ISSN 0013–8738, Entomological Review, 2010, Vol. 90, No. 3, pp. 333–371. © Pleiades Publishing, Inc., 2010.
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published in Entomologicheskoe Obozrenie, 2010, Vol. 89, No. 1, pp. 178–218.

Analysis of the Ways of Formation of the Entomofaunistic Complexes in the Northwest Caucasus Based on the Material on Coleopterous Insects (Coleoptera)

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Received September 22, 2009

Abstract—By the example of 14 coleopterous insect families, namely Gyrinidae, Haliplidae, Noteridae, Dytiscidae, Carabidae, Hydrophilidae, Staphylinidae, Lucanidae, Trogidae, Scarabaeidae, Elateridae, Alleculidae, Tenebrionidae, and Chrysomelidae, regularities and the basic sources of formation of the most typical landscape-coenotic complexes in the Northwest Caucasus are discussed. The total number of the species included in the material analyzed amounts to about 2000. The maximal species diversity (854 species) is registered for the deciduous forests and dry open woodlands. In total, 11 types of the chorological complexes and distributional ranges (chorotypes) of the regional beetle fauna are distinguished. Significant concordance of the chorologic patterns in some groups of beetles is established. In this respect, Carabidae and Tenebrionoidea seem to be the closest on the one hand, and also Elateridae and Scarabaeoidea, on the other. The zonal fauna of the Northwest Caucasus is formed basically by species possessing Boreal ranges, while the azonal fauna, predominantly by species with the Ancient Mediterranean ranges. Allocation of coleopterous insects within regional zoochorones is investigated as well. It is established, that in different zoochorones of the upland part of the region the majority of coenofaunas show significant similarity of the arealogical pattern, even though being composed frequently by different taxa. The fauna of agrarian landscapes of the Northwest Caucasus is also examined. It includes 382 beetle species. The overwhelming majority of them belongs to the ground beetles (229 species), leaf beetles (78), and Scarabaeoidea (30). This fauna reveals the maximal similarity with the coenofaunas of the lowland steppe and meadows. It is established that the major role in formation of the agrocenoses beetle fauna belongs to the natural plain and upland steppe and treeless fields, foothill broad-leaf forests and open woodlands, and also to the floodplain and lowland forests. The bulk of the species occurring in the agrocenoses possesses wide ranges, predominantly of the Boreal type. Some peculiarities of the regional endemism are discussed as well.

DOI: 10.1134/S0013873810030048

INTRODUCTION

Coleopterous insects constitute about a half of the biodiversity of hexapods of the Palaearctic Region (Konstantinov et al., 2009). Thus, the study of this group in any natural division of the Palaearctics provides representative material on insects as a whole. The beetle fauna of the Northwest Caucasus, discussed

below, is rather original and complicated in zoogeographical respect. The Northwest Caucasus is actually a unique region of Russia inhabited by species of the Colchic and Hyrcanian origin; besides it is characterized by a considerable number of endemic taxa. The region also possesses a wide variety of landscapes and types of plant formations.

The Northwest Caucasus is defined as a terrain bounded by the Manych Depression and a line between the mouth of the Don River and Lake Manych in the north, the border between Russia and Abkhazia in the south, the coast of the Azov and Black seas in the west, and the valley of the Urup and the watershed of the Urup and the Bolshaya Laba rivers in the east (Kanonnikov, 1977, 1984). Thus, the Northwest Caucasus includes the historical ranges traditionally called Kuban and the Western Black Sea Coast (Zamotajlov, 1992b). The region in question is accepted as a solid unit by numerous authors in their layouts of the biogeographical subdivision of the Caucasus, thus justifying its treatment as a natural zoogeographical area. On the other hand, the Northwest Caucasus is located at a junction of several large faunal regions and besides represents an arena of intensive speciation processes (in some groups resulting in differentiation of peculiar genus-group taxa) leading to significant diversification and originality of the regional entomofauna. The beetle fauna of the western part of the Gagra Mt. Range and adjacent massifs reveals a significant similarity to regional beetle fauna; therefore, this analysis also involves material from the abovementioned terrains. Administratively, the investigated region mainly embraces the territories of Krasnodar Territory, the Republic of Adygea, the extreme west of the Karachai-Cherkess Republic, the southwest areas of Rostov Province, and the northwesternmost part of the Republic of Abkhazia. Within these limits the surface of the Northwest Caucasus comprises approximately 87000 km^2.

