna of the Central Caucasus. They are hosts of 18 flea species, including 7 species that inhabit nests of swallows (Hirundinidae): *C. waterstoni* (Jordan, 1925), *Ceratophyllus styx* Rothschild, 1900, *C. farreni* Rothschild, 1905, *C. rusticus* Wagner, 1903, *C. caliotes* Jordan, 1937, *C. hirundinis* (Curtis, 1826), and *F. laeta* Jordan, Rothschild, 1920.

There are also fleas associated with hosts from 10 other passerine families: Motacillidae, Corvidae, Troglodytidae, Prunellidae, Sylviidae, Muscicapidae, Paridae, Sittidae, Passeridae, and Fringillidae, without specific preference of hosts from a certain family by each parasite species. All these fleas belong to the family Ceratophyllidae: *C. gallinae* (Schrank, 1803), *C. pullatus* Jordan et Rothschild, 1920, *C. tribulis* Jordan, 1926, *C. fringillae* (Walker, 1856), *C. garei* Rothschild, 1902, *C. frigoris* Darskaya, 1950, *C. borealis* Rothschild, 1907, and *Dasypsyllus gallinulae* (Dale, 1758).

2. Fleas distributed in the Central Caucasus to the west of the upper reaches of the Cherek-Bezengy and Enguri rivers.

Table 2. Distribution of fleas by orders and families of birds in the Central Caucasus

Flea genera and subgenera	Fl.		Gl.	Ch.	Cl.	Pc.	Passeriformes											Total
	Falconidae (1)	Gypaetidae (1)	Phasianidae (1)	Scolopacidae (1)	Columbidae (1)	Picidae (1)	Hirundinidae (3)	Motacillidae (3)	Corvidae (2)	Troglodytidae (1)	Prunellidae (!)	Sylviidae (1)	Muscicapidae (1)	Paridae (3)	Sittidae (1)	Passeridae (2)	Fringillidae (3)	
Callopsylla (*Orneacus*)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Callopsylla (*Geminopsylla*)	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Ceratophyllus (*Emmareus*)	0	0	0	0	0	0	0	3	0	0	0	1	3	0	0	2	1	3
Ceratophyllus (*Ceratophyllus*)	0	0	0	0	0	1	5	3	1	0	1	0	2	2	1	0	1	11
Dasypsyllus (*Dasypsyllus*)	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	1
Frontopsylla (*Orfrontia*)	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
Total	1	1	1	1	1	1	7	7	1	1	1	2	5	3	1	2	2	20

The number of species recorded as flea hosts is given in parentheses. Orders of birds: Fl., Falconiformes; Gl., Galliformes; Ch., Charadriiformes; Cl., Columbiformes; Pc., Piciformes.

These are parasites of the Caucasian mountain ground squirrel *Spermophilus musicus* Menetries: *Oropsylla idahoensis* (Baker, 1904), *Citellophilus tesquorum* (Wagner, 1898), *F. semura* Wagner et Ioff, 1926, *Ctenophthalmus orientalis* (Wagner, 1898), *R. li* Argyropulo, 1941, and *Neopsylla setosa* (Wagner, 1898), and also the vole fleas *C. kirschenblatti* Argyropulo, 1936 and *R. ucrainica* Wagner et Argyropulo, 1934.

3. Fleas distributed only in the eastern part of the Central Caucasus.

These are the vole parasites *Callopsylla saxatilis* (Ioff et Argyropulo, 1934), *C. kazbegiensis* Goncharov, 1980, *Amphipsylla georgica* Savenko, 1949, *Ctenophthalmus bifurcus* Ioff, 1940, *C. shovi* Rostigayev, 1948, *C. bogatschevi* Wagner et Argyropulo, 1934, and *C. kazbek* Tiflov, 1953. The Norway rat *Rattus norvegicus* (Berkenhout) was found to be infested with fleas typical of wild rodents in the mountain shepherds' bases, and with its specific parasite *Nosopsyllus fasciatus* under the urban conditions in the foothills (Labunets and Korzhov, 1983).

Three species are endemic to the Central Caucasus: *Callopsylla kazbegiensis*, *Ctenophthalmus bifurcus*, and *C. kazbek*, associated with voles. The southern macroslope is much less studied than the northern one, and some more flea species are likely to be found there in the future. Still it may be stated that, for instance, the monoxenous parasites of the Caucasian mountain ground squirrel are absent on the southern macroslope due to the absence of suitable hosts. At the same time, *C. shovi* was not recorded on the northern macroslope although its hosts are widely distributed on both sides of the Main Caucasian Range and collections off them are abundant.

