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ECOLOGY AND ZOOGEOGRAPHY

The Structure and Spatial Organization of the Butterfly Fauna (Lepidoptera, Rhopalocera) of the Ural Mountains

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Abstract—The butterfly fauna of the Ural Mountains contains 233 species: Papilionidae (6 species), Pieridae (23), Lycaenidae (64), Nymphalidae (60), Satyridae (57), and Hesperiidae (23). The number of butterfly species in seven regional and 29 local faunas generally increases gradually from north to south. The mean number of species in the local butterfly faunas is 127 in the southern Urals and slightly over 50 in the Polar Urals. The arealogical structure of the fauna is determined by the distribution of species recorded in 24 meridional and 19 latitudinal groups which together result in 80 distribution patterns. Based on comparison of the local butterfly faunas of the Urals, two large, historically formed faunistic complexes are distinguished: southern and northern. Either complex contains two faunistic complexes of the second order, hypoarctic and boreal in the former, and southern boreal and subboreal in the latter. The faunas of the Kazakhstan part of the Urals form a separate subboreal semi-arid complex, whereas the extreme boreal fauna of Pay-Khoy forms an independent arctic complex.

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The Ural mountain country extends for 2400 km from north to south and crosses eight natural zones and belts: tundra, forest-tundra, taiga, subtaiga, broad-leaved forests, forest-steppe, steppe, and semi-desert. It therefore represents a convenient model territory for studying the spatial distribution of species of some large taxa. In its turn, the group of diurnal butterflies (Rhopalocera) is an interesting and promising object of eco-chorological research due to its diversity and to its being relatively well studied.

The history of the studies of the Ural butterfly fauna counts over 200 years. The accumulated data allow one to analyze its taxonomic and arealogical structure and to reveal the specific traits of its spatial organization. The results of this analysis are reported below.

MATERIALS AND METHODS

This work is mostly based on the material collected by the authors in different regions of the Urals from 1984 to 2013, as well as on published data and information shared by our colleagues. As a result, more or less complete species lists of butterflies were compiled for 7 regions of the Ural mountain country and 29 local faunas (Fig. 1). In this communication, the term "local fauna" refers to the known fauna of a particular geographic region or a sample of this fauna reflecting the results of species surveys, by analogy with the "local flora" concept (Makarov and Matalin, 2009).

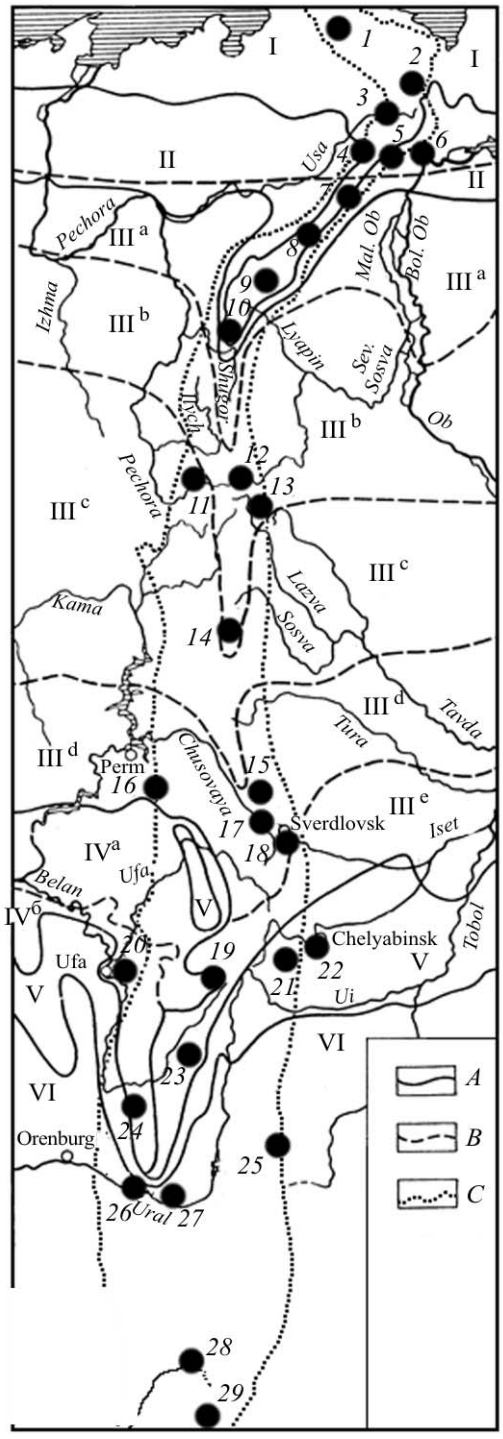
The local faunas were compared by their composition using cluster analysis. The similarity of species lists was assessed using the Jaccard index (I_J) for qualitative data. The similarity dendrogram was built by the unweighted arithmetic mean group method (Pesenko, 1982).

The names of butterflies are given according to the *Catalog of Lepidoptera of Russia* (2008) with minor changes. The species ranges are classified by the typology of Gorodkov (1984, 1992).

RESULTS AND DISCUSSION

Species Diversity of the Regional and Local Faunas

According to our data, the total butterfly fauna of the Ural mountain country includes 233 species representing six families (Table 1). Since the territory in question is vast and has highly heterogeneous natural and climatic conditions, this estimate is certainly not



final; however, proceeding from the results of our long-term studies and the critical analysis of published data, we can reasonably assume that the above number is close to the probable maximum for this group of insects. One may expect relatively few new findings in the future, less than a dozen species.

The South Urals have the richest fauna of butterflies which includes more than 80% of the total fauna of this mountain country (Fig. 2). The species diversity of regional faunas declines almost 2.5-fold towards the Polar Urals. The fauna of the Pay-Khoy Range comprises only 11% of the species recorded in the Urals. Along the latitude gradient, the number of species in the regional faunas of the North and Subpolar Urals is clearly smaller than in the more southern regions; however, a drastic decline in species diversity at the transition from the taiga to the tundra zone, typical of many groups of terrestrial invertebrates, is not observed in butterflies. Moreover, the number of species in the Polar Ural forest-tundra is even slightly greater than in the northern taiga. Here we are dealing with a phenomenon similar to the "ecotone effect" but at the macrogeographic level: the boreal and hypoarctic sets of species combine at the boundary of the two geographic zones, increasing the species richness in the transitional belt. The species diversity drops abruptly between the subzones of shrub tundras and typical tundras in Pay-Khoy (about 69°N). However, this is only a preliminary conclusion since the butterflies of this region, and particularly their intrazonal assemblages, are poorly studied.

The local faunas included in our analysis together comprise 99% of the species of Rhopalocera known from the Urals. The species diversity of the local faunas also distinctly decreases toward the north (Fig. 3). The mean number of species in the local faunas is 127 in the South Urals and slightly above 50 in the Polar Urals (Table 2).

The level of species diversity of the local faunas along the latitude gradient is determined by a set of abiotic, biotic, faunogenetic, and anthropogenic factors acting in various combinations and proportions (Begon et al., 1989; Chernov and Penev, 1993). Of certain importance among the biotic factors are, for instance, trophic associations (Bogacheva, 1997), even though their effect on the geographic distribution of species is weaker than the effect of climatic parameters (Dowries, 1964; Danks, 1986); this was demonstrated for various groups including Lepidoptera (Virtanen and Neuvonen, 1999). In some groups of terrestrial arthropods, the number of species was shown to depend on the temperature parameters (Chernov and Penev, 1993; Esyunin, 1995; Esyunin and Efimik, 2000; Esyunin and Kozminykh, 2000; Chernov, 2002). We have also observed a considerable effect of temperatures on the number of species in the local butterfly faunas in the mountain part of the Urals. In particu-