During the last 20–25 years, considerable progress has been achieved in entomofaunistic research in Krasnodar Territory and the Adygea Republic. The most comprehensive results were achieved in the monographic study of several insect groups of the Northwest Caucasus. First of all, a number of coleopterous families should be mentioned: ground beetles (Zamotajlov, 1989, 1992, etc.), rove beetles (Solodovnikov, 1997), longhorn beetles (Miroshnikov, 1984; Danilevsky and Miroshnikov, 1985, etc.), chrysomelids (Okhrimenko, 1992; Yaroshenko, 1994), click beetles (Orlov, 1994), malachiid beetles (Solodovnikov, 1994), blister beetles (Tkhabisimova, 2007), several groups of xylophylic beetles (Bibin, 2008, Nikitsky et al., 2008), a part of aquatic beetles (Shapovalov, 2009). According to preliminary estimation (Shchurov and Zamotajlov, 2006), the already revealed insect fauna of the Northwest Caucasus totals about 10000 species (i.e., about 5% of the Palaearctic fauna, see Konstantinov et al., 2009), more than one-third of it being represented by beetles.

The hitherto accumulated material allows us to carry out a preliminary general and comparative evaluation of the biodiversity and similarity of the main landscape-coenotic beetle complexes of the region in question, the arealogical structure of beetle fauna as a whole, and its separate coenofaunas, to estimate the similarity of faunas of different biogeographical units aiming at further interpretation and reconstruction of the regularities of the formation of the entomofaunistic complexes of the Northwest Caucasus. Hereafter the geographic distribution and biocoenotic allocation of about 2000 beetle species belonging to 14 families (comprising the bulk of the known regional beetle fauna) are analyzed. Of all the families discussed below, the most important role in formation of the regional coleopterous insects taxocenes is plaied by ground beetles (more than 600 species), rove beetles (more than 400 species), chrysomelids (over 350 species), lamellicorn beetles and click beetles (more than 150 species respectively).

Besides the authors' unpublished data on geographic distribution and landscape-biotopic diffusion of beetles within the region and beyond its bounds, similar information from numerous references, critically revised taking into account the modern state of systematics and nomenclature of beetles has been used as well. These sources include first of all a number of summarizing faunistic researches on separate families or family groups of Coleoptera within the limits of the Northwest Caucasus (Okhrimenko, 1992; Zamotajlov, 1992b; Orlov, 1994a; Solodovnikov, 1997, 1998b; Shapovalov, 2007c, 2009; Shapovalov and Shokhin, 2007). Catalogs, check lists (annotated lists), faunistic and ecological-faunistic researches on separate coleopterous groups or beetles as a whole within the limits of the entire Caucasus or South Russia (including Ciscaucasia), or covering territories adjacent to the Northwest Caucasus were also widely used (Zaitzev, 1908, 1917, 1923, 1927, 1928, 1947; Olsoufieff, 1916, 1918; Bogdanov-Katjkov, 1921; Bogatchev, 1938;