Fleas of 18 species mainly occur in the subalpine and alpine meadow belt: *Callopsylla caspia*, *C. waterstoni*, *C. gemina*, *C. gypaetina*, *Ceratophyllus caliotes*, *C. rusticus*, *Amalaraeus improvisus*, *Paradoxopsyllus hesperius*, *Frontopsylla caucasica*, *F. laeta*, *Amphipsylla kuznetzovi*, *Ctenophthalmus chionomydis*, *C. bifurcus*, *C. shovi*, *C. schuriscus*, *Rhadinopsylla caucasica*, *R. li*, and *Paraneopsylla dampfi.* On the contrary, such species as *N. consimilis* and *C. wagneri* are limited to the steppe foothills and mid-mountain areas.

CONCLUSIONS

There are 87 species of fleas recorded in the Central Caucasus. The known flea fauna of Russia comprises

255 species (Medvedev, 2013); thus, the species diversity of the order Siphonaptera in the Central Caucasus is rather high.

Among mammal fleas in the Central Caucasus, monoxenous and pleioxenous parasites make up 43% of species each, whereas the fractions of oligoxenous and polyxenous species are much smaller. The main groups of hosts for each flea family can be distinguished. These are Carnivora for Pulicidae and Vermipsyllidae, Chiroptera for Ischnopsyllidae, and cricetid rodents for Ceratophyllidae, Leptopsyllidae, and Hystrichopsyllidae (Table 1). It is cricetid hosts that determine the species diversity of mammal fleas in the Central Caucasus. On the whole, the Euro-Siberian Subregion that includes the Greater Caucasus (Medvedev, 2013) has the greatest known number of cricetid rodents parasitized by fleas for the whole Palaearctic (Medvedev, 1998).

The bird fleas include only 2 monoxenous and 6 pleioxenous species, the absolute majority being polyxenous. The association of fleas with particular host species is mainly determined by the construction of their nests. At the same time, the orders and families of birds that are most important for fleas can be distinguished. Most flea species (18) are associated with passerine birds, including the families Hirundinidae, Motacillidae (7 species each), and Muscicapidae (5 species) (Table 2). Fleas parasitizing these hosts make up the considerable number of bird fleas.

The richness of the flea fauna is related to the diversity of hosts and their shelters. Endemism at the species level is not high (3%). The overwhelming majority, 65 species, are widespread in the Central Caucasus. The ranges of the remaining species are narrower in accordance with comparatively small ranges of their specific host (the Caucasian mountain ground squirrel) or for some other reasons, as is the case with certain fleas living on the practically ubiquitous voles.

The flea fauna of the Central Caucasus is highly similar in species composition to the faunas of the Western and Eastern Caucasus. The Jaccard coefficient of faunistic similarity is fairly high: 0.7 for each pair of the groups compared. This is primarily accounted for by the wide distribution of many flea hosts: moles, shrews, the Northern white-breasted hedgehog, bats, canid and mustelid carnivores, dormice, the common, bank, pine, and snow voles, field and house mice, the Norway rat, the bearded vulture, and many passerine birds.

The specific patterns of flea distribution are associated with the limited ranges of specific hosts. These are, for example, the introduced red squirrel with the flea *Tarsopsylla octodecimdentata* (Kolenati, 1863) in the forests of the West Caucasus, and also the inhabitants of meadows: the Prometheus' vole and its parasite *Ctenophthalmus inornatus* in the West and Central Caucasus, the Caucasian mountain ground squirrel with its fleas on the northern slope of the Central Caucasus. A special complex of rodents and fleas on the southern slope of the East Caucasus is formed by inhabitants of semi-desert biotopes: the small five-toed and Williams' jerboas with their parasites *Ophthalmopsylla volgensis* (Wagner et Ioff, 1926) and *Mesopsylla apscheronica* Wagner et Argyropulo, 1911, the social vole with *C. secundus* Wagner, 1916 and *Rhadinopsylla ucrainica* Ioff et Argyropulo, 1934, and the Libyan jird with *Xenopsylla conformis* (Wagner, 1903), *Nosopsyllus laeviceps* (Wagner, 1909), *Stenoponia tripectinata* (Tiraboschi, 1902), *R. ucrainica*, and *Coptopsylla caucasica* Isayeva-Gurvich, 1950.

At the same time, despite large ranges of suitable hosts, many fleas are characterized by local distribution in the Greater Caucasus. These are the marten flea *Chaetopsylla caucasica* (West and Central Caucasus) and the vole fleas *Callopsylla kazbegiensis* Goncharov, 1980, *Ctenophthalmus bifurcus* Ioff, 1940, *C. shovi* Rostigayev, 1948, *C. kazbek* Tiflov, 1953 (Central Caucasus), *Callopsylla saxatilis*, *Stenoponia ivanovi* (Central and East Caucasus), *Amalaraeus dissimilis* (Jordan, 1938), *Ctenophthalmus dagestanicus* Rostigayev, 1967, and *Neopsylla pleskei* Ioff, 1928 (East Caucasus).

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