Fig. 1. Schematic map of the study area. Vegetation zones (after Gorchakovskii, 1975): (I) tundra; (II) forest-tundra; (III) boreal forests [(IIIa) sub-forest-tundra sparse forests (extreme northern taiga); (IIIb) northern taiga; (IIIc) middle taiga; (IIId) southern taiga; (IIIe) sub-forest-steppe pine and birch forests]; (IV) broad-leaved forests [(IVa) mixed broad-leaved-conifer forests; (IVb) broad-leaved forests]; (V) forest-steppe; (VI) steppe.
Boundaries: (A) zones; (B) subzones; (C) the Ural mountain country.
Local faunas (black circles): (***1***) Pay-Khoy, Malaya Padeya Upland, upper reaches of the Vasyakha, Greater Ngoyu, and Yangorei rivers, coll. of A.G. Tatarinov (2010), 15 species; (***2***) Polar Urals, Ochenyrd Range as far as the confluence of the Greater and Lesser Kara, coll. of A.G. Tatarinov and O.I. Kulakova (2007, 2008, 2010), published data (Kusnetzov, 1925), 45 species; (***3***) Polar Cis-Ural region and the Urals from Vorkuta to Enganepe Ridge, coll. of A.G. Tatarinov and O.I. Kulakova (1993, 2004, 2007–2010), published data (Sedykh, 1974, 1977; Gorbunov and Olshvang, 1993), 56 species; (***4***) Polar Urals, branch railway line Seida–Labytnangi from Polyarnyi Ural station (98th km) to Sob station (120th km), coll. of V.N. Olshvang, P.Yu. Gorbunov, A.G. Tatarinov, and O.I. Kulakova (1970–2010), published data (Sedykh, 1974, 1977; Korshunov et al., 1985; Lvovsky and Morgun, 2007, etc.), 60 species; (***5***) Polar Urals, branch railway line Seida–Labytnangi from Sob station to Krasnyi Kamen' station (141st km), Rai-Iz Range, coll. of V.N. Olshvang, I.A. Bogacheva, P.Yu. Gorbunov, A.G. Tatarinov, O.I. Kulakova, S.P. Reshetnikov, Yu.A. Shevnin, V.O. Zurilina, and others (1970–2008), published data (Sedykh, 1974, 1977; Korshunov et al., 1985; Lvovsky and Morgun, 2007, etc.), 69 species; (***6***) Polar Trans-Ural region along the left bank of the Ob, from Kharp station to Labytnangi and lower course of the Khadyta-Yakha, coll. of V.N. Olshvang, I.A. Bogacheva, P.Yu. Gorbunov, A.G. Tatarinov, and O.I. Kulakova (1970–2008), published data (Korshunov et al., 1985), 54 species; (***7***) Polar Cis-Ural region and the Ural Mountains, Pagaty, Bolshaya Lokhorta Lakes, Kokpel Pass, coll. of A.G. Tatarinov and O.I. Kulakova (2007, 2010), 57 species; (***8***) Subpolar Urals, middle course of the Kozhim, Maldy-Nyrd Range, coll. of A.G. Tatarinov and O.I. Kulakova (2000), 51 species; (***9***) Subpolar Urals, Manaraga Mt., Olenevodov Plateau as far as the upper reaches of the Vangyr, coll. of A.G. Tatarinov and O.I. Kulakova (2006, 2011), 47 species; (***10***) Subpolar Urals, middle course of the Lesser Patok as far as Telposiz Mt., coll. of A.G. Tatarinov (1995, 1996), 58 species; (***11***) North Cis-Ural region, Ust-Unya to Garevka Levoberezhnaya field station, coll. of A.G. Tatarinov and O.I. Kulakova (1992, 1993, 1998, 2008), pers. comm. of A.V. Bobretsov and N.D. Neufeld, 79 species; (***12***) North Urals, Medvezhya, Koip, Yany-Pupu-N'er, and Man'-Pupu-N'er Mts, coll. of A.G. Tatarinov (1992, 1993), and A.A. Medvedev (2002), pers. comm. of A.V. Bobretsov and N.D. Neufeld, 73 species; (***13***) North Trans-Ural region, upper reaches of the Lozva, Burmantovo and Vizhai settl., coll. of P.Yu. Gorbunov (1991, 1993) and L.K. Korshikov (2005), 71 species; (***14***) North Urals, upper reaches of the Lobva, Kytlym, Denezhkin Kamen and Konzhakovskii Kamen Mts, coll. of P.Yu. Gorbunov (1991) and S.F. Melyakh (2007), published data (Baranchikov, 1980), 72 species; (***15***) Middle Urals, Visim Reserve, published data (Olshvang et al., 2006), 89 species; (***16***) Middle Cis-Ural region, lower course of the Sylva, Kungur, coll. of N.A. Litvinov and students of Perm State University (1953–1988), published data (Gelzermann, 1906), 122 species; (***17***) Middle Urals, N part of Kirgshan Ridge, Kuzino and Staroutkinsk settl., coll. of P.Yu. Gorbunov and Yu.A. Shevnin (1984–1991), 103 species; (***18***) Middle Trans-Ural region, Yekaterinburg, including Sysert Distr., coll. of P.Yu. Gorbunov (1984–1996) and students of Ural State University (1958–1991), published data (Gorbunov and Olshvang, 1997), 111 species; (***19***) South Urals, Iremel Mt., Tyulyuk, coll. of V.N. Olshvang, K. Nupponen, T. Nupponen, and others (1977–1991, 1995–2007), published data (Gorbunov et al., 1992), 107 species; (***20***) South Cis-Ural region, Ufa, coll. of M.G. Migranov and A.Sh. Gabidullin (1972–1991), published data (Grosser, 1983), 125 species; (***21***) South Urals, Miass and Chebarkul, coll. of A.V. Lagunov, B.V. Krasutskii, and V.O. Zurilina (1970–2007), 125 species; (***22***) South Trans-Ural region, Chelyabinsk, including the south of Sosnovsky Distr., coll. of A.V. Razboinikov, V.G. Barkhatov, and V.O. Zurilina (1968–2007), 124 species; (***23***) South Urals, S part of Bashkir Reserve, coll. of P.Yu. Gorbunov (1991), published data (Gorbunov et al., 1992), 124 species; (***24***) South Urals, interfluve of the Belaya and the Greater Ik between Bugulchan and Mrakovo, coll. of M.G. Migranov and A.Sh. Gabidullin (1980–1990), 128 species; (***25***) South Trans-Ural region, Arkaim Reserve and Bredinsky pine forest, coll. of E.A. Kulyginsky, V.G. Barkhatov (1968–1990), and P.Yu. Gorbunov (1998, 2007), 145 species; (***26***) South Urals, interfluve of the Ural and the Sakmar S of Kuvandyk and the Ural valley near Donskoe, coll. of P.Yu. Gorbunov, V.O. Zurilina, and V.G. Barkhatov (1991–2005), 153 species; (***27***) South Trans-Ural region, Guberlinskie Mts near Novotroitsk, coll. of P.Yu. Gorbunov (2004, 2007), published data (Lukhtanov and Lukhtanov, 1994), 116 species; (***28***) Upper reaches of the Emba, coll. of P.Yu. Gorbunov, 42 species; (***29***) Mugodzhary, S part between Berchogur and source of the Emba, coll. of P.Yu. Gorbunov (2007–2012), published data (Lukhtanov and Lukhtanov, 1994), 62 species.

lar, according to the data of the weather stations positioned in the foothills and valleys, the number of species along the vast Ural Range (local faunas 1–26) is strongly and significantly correlated ($p < 0.05$) with the mean temperatures of January ($r = 0.76$) and July ($r = 0.87$), the mean annual air temperature ($r = 0.80$), and the duration of the frost-free season ($r = 0.92$). The minimum temperatures affect the wintering success of butterflies, especially the species hibernating as pupae or eggs. The maximum and mean annual temperatures, and also the duration of the frost-free season usually determine the possibility of completing the development cycle in one year (Danilevsky, 1949).

The highest species diversity of butterflies in the Urals (153 species) is observed at the south boundary of the mountain forest-steppe, in the Ural-Sakmara interfluve (local fauna 26). In more southern regions, such as the Guberlinskie Mountains, the adjacent mountain areas of Aktyubinsk Province (Kazakhstan), Mugodzhary, and the upper reaches of the Emba, diversity drops drastically down to 40–60 species due to