Iablokoff-Khnzorian, 1967; Dzhambazishvili Ya.S., 1973, 1979; Abdurakhmanov, 1984; Boháč, 1986; Komarov, Khatschikov, et al., 1992; Abdurakhmanov and Medvedev, 1994; Yaroshenko, 1994; Khatschikov, 1995, 1996, 1997a, 1997b, 1998, 2005a; Arzanov, Arzanov, Shokhin, Komarov, et al., 1996; Nabozhenko, 1999, 2000, 2005, 2007; Dzhambazishvili M.Ya., 2000; Gildenkov and Khatschikov, 2000; Shokhin, 2000, 2007; Abdurakhmanov and Abdulmuslimova, 2002; Orlov, 2002; Shokhin and Bozadzhiev, 2003; Yaroshenko and Shapovalov, 2004). Publications on the fauna and ecology of insects as a whole and the order Coleoptera wholly or partly in separate biogeographical, ecological, territorial or administrative constituents of the Northwest Caucasus have been taken into account (Ghilarov and Arnoldi, 1957, 1969; Arnoldi and Ghilarov, 1958; Kosmachevsky et al., 1974; Ghilarov, 1979; Yaroshenko and Tsuprikova, 1984; Zamotajlov, 1989, 1993, 2004; Sushentsova, 1999; Gongalsky and Zamotajlov, 2002; Pushkin, 2004; Shapovalov and Yaroshenko, 2004; Shapovalov, 2007b; Nikitsky et al., 2008). Different investigations of various aspects of the fauna and problems of beetle protection in the Northwest Caucasus, making an appreciable contribution to the knowledge of the regional fauna and its distributional peculiarities are also used (Medvedev, 1962; Stepanova, 1967, 1969; Kosmachevsky, 1974; Fomitschev et al., 1977; Yaroshenko, 1982; Orlov, 1990; *The Red Data Book of Republic of Adygea*, 2000; Knysh and Zamotajlov, 2001, 2004; Brekhov, 2005; *The Red Data Book of Krasnodar Territory*, 2007; Shapovalov, 2007a).

The data obtained from numerous publications on taxonomy of Coleoptera are involved, of which only the most important works and researches on the systematics and fauna of separate groups (genera complexes, genera, large species-groups), comprising extensive data on the fauna of the Northwest Caucasus are listed below (Reichardt, 1936b; Kurnakov, 1961; Iablokoff-Khnzorian, 1976; Ushakov, 1988; Ryvkin, 1990; Gusarov, 1992, 1995; Zamotajlov, 1992a, etc.; Orlov, 1994b; Belousov, 1998; Solodovnikov, 1998a, 2000, 2001, 2002, 2004; Nabozhenko, 2001; Khatschikov, 2003, 2005b; Egorov, 2006). The World and Palaearctic catalogs presenting information on the general distribution of the coleopterous species in the Northwest Caucasus are widely used (Balthasar, 1936; Herman, 2001; Nilsson, 2001; Löbl and Smetana, 2003, 2004, 2006, 2007, 2008) as well as some issues of "*The Fauna of the USSR*" series, keys to the fauna of the USSR, catalogs, check lists and other publications containing important actual or historically valuable information on the taxonomy and distribution of some voluminous taxa, geographical complexes or biological groupings of coleopterous insects of some extensive terrains (Ogloblin, 1936; Reichardt, 1936a; Ogloblin and Znojko, 1950; Dobrovolsky, 1951; Medvedev S.I., 1949, 1951, 1952, 1960, 1964; Medvedev G.S., 1965, 1968, 1974; Tikhomirova, 1973; Guryeva, 1979, 1989; Nikitsky, 1980; Dolin, 1982, 1988; Kryzhanovskij, 1983; Nikolaev, 1987; Egorov, 1990, 2009; Kryzhanovskij et al., 1995 and later on-line versions of this work; Zamotajlov, 2005; Kabakov, 2006). Some data published by V.A. Yaroshenko (Yaroshenko, 1994; Yaroshenko and Shapovalov, 2004) and V.G. Knysh (Knysh, 2002) are also partly used hereafter.