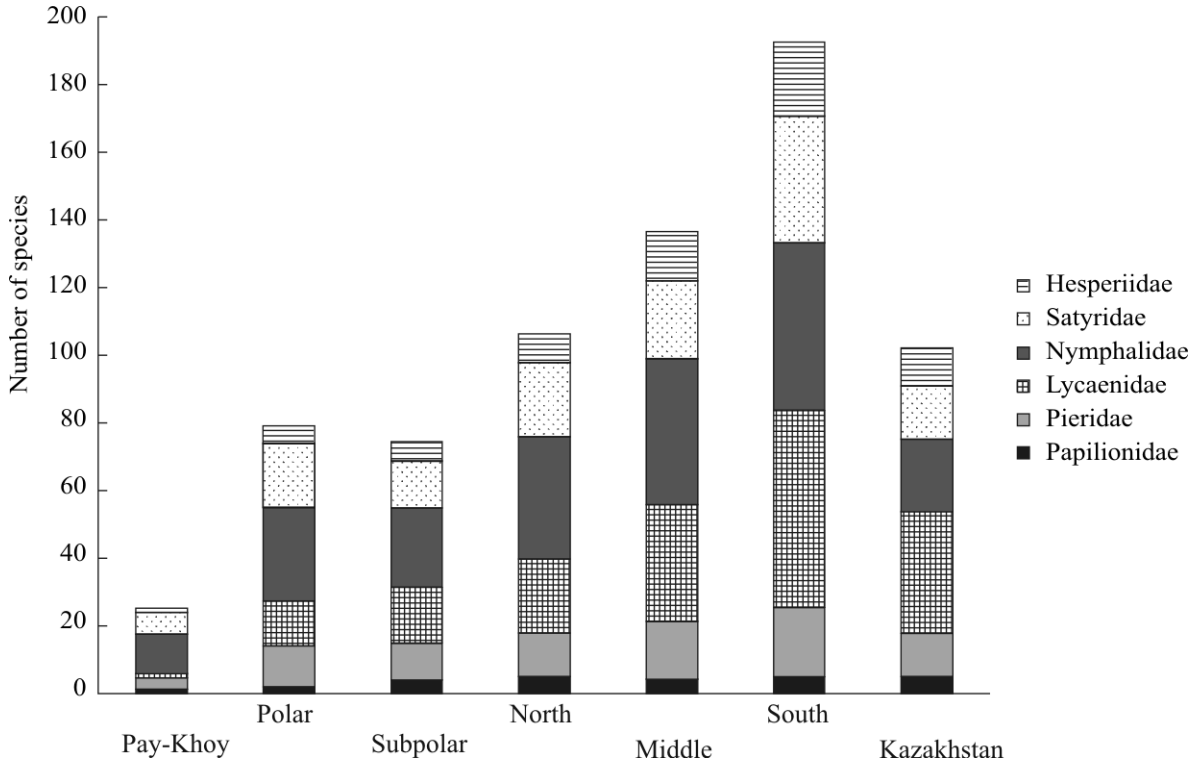


Fig. 2. The species richness and taxonomic structure (relative abundance of different families) of the butterfly fauna in different regions of the Urals.

a higher aridity and lower altitudes of the mountain ridges and the plateau. The coefficients of correlation between the number of species in the local faunas and humidity are low and non-significant in the Russian part of the Ural Range, whereas in the extreme south of this mountain country within the Kazakhstan territory, the species diversity of butterflies is positively correlated with annual precipitation ($r = 0.86$, $p < 0.05$).

Thus, the main trend in the species diversity of Rhopalocera in the Urals, namely a decrease in the number of species and genera toward the north, is determined by the regional heat supply, whereas dependence on humidity can be observed only under the extreme continental conditions in the southern part of this mountain country.

The Taxonomic Structure of the Fauna

The core of the butterfly fauna of the Urals is almost equally formed by the families Lycaenidae (64 species), Nymphalidae (60), and Satyridae (57), which together comprise about 78% of the species (Table 3). These families also include the greatest number of recorded genera: 20, 18, and 18, respectively. The families Pieridae and Hesperiidae are represented by the same number of species (23) and nearly the same number of genera (9 and 10). The family Papilionidae is represented by 6 species (2.5%) in 5 genera.

The largest butterfly genera in the Ural fauna are *Clossiana* of the family Nymphalidae and *Erebia* of the family Satyridae. The representation (fraction of the global diversity) of the former genus in the Urals is about 35%, that of the latter, about 15%.

The species diversity of all the families decreases northwards, this trend being the most distinct in Lycaenidae and Hesperiidae (Table 2). These families are represented by 4 times as many species in the South as in the Polar Urals. The number of species of Nymphalidae and Satyridae even slightly increases in the Polar Ural local faunas due to the genera *Clossiana*, *Erebia*, and *Oeneis* which are represented by species from different landscape-zonal categories in this region. The presence of these butterflies determines the above-mentioned “ecotone effect” in the forest-tundra belt.

In addition to changes in the number of species and genera, considerable changes in the composition of the butterfly families are observed along the latitude gradient of the Urals. For example, only two species, the

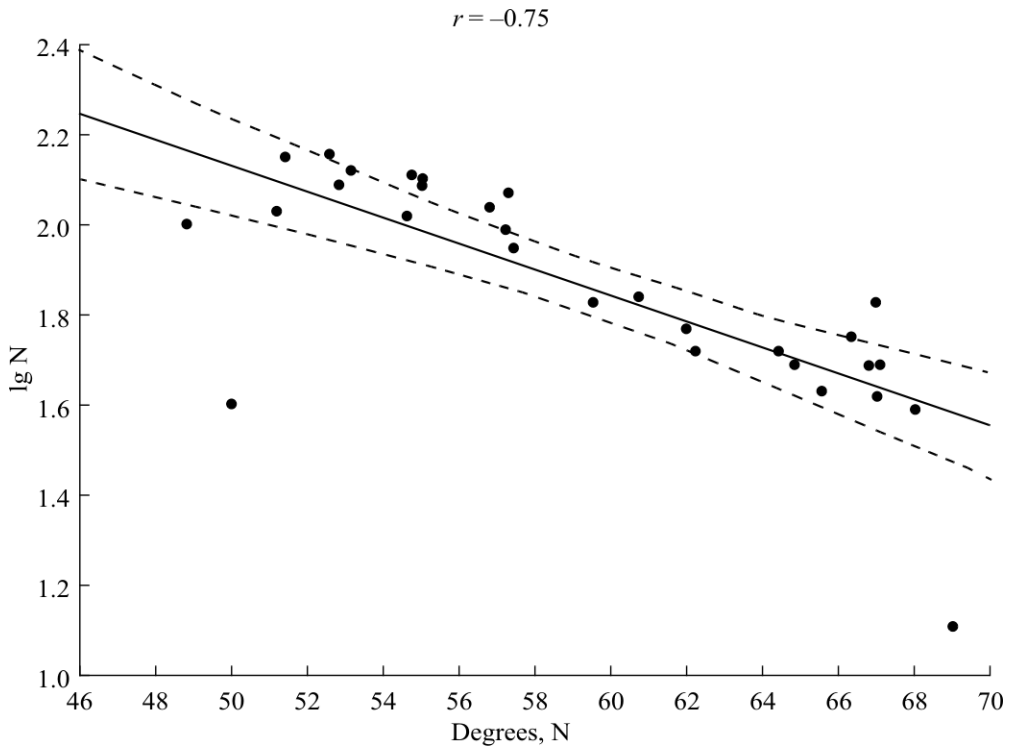


Fig. 3. Relation between the number of species (lg *N*) in the local butterfly faunas of the Urals (1–29) and the latitude; *r* is Spearman's correlation coefficient ($p < 0.05$); the confidence intervals are shown as dashed lines.

polyzonal *Pieris napi* and the subcosmopolitan *Vanessa cardui*, are shared by local faunas 1 and 29 positioned at the opposite ends of the mountain country. The two most diverse local faunas of the Polar and South Urals (5 and 26) reveal 13%, 15%, 24%, and 35% similarity in the species composition of the families Lycaenidae, Hesperiidae, Nymphalidae, and Pieridae, respectively, and have no shared species of the family Satyridae.

The Arealogical Structure of the Fauna

The arealogical structure of the butterfly fauna of the Ural mountain country is highly heterogeneous. Its species belong to 19 latitudinal and 24 longitudinal groups (Table 4). The largest latitudinal groups are the subboreal (74 species, 31.8%) and the temperate ones (46 species, 19.7%), which agrees well with the geographic position of the mountain range. The southern latitudinal elements (nemoral, temperate-subtropical, and subboreal-subtropical ones) together comprise 37 species, or 15.9% of Rhopalocera occurring in the Urals. The ranges of 33 species (14.2%) lie mostly within the boreal belt while their peripheral parts may extend into the Hypoarctic, the mixed and deciduous forest zone, and the subboreal mountain areas (the hypoarctic-boreomontane, hypoarctic-boreal, boreomontane, and boreal species). The representatives of the Arctic fauna (in the broad sense) are less diverse: there are only 16 such species (6.9%) even if we include those extending far into the boreal and subboreal belts in the mountains (the arctic-goltsy, hypoarctic-goltsy, and hypoarctic-goltsy-alpine ones). A characteristic trait of the Ural butterfly fauna is a small number of strictly mountain-dwelling (goltsy, goltsy-alpine, and montane) elements, which together comprise only 8 species (3.4%).