MATERIAL AND METHODS

The present synthesis is based on information from several databases belonging to the specialists involved in team-work. It includes the following coleopterous families (the number of species of the regional fauna analyzed and the author's name for each taxonomic group are given in brackets): Gyrinidae (8, Shapovalov), Haliplidae (7, Shapovalov), Noteridae (2, Shapovalov), Dytiscidae (72, Shapovalov), Carabidae (including Cicindelinae) (627, Zamotajlov), Hydrophilidae (49, Shapovalov), Staphylinidae (excluding Aleocharinae) (398, Khatschikov), Lucanidae (8, Shokhin), Trogidae (3, Shokhin), Scarabaeidae (164, Shokhin), Elateridae (156, Orlov), Alleculidae (16, Nabozhenko), Tenebrionidae (64, Nabozhenko), Chrysomelidae (365, Okhrimenko, Shapovalov). All the types of calculations and similarity measurements were carried out at a species-level, subspecific forms not being taken into account.

The initial data are based on the material collected mainly by the authors and their colleagues on numerous expeditions to the region carried out mainly since the seventies of the XX century till the present time. Collections of the above institutions and those of the private persons listed above were also used as well as the ones deposited at the Entomological Museum of the Kuban State Agrarian University and Faculty of Zoology of the Kuban State University (Krasnodar), and G.N. Prozritelev and G.K. Prave Museum of Local Lore, History and Economy (Stavropol).

The following landscape-coenotic complexes (coenofaunas) of the coleopterous insects of the Northwest Caucasus were investigated (a number of types of plant formations distinguished by some authors was integrated due to a considerable resemblance of populating complexes of beetles). A 3-letter coding system is used for the complexes' indication, which is given below.

Land Zonal Types of Communities

(1) StP—natural steppes and pastures of the steppe and forest-steppe zones (Figs. 1–12).

(2) StM—steppe habitats, treeless mountain tops, glades, other meadow-steppe coenoses of the upland part of the region (Fig. 2).

(3) IPF—inundated and plain forests (mainly situated on the right bank of the Kuban River) (Fig. 3).

(4) DeF—deciduous forests and dry light forests with "Shybliak" (Fig. 4).

(5) MCF—mixed and coniferous forests (including crooked forests) (Fig. 5).

(6) Alp—alpestrine and alpine belts (herb meadows, carpets) (Fig. 6).

Land Azonal Types of Communities

(7) Mar—marshes, temporarily flooded bottomlands, and wetlands of the plain and seaside parts of the region (Fig. 7).

(8) MBo—moors, salinized and mineralized habitats of the upland part of the region (Fig. 8).

(9) Sal—solonchaks and other salinized habitats (Fig. 9).

(10) Sea—sea coasts and beaches (sandy and coquina) (Fig. 10).

(11) SuN—subnival (adnival) belt (Fig. 11).

(12) Flo—floodlands (bottomlands) of the rivers and brooks, including gravel and sandy banks and organic depositions (inwashes) (Fig. 12).

(13) Kar—subterranean forms of karst.

Freshwater Reservoirs (Communities)

(14) RSS—stagnant reservoirs of the steppe and the forest-steppe zones.

(15) RCS—running and circulating reservoirs of steppe and forest-steppe zones.

(16) RSF—stagnant reservoirs of the foothill part of the region.

(17) RCF—running and circulating reservoirs of the foothill part of the region.

(18) RSM—stagnant reservoirs of the mountain and high-mountain parts of the region.

(19) RCM—running and circulating reservoirs of the mountain and high-mountain parts of the region.

(20) RAr—artificial reservoirs of different types.

Agrocenoses

(21) Agr—agrocenoses of all the altitudinal belts, including meadow formated gardens and shelter belts (agrarian landscapes).

The nomenclature of zoogeographical divisions of the Palaearctic Region for land animals after Semenov-Tian-Shanskij (1935) is mainly used hereafter for classification of the ranges, with some changes after Kryzhanovskij (1965) and addition of several terms suggested by Emeljanov (1974) and Gorodkov (1984) (cited after: Zamotajlov, 1992b). The proposed classification is merely simplified, and accepted ranges actually combine some groups of more restricted ranges, or chorotypes (Vigna Taglianti et al., 1999), the latter still not outlined thoroughly for a significant portion of the analyzed species. The following types of chorological complexes and ranges of the regional beetle fauna are discussed in the present analysis (a 3-letter coding system being used below for their indication).