As can be expected, the largest longitudinal groups are the trans-Palaearctic and trans-Eurasian ones, which together include 69 species (29.6%). The fraction of Holarctic elements (trans-Holarctic, sub-trans-Holarctic, and Eurasian-Alaskan ones) includes 32 species, or 13.7% of the fauna. The relatively small fraction of these groups can be explained by the revised taxonomic status of the Eurasian and North American populations of many species which used to be regarded as Holarctic. For example, the ranges of *Pieris napi*, *Celastrina argiolus*, *Clossiana selene*, *Coenonympha tullia*, *Oeneis jutta*, and some other species are now believed to be restricted to the Palaearctic. The Ural Range forms the eastern distribution

Table 1. Species composition of the regional and local (1–29) butterfly faunas of the Urals

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
Papilionidae							
Papilio machaon Linnaeus, 1758, Pan-Holarctic (trans-Holarctic polyzonal)	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
Iphiclides podalirius (Linnaeus, 1758), Western-Central Eurasian subboreal	–	–	–	11	15, 16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
Zerynthia polyxena ([Denis et Schiffer-müller], 1775), European nemoral	–	–	–	–	–	26, 27	+
Parnassius apollo (Linnaeus, 1758), Euro-Siberian-Central Asian temperate	–	–	+	+	15, 16, 17, 18	19, 21, 22, 24, 25, 26	+
P. corybas Fischer de Waldheim, 1823 Eurasian-Alaskan hypoarctic-goltsy-alpine	?	2, 3, 4, 5, 7	8, 9, 10	12, 14	–	–	–
Driopa mnemosyne (Linnaeus, 1758), European-Central Asian temperate	–	–	+	11, 12	15, 16, 17, 18	19, 20, 23, 24, 26, 27	+
Pieridae							
Leptidea morsei (Fenton, 1881), Central European–Trans-Asian temperate	–	–	?	13, 14	15, 16, 17, 18	19, 20, 21, 22, 23	–
L. reali Reissinger, 1989, Euro-Siberian-Central Asian temperate	–	–	?	+	16, 18	20, 21, 22, 23, 24, 25, 26	–
L. sinapis (Linnaeus, 1758), Euro-Siberian-Central Asian temperate	–	5, 7	10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	–
Aporia crataegi (Linnaeus, 1758), Trans-Palaearctic temperate	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
Pieris brassicae (Linnaeus, 1758), Trans-Palaearctic temperate	–	7	10	11, 12	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
P. napi (Linnaeus, 1758), Trans-Palaearctic polyzonal	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
P. rapae (Linnaeus, 1758), multiregional	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
Pontia chloridice (Hübner, [1813]), Central European–trans-Asian subboreal-subtropical	–	–	–	–	16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
P. daplidice (Linnaeus, 1758), Trans-Palaearctic temperate-subtropical	–	–	10	11, 12, 13	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
P. callidice (Hübner, [1800]), Eurasian-Alaskan hypoarctic-goltsy-alpine	?	2, 3, 4, 5, 6, 7	8, 9, 10	12, 14	15, 17, 18	21, 22	–
Zegris eupheme (Esper, [1805]), Western-Central Palaearctic subboreal-subtropical	–	–	–	–	–	26, 27	28, 29
Euchloe ausonia (Hübner [1803]), Western-Central Eurasian subboreal-subtropical	–	–	–	–	16, 17, 18	20, 23, 25, 26, 27	28, 29
Anthocharis cardamines (Linnaeus, 1758), trans-Eurasian hypoarctic-temperate	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
Gonepteryx rhamni (Linnaeus, 1758), Western-Central Palaearctic temperate	–	3, 5, 6	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
Colias alfacariensis Ribbe, 1905, Western-Central Eurasian subboreal	–	–	–	–	–	26, 27	28
C. chrysotheme (Esper, [1781]), Western-Central Eurasian subboreal	–	–	–	–	16, 18	20, 22, 24, 25, 26, 27	+
C. crocea (Geoffroy, 1785), Western Palaearctic subboreal-subtropical	–	–	–	–	16	20, 24, 25, 26	?
C. erate (Esper, [1805]), Trans-Eurasian subboreal-subtropical	–	–	–	–	–	20, 22, 23, 24, 25, 26, 27	28, 29
C. hecla Lefebvre, 1836, Trans-Holarctic arctomontane	1	2, 3, 4, 5, 6	–	–	–	–	–
C. hyale (Linnaeus, 1758), Euro-Siberian–Central Asian temperate	–	5, 6, 7	8, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
C. myrmidone (Esper, [1781]), European subboreal	–	–	–	–	16, 17, 18	20, 21, 22, 23, 24, 25, 26	–
C. palaeno (Linnaeus, 1761), Trans-Holarctic hypoarctic-boreomontane	+	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 21	–
C. tyche (Boeber, 1812), Trans-Holarctic arctomontane	+	4	–	–	–	–	–
Lycaenidae							
Thecla betulae (Linnaeus, 1758), Trans-Eurasian temperate	–	–	–	11	16, 18	20, 21, 22, 24, 26	–
Favonius quercus (Linnaeus, 1758), Western Palaearctic nemoral	–	–	–	–	–	23, 24, 26	–
Nordmannia acaciae (Fabricius, 1787), Western Eurasian nemoral	–	–	–	–	–	20, 24, 26, 27	29
N. ilicis (Esper, 1779), Western Eurasian nemoral	–	–	–	–	–	20, 24, 26	–
N. pruni (Linnaeus, 1758), Trans-Eurasian temperate	–	–	–	11, 12, 13	16, 17, 18	19, 20, 21, 22, 23, 24, 26, 27	+
N. spini ([Denis et Schiffermüller], 1775), Western Eurasian nemoral	–	–	–	–	16	24, 25, 26, 27	29
N. w-album (Knoch, 1782), Amphi-Eurasian nemoral	–	–	–	–	18	19, 20, 21, 22, 24, 25, 26	+
Neolycaena rhymnus (Eversmann, 1832), Central Eurasian subboreal	–	–	–	–	?	20, 21, 22, 23, 24, 25, 26, 27	28, 29
Callophrys rubi (Linnaeus, 1758), Trans-Palaearctic hypoarctic-temperate	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
C. suaveola (Staudinger, 1881), Central Eurasian subboreal	–	–	–	–	–	26, 27	29
Ahlbergia frivaldszkyi (Lederer, 1853), Ural–Trans-Asian boreomontane	–	–	–	13	–	–	–
Lycaena belle ([Denis et Schiffermüller], 1775), Trans-Eurasian hypoarctic-temperate	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
L. phlaeas (Linnaeus, 1761), Pan-Holarctic (Trans-Holarctic polyzonal)	–	2, 3, 4, 5, 6	+	11, 12	15, 16, 17, 18	20, 21, 22, 23, 24, 25, 26, 27	+
L. alciphron (Rottemburg, 1775), Western-Central Palaearctic subboreal	–	–	–	–	+	20, 21, 22, 23, 24, 25, 26, 27	29
L. dispar ([Haworth], 1802), Trans-Eurasian subboreal	–	–	–	9	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
L. thersamon (Esper, [1784]), Western-Central Eurasian subboreal-subtropical	–	–	–	–	–	21, 22, 23, 24, 25, 26, 27	28, 29
L. tityrus (Poda, 1761), Western-Central Eurasian subboreal	–	–	–	–	16	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
L. virgaureae (Linnaeus, 1758), Trans-Eurasian temperate	–	–	10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
L. hippothoe (Linnaeus, 1761), Trans-Eurasian hypoarctic-boreomontane	–	2, 3, 4, 5, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 25	–
Athamantia athamantis (Eversmann, 1854), Turanian	–	–	–	–	–	–	28
A. japhetica (Nekrutenko et Effendi, 1983), Turanian	–	–	–	–	–	27	29
Lampides boeticus (Linnaeus, 1767), Paleotropical	–	–	–	–	–	26	28, 29
Cupido minimus (Fuessly, 1775), Trans-Eurasian hypoarctic-temperate	–	2, 3, 4, 5, 7	9, 10	11, 12	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
C. osiris (Meigen, 1829), Western-Central Eurasian subboreal	–	–	–	–	–	20, 21, 22, 24, 25, 26, 27	–
C. alcetas (Hoffmannsegg, 1804), Western-Central Eurasian temperate	–	–	–	11, 13, 14	15, 16, 17, 18	19, 20, 21, 23, 24, 25	–
C. argiades (Pallas, 1771), Trans-Eurasian temperate	–	–	–	?	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	?
Tongea fischeri (Eversmann, 1843), Ural–Trans-Asian subboreal	–	–	–	–	–	21, 22, 24, 25, 26, 27	+
Celastrina argiolus (Linnaeus, 1758), Trans-Eurasian temperate	–	5, 6, 7	9	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
Scolitantides orion (Pallas, 1771), Trans-Eurasian temperate	–	–	–	–	17	19, 20, 21, 22, 23, 24, 25, 26, 27	+
S. bavius (Eversmann, 1832), Western Palaearctic subboreal	–	–	–	–	–	25, 26, 27	?
S. vicrama (Moore, 1865), Western-Central Eurasian subboreal-subtropical	–	–	–	–	–	21, 25, 26, 27	28, 29
S. antracias (Christoph, 1877), Turanian	–	–	–	–	–	–	28
Glaucopsyche alexis (Poda, 1761), Western-Central Palaearctic temperate	–	–	–	+	16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
Maculinea alcon ([Denis et Schiffer-müller], 1775), Trans-Eurasian subboreal	–	–	–	–	16	19, 20, 21, 22, 23, 24, 25, 26, 27	–