The Ranges Exceeding the Holarctic Region

(1) ExH—extraholarctic multiregional, including cosmopolitan.

The Boreal Complex

(2) WBo—wide polysector and polyzonal (predominantly boreal: Holarctic, Transpalaearctic, Amphipalaearctic, West Palaearctic, Euro-Siberian, etc.).

(3) Nem—Forest European and Euro-Caucasian.

The Ancient Mediterranean (Tethyan) Complex

(4) Ste—Steppe (Scythian and Pontic, Euro-Scythian, partly polysector).

(5) CAs—Wide Tethyan (Ancient Mediterranean), Anterior-Middle Asian and Euro-Turanian polysector.

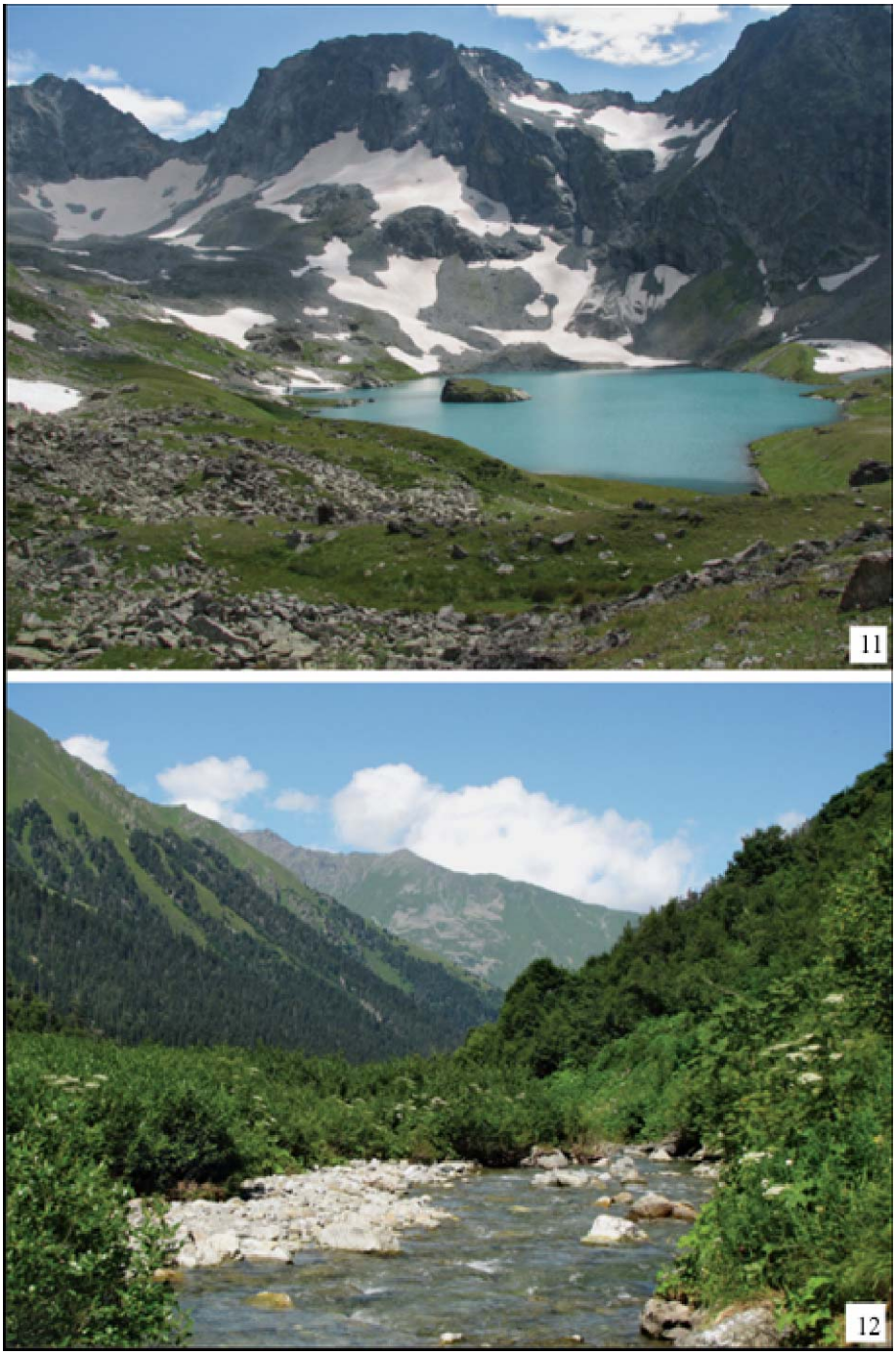
Figs. 1, 2. (1) Feather-motley grass steppe at slopes of Mt Lysaya, bank of Kiziltash Estuary (Taman Peninsula), July 2005; (2) secondary (after deforestation) meadows at slopes of Chernomorskiy Mt Range near Lake Krugloye, 800–850 m (environs of Akhmetovskaya Stanitsa), May 2008.