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
M. arion (Linnaeus, 1758), Trans-Eurasian subboreal	–	–	–	–	16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
M. nausithous (Bergsträsser, 1779), Western-Central Eurasian subboreal	–	–	–	–	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	?
M. teleius (Bergsträsser, 1779), Trans-Eurasian subboreal	–	–	–	–	16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
Plebeius argus (Linnaeus, 1758), Trans-Eurasian temperate	–	+	10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
P. argyrognomon (Bergsträsser, 1779), Trans-Eurasian subboreal	–	–	–	–	+	19, 20, 21, 22, 23, 24, 25, 26, 27	?
P. maracandicus (Erschoff, 1874), Turanian	–	–	–	–	+	–	28
P. idas (Linnaeus, 1761), Trans-Holarctic hypoarctic-temperate	–	3, 7	9, 10	11, 12	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	?
P. pylaon (Fisher de Waldheim, 1832), Western-Central Eurasian subboreal	–	–	–	–	–	24, 25, 26, 27	28, 29
P. cyane (Eversmann, 1837), Central Eurasian subboreal	–	–	–	–	–	26	+
P. optilete (Knoch, 1781), Sub-trans-Holarctic hypoarctic-boreomontane	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 21, 22, 23	–
Agriades glandon (de Prunner, 1798), Trans-Holarctic hypoarctic-goltsy-alpine	?	2, 3, 4, 5	?	–	–	–	–
A. orbitulus (Püngeler, 1798), Trans-Eurasian goltsy-alpine	–	–	–	13	–	19	–
Aricia agestis ([Denis et Schiffermüller], 1775), Western-Central Palaearctic subboreal-subtropical	–	–	–	–	–	26	?
A. artaxerxes (Fabricius, 1793), Trans-Eurasian temperate	–	–	9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
A. nicias (Meigen, 1830), Western-Central Eurasian boreomontane	–	–	?	11, 12, 13, 14	15, 16, 17, 18	19, 21, 22, 23	–
Eumedonia eumedon (Esper, [1780]), Trans-Eurasian temperate	–	–	10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	–
Polyommatus amandus (Schneider, 1792), Trans-Palaearctic temperate	–	–	+	11, 12, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
P. icarus (Rottemburg, 1775), Trans-Palaearctic polyzonal	–	3, 5, 6, 7	8, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
P. (*eros*) *boisduvalii* (Herrich-Schaffer, [1844]), Eastern European subboreal	–	–	–	–	–	22, 24, 26	–
P. (*eros*) *erotides* (Staudinger, 1886), Eastern European–trans-Asian subboreal	–	–	–	–	–	20, 22, 23, 25, 26, 27	+
P. (*eros*) *kamtchadalis* (Sheljuzhko, 1933), Ural–trans-Asian hypoarctic-boreomontane	?	2, 3, 4, 5, 7	8	–	–	–	–
P. thersites (Cantener, 1834), Western-Central Palaearctic subboreal	–	–	–	–	–	19, 20, 21, 22, 23, 24, 25, 26, 27	29

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
P. coridon (Poda, 1761), European subboreal	–	–	–	–	–	20, 24	–
P. coelestinus (Eversmann, 1843), Western Eurasian subboreal	–	–	–	–	–	20, 24, 25, 26, 27	29
P. daphnis ([Denis et Schiffermüller], 1775), Western Eurasian subboreal	–	–	–	–	–	20, 24, 25, 26, 27	29
P. damocles (Herrich-Schäffer, [1844]), Eastern European subboreal	–	–	–	–	–	26, 27	?
P. damon ([Denis et Schiffermüller], 1775), Western-Central Eurasian subboreal	–	–	–	–	16	20, 21, 22, 23, 25, 26	–
P. damone (Eversmann, 1841), Central Eurasian subboreal	–	–	–	–	–	25, 26	+
P. ripartii (Freyer, 1830), Western-Central Eurasian subboreal	–	–	–	–	–	21, 25	–
Cyaniris semiargus (Rottemburg, 1775), Trans-Palaearctic temperate	–	3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
Nymphalidae							
Apatura ilia ([Denis et Schiffermüller], 1775), Amphi-Eurasian subboreal	–	–	–	–	16, 17, 18	19, 20, 21, 22, 24, 25, 26, 27	–
A. iris (Linnaeus, 1758), Amphi-Eurasian subboreal	–	–	–	–	15, 16, 17, 18	19, 20, 21, 22, 25	–
Limenitis camilla (Linnaeus, 1764), Amphi-Eurasian subboreal	–	–	–	–	16, 17, 18	19, 20, 22, 23, 24, 25, 26	–
L. populi (Linnaeus, 1758), Trans-Eurasian temperate	–	–	?	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 25	–
Neptis rivularis (Scopoli, 1763), Central European–trans-Asian temperate	–	5	–	11, 13	16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	–
N. sappho (Pallas, 1771), Central European–trans-Asian subboreal	–	–	–	13, 14	15, 16, 17, 18	19, 20, 21, 22, 24, 26	–
Nymphalis antiopa (Linnaeus, 1758), Circumtemperate	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
N. polychloros (Linnaeus, 1758), Western-Central Palaearctic subboreal	–	–	–	?	?	20, 23, 24, 25, 26	–
N. vaualbum ([Denis et Schiffermüller], 1775), circumtemperate	–	–	–	11	15, 16, 17, 18	20, 21, 22, 23, 24, 25, 26	–
N. xanthomelas (Esper, [1781]), Central European–trans-Asian hypoarctic-temperate	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
N. urticae (Linnaeus, 1758), Trans-Eurasian temperate	–	3, 4, 5, 6, 7	8, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 25, 26, 27	29
N. io (Linnaeus, 1758), Trans-Eurasian temperate	–	–	–	11	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
Polygonia c-album (Linnaeus, 1758), Trans-Palaearctic temperate	–	5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
Vanessa atalanta (Linnaeus, 1758), multiregional	–	3, 5, 7	10	11, 12	16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
V. cardui (Linnaeus, 1758), subcosmopolitan	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
Araschnia levana (Linnaeus, 1758), Trans-Eurasian temperate	–	5, 6	+	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	–
Euphydryas aurinia (Rottemburg, 1775), Western-Central Palaearctic subboreal	–	–	–	–	18	21, 23, 25, 26, 27	29
E. ichnea (Boisduval, [1833]), Trans-Eurasian (European disjunctive) boreomontane	–	–	–	11, 13, 14	17	19, 25	–
E. iduna (Dalman, 1816), Trans-Eurasian hypoarctic-goltsy-alpine	–	2, 3	–	–	–	–	–
E. maturna (Linnaeus, 1758), Western-Central Eurasian temperate	–	5, 6, 7	8, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 25, 26, 27	–
Melitaea arduinna (Esper, [1784]), Central Eurasian subboreal	–	–	–	–	–	20, 22, 23, 24, 26, 27	+
M. cinxia (Linnaeus, 1758), Trans-Palaearctic subboreal	–	–	–	–	16, 18	20, 21, 22, 23, 24, 25, 26, 27	+
M. diamina (Lang, 1789), Trans-Eurasian temperate	–	–	?	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 25, 26	–
M. didyma (Esper, [1779]), Western-Central Palaearctic subboreal-subtropical	–	–	–	–	16	20, 21, 22, 23, 24, 25, 26, 27	29
M. trivia ([Denis et Schiffermüller], 1775), Western-Central Eurasian subboreal	–	–	–	–	–	20, 25, 26	–
M. robertsi Butler, 1880, Irano-Turanian subboreal-subtropical	–	–	–	–	–	26, 27	29
M. athalia (Rottemburg, 1775), Trans-Eurasian temperate	–	–	?	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	–
M. aurelia Nickerl, 1850, Western-Central Eurasian subboreal	–	–	–	–	16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
M. brithomartis Assmann, 1847, Central European–trans-Asian subboreal	–	–	–	–	15, 16, 17, 18	20, 21, 22, 23, 24, 25, 26, 27	+
M. phoebe ([Denis et Schiffermüller], 1775), Trans-Eurasian subboreal	–	–	–	–	16, 17	20, 21, 22, 23, 24, 25, 26, 27	28, 29
M. ornata (Christoph, 1893), Western Eurasian subboreal-subtropical	–	–	–	–	–	24, 25, 26	29
Argynnis paphia (Linnaeus, 1758), Trans-Palaearctic temperate	–	5	10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24	–
Pandoriana pandora ([Denis et Schiffermüller], 1775), Western-Central Palaearctic subboreal-subtropical	–	–	–	–	–	+	28, 29