Figs. 3, 4. (3) Floodland forest on the Kuban River within Krasnodar boundaries ("Kirgizskie Plavni" Tract), July 2006; (4) xerophytic woodland and "shibliak" near Mt Kobyla (environs of Cape Bolshoy Utrish), April 2009.

Figs. 5, 6. (5) Mixed forest in the valley of the Malaya Laba River at confluence with the Bezymianka River, 1600–2000 m, July 2008; (6) alpine meadow, upper reaches of the Vorovskaya Balka River near Pass Krutoy, 2000–2400 m (Tsakhvoa River basin), July 2007.

Figs. 7, 8. (7) Temporarily flooded bottomlands at the mouth of the Kulikov Estuary (environs of Temryuk, Verbianaya Spit), July 2008; (8) mountain marsh at the source of the Imeretinka River, 2500 m, August 2009.

Figs. 9, 10. (9) Saline habitat near "Hephaest" mud volcano (environs of Temryuk), August 2008; (10) Black Sea coast between brooks Vodopadnaya Shchel' and Bazovaya Shchel' (environs of Cape Bolshoy Utrish), April 2009.



Figs. 11, 12. (11) Subnival belt near Lake Bolshoye Imeretinskoye, 2500–3200 m, August 2009; (12) Imeretinka River valley, 1900–2000 m, August 2009.

(6) WMe—Wide Mediterranean.

(7) EMe—East Mediterranean.

(8) EuM—Euro-Mediterranean.

The Caucasian (Euxine) Complex

(9) Cau—Wide Euxine (including Caucaso-Hyrcanian or penetrating Anatolia, the Anterior Asia, Crimea or steppe zone of South Russia).

(10) WCa—West Caucasian.

(11) End—Northwest Caucasian of different types (zonal, local, etc.). The ranges of endemic taxa are not considered in details within the framework of the present study.

The biogeographical division of the Northwest Caucasus given below follows that of Shiffers (1953), with some modifications based on the data on coleopterous