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
Argyronome laodice (Pallas, 1771), Amphi-Eurasian nemoral	–	–	–	–	16, 18	21	?
Speyeria aglaja (Linnaeus, 1758), Trans-Palaearctic temperate	–	5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
Fabriciana adippe (Rottemburg, 1775), Trans-Eurasian temperate-subtropical	–	–	?	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
F. niobe (Linnaeus, 1758), Western-Central Eurasian subboreal-subtropical	–	–	–	14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
Issoria lathonia (Linnaeus, 1758), Western-Central Palaearctic temperate-subtropical	–	–	10	11, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	29
I. eugenia (Eversmann, 1847), Eastern European–trans-Asian hypoarctic-boreomontane	+	2, 3, 4, 5, 6, 7	8, 9	+	–	–	–
Brenthis daphne ([Denis et Schiffermüller], 1775), Amphi-Eurasian subboreal	–	–	–	–	–	19, 20, 21, 22, 23, 24, 25, 26, 27	+
B. hecate ([Denis et Schiffermüller], 1775), Western-Central Eurasian subboreal	–	–	–	–	–	22, 23, 24, 25, 26	–
B. ino (Rottemburg, 1775), Trans-Eurasian temperate	–	3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
Boloria aquilonaris (Stichel, 1908), Trans-Eurasian hypoarctic-boreal	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17	19	–
B. alaskensis (Holland, 1900), Eurasian-Alaskan arcto-goltsy	1	2, 3, 4, 5, 6, 7	8, 9	12	–	–	–
B. napaea (Hoffmannsegg, 1804), Trans-Eurasian goltsy-alpine	–	?	9	14	–	–	–
Clossiana eunomia (Esper, [1799]), Trans-Holarctic hypoarctic-boreomontane	+	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 21, 22, 23	–
C. angarensis (Ershoff, 1870), Eastern European–trans-Asian hypoarctic-boreal	–	2, 3, 4, 5, 6, 7	8, 9	13, 14	15, 17	–	–
C. chariclea (Schneder, 1792), Trans-Holarctic arcto-goltsy	1	2, 3, 4, 5	–	–	–	–	–
C. titania (Esper, [1793]), Trans-Eurasian boreomontane	–	–	10	11, 12, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25	–
C. dia (Linnaeus, 1758), Trans-Eurasian temperate	–	–	–	+	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	+
C. thore (Hübner, [1803]), Trans-Eurasian hypoarctic-boreomontane	+	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 21	–
C. euphrosyne (Linnaeus, 1758), Trans-Eurasian temperate	–	3, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
C. selene ([Denis et Schiffermüller], 1775), Trans-Eurasian hypoarctic-temperate	+	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25	–

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
C. selenis (Eversmann, 1837), Eastern European–trans-Asian temperate	–	6	–	11	16, 18	22, 23	–
C. oscarus (Eversmann, 1844), Ural–trans-Asian boreal	–	–	–	–	+	–	–
C. freija (Thunberg, 1791), Trans-Holarctic hypoarctic-boreal	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	?	21	–
C. frigga (Thunberg, 1791), Trans-Holarctic hypoarctic-boreal	1	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	16	–	–
C. improba (Butler, 1877), Circumpolar (trans-Holarctic metaarctic)	1	2, 3, 4, 5, 6	–	–	–	–	–
C. polaris (Boisduval, 1829), Circumpolar (trans-Holarctic metaarctic)	1	2, 3, 4, 5, 7	–	–	–	–	–
C. tritonia (Boeber, 1812), Ural-Alaskan montane	–	4, 5	–	–	–	–	–
Satyridae							
Melanargia galathea (Linnaeus, 1758), Western Palaearctic nemoral	–	–	–	–	–	20, 21, 24, 26	–
M. russiae (Esper, [1784]), Western-Central Eurasian subboreal	–	–	–	–	16, 17	19, 20, 22, 23, 24, 25, 26, 27	28, 29
Pararge aegeria (Linnaeus, 1758), Western Palaearctic subboreal-subtropical	–	–	–	11, 12	15, 16, 17	19, 21, 23	–
Lopinga achine (Scopoli, 1763), Trans-Eurasian subboreal	–	–	–	+	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
L. deidamia (Eversmann, 1851), Ural–trans-Asian boreomontane	–	–	–	11, 12, 13, 14	15, 16, 17	19	–
Lasiommata maera (Linnaeus, 1758), Western-Central Palaearctic temperate	–	–	–	11, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
L. petropolitana (Fabricius, 1787), Trans-Eurasian boreomontane	–	–	10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23	–
Coenonympha amaryllis (Stoll, 1782), Ural–trans-Asian subboreal	–	–	–	–	–	25	–
C. arcania (Linnaeus, 1758), Western Eurasian subboreal	–	–	–	–	16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
C. glycerion (Borkhausen, 1788), Trans-Eurasian temperate	–	–	–	11, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
C. hero (Linnaeus, 1758), Trans-Eurasian temperate	–	–	–	13	15, 16, 17, 18	19, 20, 23, 24, 25	–
C. leander (Esper, [1784]), Western Eurasian subboreal	–	–	–	–	–	23, 24, 25, 26, 27	+
C. oedippus (Fabricius, 1797), Trans-Eurasian subboreal	–	–	–	–	–	21, 25	–
C. pamphilus (Linnaeus, 1758), Western-Central Palaearctic temperate-subtropical	–	–	–	13	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
C. tullia (Müller, 1764), Trans-Eurasian hypoarctic-boreomontane	+	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	16, 18	22, 25	–

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
Triphysa phryne (Pallas, 1771), Central Eurasian subboreal	–	–	–	–	–	23, 24, 25, 26, 27	28, 29
T. dohrnii (Zeller, 1850), Ural–trans-Asian hypoarctic-boreomontane	–	–	–	+	–	–	–
Oeneis jutta (Hübner, [1806]), Trans-Eurasian hypoarctic-boreal	–	3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 17	19	–
Oe. magna Graeser, 1888, Ural–trans-Asian hypoarctic-boreomontane	–	4, 5	8	–	–	–	–
Oe. melissa (Fabricius, 1775), Sub-trans-Holarctic goltsy	?	2, 3, 4, 5, 7	8, 9, 10	12, 14	–	–	–
Oe. bore (Schneider, 1792), Trans-Holarctic hypoarctic-goltsy	+	2, 3, 4, 5, 6, 7	8, 9	+	–	–	–
Oe. ammon Elwes, 1899, Ural-Siberian goltsy	?	4, 5, 6	?	–	–	–	–
Oe. norna (Thunberg, 1791), Eurasian-Alaskan hypoarctic-goltsy-alpine	+	2, 3, 4, 5, 6, 7	8, 9, 10	12, 14	–	–	–
Oe. polixenes (Fabricius, 1775), Sub-trans-Holarctic arcto-goltsy	?	2, 4	–	–	–	–	–
Oe. tarpeia (Pallas, 1771), Central Eurasian subboreal	–	–	–	–	18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
Maniola jurtina (Linnaeus, 1758), Western Palaearctic temperate-subtropical	–	–	–	11, 14	16, 17, 18	19, 20, 21, 23, 24, 25, 26	–
Hyponephele lupina (Costa, 1836), Western-Central Palaearctic subboreal	–	–	–	–	–	24, 25, 26, 27	28, 29
H. lycaon (Rottemburg, 1775), Trans-Eurasian subboreal	–	–	–	?	16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	28, 29
H. narica (Hübner, [1813]), Turanian	–	–	–	–	–	–	28
H. naricina (Staudinger, 1870), Turanian	–	–	–	–	–	–	28
Aphantopus hyperantus (Linnaeus, 1758), Trans-Eurasian temperate	–	–	–	11, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
Satyrus ferula (Fabricius, 1793), Trans-Palaearctic subboreal	–	–	–	–	–	23, 24, 25, 26, 27	28, 29
S. dryas (Scopoli, 1763), Trans-Eurasian subboreal	–	–	–	–	16, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
Arethusana arethusa ([Denis et Schiffer-müller], 1775), Western-Central Palaearctic subboreal	–	–	–	–	–	23, 24, 25, 26, 27	?
Brintesia circe (Fabricius, 1775), Western Eurasian subboreal	–	–	–	–	–	26	–
Hipparchia autonoe (Esper, [1783]), Eastern European–trans-Asian subboreal	–	–	–	–	+	23, 24, 25, 26, 27	–
H. volgensis (Mazochin-Porshnyakov, 1952) Western Palaearctic subboreal	–	–	–	–	–	25	–
H. statillinus (Hüfnagel, 1766), European subboreal	–	–	–	–	–	25	–

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
Chazara briseis (Linnaeus, 1764), Western-Central Palaearctic subboreal	–	–	–	–	–	20, 21, 22, 23, 24, 25, 26, 27	28, 29
Ch. persephone (Hübner, [1805]), Central Eurasian temperate	–	–	–	–	–	22, 25, 26, 27	28, 29
Pseudochazara hippolyte (Esper, [1784]), Western-Central Eurasian European disjunctive subboreal	–	–	–	–	–	22, 23, 25, 26, 27	28, 29
Proterebia afra (Fabricius, 1787), Western-Central Eurasian subboreal	–	–	–	–	–	23, 24, 25, 26, 27	28, 29
Erebia ligea (Linnaeus, 1758), Trans-Eurasian boreomontane	–	3, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 21, 23, 25	–
E. euryale (Esper, [1805]), European hypoarctic-boreomontane	?	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17	19, 21, 22	–
E. jeniseiensis (Trybom, 1877), Eastern European–trans-Asian hypoarctic-boreomontane	?	4	–	–	–	–	–
E. aethiops (Esper, [1777]), Western-Central Eurasian subboreal	–	–	–	–	15, 16, 17, 18	19, 20, 21, 22, 23, 25	–
E. (*callias*) *churkini* Bogdanov, 2008, Sub-trans-Holarctic goltsy	–	4	–	–	–	–	–
E. medusa ([Denis et Schiffermüller], 1775), Trans-Eurasian hypoarctic-boreomontane	–	–	–	–	–	19, 21, 22, 25, 26, 27	+
E. rossii (Curtis, 1834), Sub-trans-Holarctic arcto-goltsy	1	2, 3, 4, 5, 6, 7	8, 9, 10	12, 14	–	–	–
E. disa (Thunberg, 1792), Eurasian-Alaskan hypoarctic-goltsy	1	2, 3, 4, 5, 6, 7	8, 9, 10	12	–	–	–
E. embla (Thunberg, 1792), Trans-Eurasian hypoarctic-boreal	–	3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 17	–	–
E. cyclopius (Eversmann, 1844), Ural–trans-Asian boreal	–	–	–	–	15, 16, 17	23	–
E. edda Ménétriès, 1851, Ural–trans-Asian boreal	–	–	?	13	+	–	–
E. discoidalis (Kirby, 1837), Sub-trans-Holarctic hypoarctic-boreomontane	–	4, 5, 6, 7	8	?	–	–	–
E. fasciata Butler, 1868, Subcircumpolar (sub-trans-Holarctic metaarctic)	1	2, 3, 4, 5, 6, 7	–	–	–	–	–
E. dabanensis Ershoff, 1871, Ural–trans-Asian goltsy	–	4, 5	+	–	–	–	–
E. (*kiferstеini*) *zaitsevi* Nikolaev, 2005, Ural-Siberian goltsy-alpine	–	4	–	–	–	–	–
Hesperiidae							
Erynnis tages (Linnaeus, 1758), Western-Central Eurasian subboreal	–	–	–	–	–	20, 27	+
Carcharodus alceae (Esper, [1780]), Western-Central Eurasian subboreal-subtropical	–	–	–	–	16	20, 23, 24, 25, 26, 27	28, 29

Table 1 (Contd.)

Family, species, range type	Regions of the Urals						
	Pay-Khoy	Polar	Subpolar	Northern	Middle	Southern	Kazakh-stan
C. flocciferus (Zeller, 1847), Western-Central Palaearctic subboreal	–	–	–	–	16, 18	20, 21, 22, 24, 25, 26	–
C. lavatherae (Esper, [1783]), Western Palaearctic subboreal	–	–	–	–	–	24	–
Spialia orbifer (Hübner, [1823]), Trans-Palaearctic subboreal-subtropical	–	–	–	–	16, 18	21, 23, 25, 26, 27	–
Muschampia cribrellum (Eversmann, 1841), Central European–trans-Asian subboreal	–	–	–	–	–	24, 25, 26, 27	29
M. proto (Ochsenheimer, [1808]), Western Palaearctic subboreal-subtropical	–	–	–	–	–	26	?
M. tessellum (Hübner, [1803]), Western-Central Asian subboreal	–	–	–	–	18	19, 20, 21, 23, 24, 25, 26, 27	+
Pyrgus alveus (Hübner, [1803]), Western-Central Palaearctic temperate	–	–	10	+	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	?
P. andromedae (Wallengren, 1853), European goltsy-alpine	?	4, 5	?	–	–	–	–
P. carthami (Hübner, [1813]), Western Eurasian subboreal	–	–	–	–	–	22, 24, 25, 26, 27	29
P. centaureae (Rambur, 1839), Trans-Holarctic hypoarctic-boreomontane	+	2, 3, 4, 5, 6, 7	8, 9, 10	12, 13	–	–	–
P. cinarae (Rambur, 1839), Western Eurasian subboreal	–	–	–	–	–	26, 27	–
P. malvae (Linnaeus, 1758), Trans-Eurasian temperate	–	–	?	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
P. serratulae (Rambur, 1839), Western-Central Eurasian subboreal	–	–	–	–	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	29
P. sidae (Esper, [1782]), Western-Central Eurasian subboreal	–	–	–	–	–	23, 24, 25, 26, 27	29
Heteropterus morpheus (Pallas, 1771), Trans-Eurasian subboreal	–	–	–	–	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–
Carterocephalus palaemon (Pallas, 1771), Trans-Holarctic hypoarctic-boreomontane	–	2, 3, 4, 5, 6, 7	8, 9, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 25, 26, 27	+
C. silvicola (Meigen, 1830), Trans-Eurasian hypoarctic-boreomontane	–	3, 4, 5, 6, 7	8, 10	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 26	–
Ochlodes sylvanus (Esper, 1777), Trans-Eurasian temperate	–	–	+	11, 12, 13, 14	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26, 27	+
Hesperia comma (Linnaeus, 1758), Trans-Holarctic hypoarctic-temperate	–	2, 3, 4, 5, 6, 7	8	11	16, 17, 18	19, 20, 21, 22, 23, 25, 26, 27	?
Thymelicus lineola (Ochsenheimer, [1808]), Trans-Holarctic temperate (circumtemperate)	–	–	–	11, 12, 13	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	28, 29
Th. sylvestris (Poda, 1761), Western Palaearctic subboreal-subtropical	–	–	–	–	15, 16, 17, 18	19, 20, 21, 22, 23, 24, 25, 26	–

Notes: (+) the species was recorded in the region but the particular local fauna was not specified; (?) the species may be present in the region; (–) the species was not found. The local faunas are numbered (1–29) as in Fig. 1.

Table 2. Parameters of taxonomic diversity of Rhopalocera as a whole and individual families of butterflies in different regions of the Urals

Parameters		Regions of the Urals						
		I	II	III	IV	V	VI	VII
Number of local faunas		1	6	3	4	4	9	2
Rhopalocera								
Number of species	Min.	12	39	44	52	89	105	42
	Max.		67	53	69	117	153	62
	Mean		51	49	62	103	127	52
Number of genera	Min.	7	25	28	42	49	53	30
	Max.		35	32	46	61	65	37
	Mean		29	29	44	56	60	34
Mean number	Papilionidae							
	Species	0	2	2	2	4	4	2
	Genera		2	2	2	4	4	2
	Pieridae							
	Species	2	8	9	10	15	15	10
	Genera	2	6	6	7	8	8	6
	Lycaenidae							
	Species	1	9	9	20	25	39	17
	Genera	1	7	6	10	11	15	9
	Nymphalidae							
	Species	7	20	17	26	34	34	7
	Genera	4	8	8	14	16	14	6
	Satyridae							
	Species	3	13	11	12	17	20	13
	Genera	1	3	3	7	9	13	9
	Hesperiidae							
	Species	0	4	3	5	11	14	5
	Genera		3	3	4	7	7	3

Notes: Regions: (I) Pay-Khoy; (II) Polar Urals; (III) Subpolar Urals; (IV) Northern Urals; (V) Middle Urals; (VI) Southern Urals; (VII) Kazakhstan. The means are rounded off to the nearest whole number.

boundary of 7 species (3.0%; the European and Eastern European elements), and the western boundary of 12 species (5.2%).

The combination of the latitudinal and longitudinal elements results in about 80 range types of butterflies in the Ural fauna. Even the largest types do not include more than 10% of the total species list: the trans-Eurasian temperate type unites 9.4% of species, the Western-Central Eurasian subboreal type, 8.2%, the trans-Eurasian subboreal type, 4.7%, whereas the trans-Palaearctic temperate, Western-Central Palaearctic subboreal, and Western Eurasian subboreal types include 3.4% each.

Similarity of the Local Faunas

Cluster analysis of the local butterfly faunas has revealed two main faunistic complexes which may be conventionally called the North Ural and South Ural ones (Fig. 4). As in the case of spiders (Esyunin and Efimik, 1994), the boundary between these complexes coincides with the boundary of the Middle and North Urals. The discontinuity probably results from the

Table 3. The taxonomic structure of the butterfly fauna of the Urals

Family and the largest genera	Number of species	Fraction (%) in the total fauna	Representation of families (% of global diversity)
Papilionidae	**6**	**2.6**	1.1
Parnassius Latreille, 1804	2	0.9	
Pieridae	**23**	**9.9**	2.0
Colias Fabricius, 1807	9	3.9	
Lycaenidae	**64**	**27.5**	1.6
Lycaena Fabricius, 1807	8	3.4	
Plebeius Kluk, 1780	7	3.0	
Polyommatus Latreille, 1804	13	5.6	
Nymphalidae	**60**	**25.6**	2.3
Melitaea Fabricius, 1807	11	4.7	
Clossiana Reuss, 1920	15	6.4	
Satyridae	**57**	**24.5**	1.9
Coenonympha Hübner, 1819	8	3.4	
Oeneis Hübner, 1819	8	3.4	
Erebia Dalman, 1816	15	6.4	
Hesperiidae	**23**	**9.9**	0.6
Pyrgus	8	3.4	

higher altitudes of the North Ural mountains and the appearance of a distinct mountain tundra belt with the associated butterfly complex. In the adjoining Cis-Ural plains the same boundary can be observed approximately 400 km further to the north (in particular, near Ukhta), whereas in the Trans-Ural region it runs at about the same latitude (close to 60°N) as in the mountains, shifting still further to the south in more eastern areas.

The faunas of the North Ural complex can be grouped into the hypoarctic (local faunas 2–8) and the

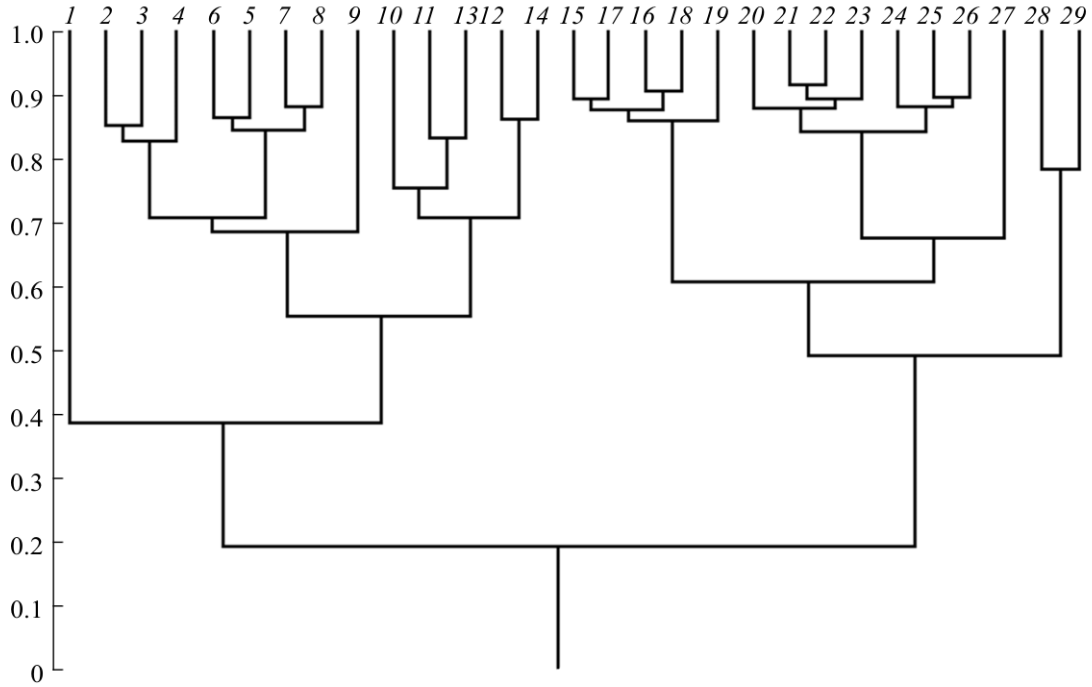


Fig. 4. The similarity dendrogram of the local butterfly faunas (*1–29*) of the Urals by species composition. Designations as in Fig. 1.

Table 4. The arealogical structure of the butterfly fauna of the Urals: the number of species with different range types

Latitudinal component	Longitudinal component																							
	Multiregional	Trans-Holarctic	Sub-Trans-Holarctic	Eurasian-Alaskan	Trans-Palaearctic	Trans-Eurasian	Amphi-Eurasian	Central Eurasian	European	Eastern European	Western Eurasian	Western Palaearctic	Western-Central Palaearctic	Western-Central Eurasian	Euro-Siberian-Central Asian	Central Eurasian	European–Central Asian	Central European–trans-Asian	Eastern European–trans-Asian	Ural–trans-Asian	Ural-Siberian	Turanian	Irano-Turanian	Palaeotropical
Metaarctic		2	1																					
Arcto-goltsy		1	2	1																				
Arctomontane		1		1																				
Hypoarcto-goltsy-alpine		1		2		1																		
Hypoarcto-goltsy		1		2																				
Hypoarcto-boreal		2				3													1					
Hypoarcto-boreomontane		4	2			5			1										2	3				
Boreomontane						4								1						2				
Boreal																				3				
Goltsy-alpine						2			1															
Goltsy			2																	1	1			
Montane				1																				
Hypoarcto-temperate		3			1	4												1						
Temperate		1			**8**	**22**		1					4	2	4		1	2	1					
Subboreal					2	**11**	4	6	3	2	**8**	3	**8**	**19**		1		4	1	2				
Nemoral							2				3	2			1									
Subboreal-subtropical					1	1					1	4	5	5				1				6	1	
Temperate-subtropical					1	1						1	1											
Polyzonal	3	2			2																			1

Note: The longitudinal and latitudinal components are named after Gorodkov (1984, 1992).

northern boreal (10–14) second-order faunistic complexes, the boundary between which runs in the northern part of the Subpolar Urals (local fauna 9: 65°N). It should be noted that this boundary, recognized already by Fridolin (1935), limits the distribution of species of many terrestrial invertebrate taxa: spiders, ground and carrion beetles, etc. (Esyunin and Efimik, 1994, 2000; Esyunin and Kuzminykh, 2000).

The hypoarctic complex can be further subdivided into the cluster of the southern tundra faunas of the Polar Urals (2–4) and that of the forest-tundra and extreme northern taiga faunas of the Polar and Subpolar Urals (5–8), which still include a considerable number of species typically associated with the forest zone. The impoverished fauna of Pay-Khoy clearly belongs to the arctic faunistic complex and occupies an isolated position in the dendrogram (Fig. 4).

The South Ural faunistic complex of butterflies can be also subdivided into the southern boreal (15–19) and subboreal humid (20–26) second-order complexes. The Kazakhstan faunas (including the boundary fauna 27: ~51°N) belong to the subboreal semi-arid complex and occupy an isolated position.

Thus, the Ural butterflies reveal distinct latitude-zonal trends not only in taxonomic diversity but also in composition of the local faunas. The ecological requirements of the species that determine the peculiar aspects of the faunas at the opposing ends of the mountain range correspond to the climate parameters of these regions: low heat supply in the north and aridity in the south.

CONCLUSION

Considering the great extent of the Ural Range from north to south and its position in the place of contact between a number of faunistic complexes (European, Siberian, Mediterranean, and Central Asian), the high diversity of its butterfly fauna is to be expected. In this respect the Urals do not yield to other mountain systems of the Eurasian temperate zone. For example, about 250 species of Rhopalocera occur in the Alpine-Carpathian mountain country, about 210 in the Great Caucasus, the same number in the Altai Mountains, and about 80 in the Verkhoyansk Range (Tolman, 2001; Kudrna, 2002; *Catalog of Lepidoptera of Russia*, 2008; Tshikolovets, 2011). The taxonomic and ecological diversity of the Ural butterfly fauna and the broad range of arealogical types seem to reflect not only the recent diversity of living conditions but also the Quaternary history of the region. The climatic fluctuations in the Neogene were probably accompanied by migrations of the eastern and western faunistic elements with different ecological preferences. The mostly allochthonic nature and relatively young age of the Ural butterfly fauna can be confirmed by the absence of endemic species and a very small number of subspecies specific to the region. The butterfly species were probably "accumulated" and preserved in the mountains, under the conditions of high diversity and relative stability of habitats, whereas the ranges of some stenotopic forms in the adjoining plains may have deteriorated due to natural or anthropogenic changes in their habitats.

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