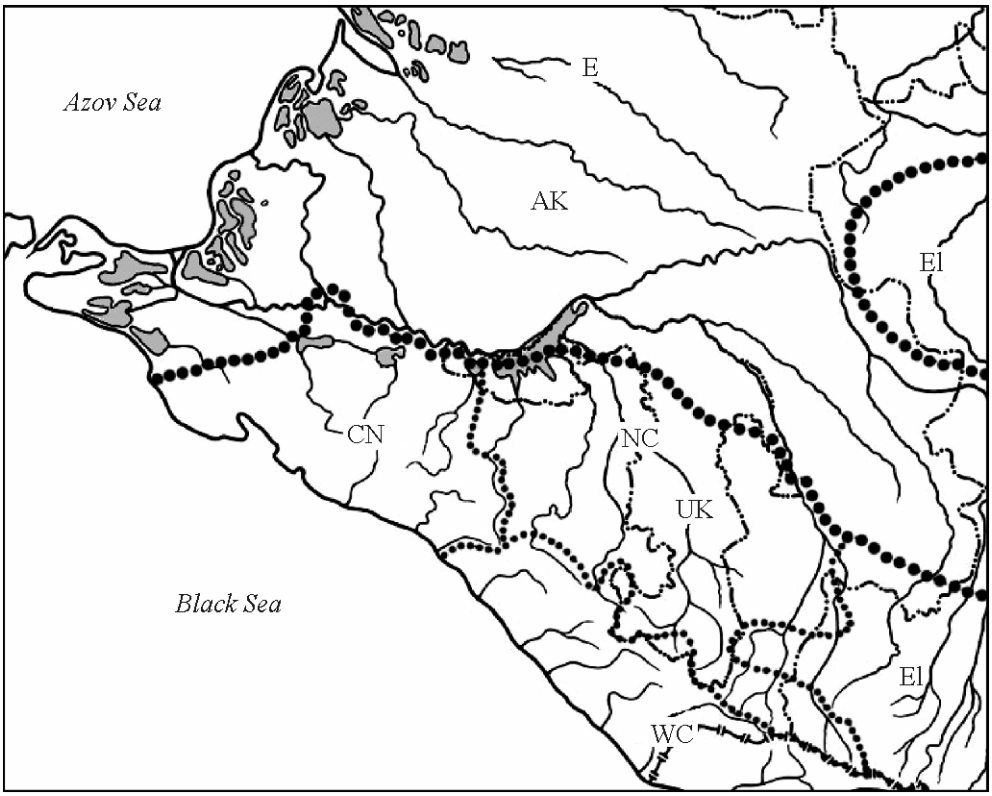


Fig. 13. Zoogeographical subdivisions of the Northwest Caucasus based on the material of the ground beetles (after Zamotajlov, 1992b, modified). E, the East European Province; NC, the North Caucasian Province; WC, the West Caucasian Province; AK, the Azov-Kuban Subprovince; KN, the Krymsk-Novorossiisk Subprovince; UK, the Upland Kuban Subprovince; El, the Elbrus Subprovince.

insects (Zamotajlov, 1992b, etc.). The following zoochorones are analyzed: AK, the Azov-Kuban Subprovince (regional fragment of the East European Province of the Eurasian Area of Steppes); KN, the Krymsk-Novorossisk Subprovince (attributed to the North Caucasian Province of the Caucasian Area of Mountain Meadows and Forests); UK, the Upland Kuban (= Kuban) Subprovince (of the same province); WC, the West Caucasian Province (regional fragment of the same area) (Fig. 13). The Elbrus and the Tersk-Manych Subprovinces are not considered within the limits of the region.

Compiling of the initial matrix and construction of diagrams were carried out using the software package Microsoft Office 2007, other calculations and graphic building were executed with the help of computer programs STATISTICA (data analysis software system), StatSoft Inc., 2001 (version 6) and BioDiversity Pro, NHM and SAMS, 1997 (version 2). Taxa ranging, considering the stability of their affiliation to certain communities or other parameters, was not made in the present work. Standard methods of analysis of the faunistic collections were implemented for construction of similarity dendrograms (Pesenko, 1982). The percent disagreement distance and the Jaccard similarity measure were used for construction of the secondary matrix; clustering was carried out using Unweighted Arithmetic Average (Pair Group Average) method.

RESULTS AND THEIR DISCUSSION

1. Species Diversity and Faunistic Similarity of the Landscape-Coenotic Complexes of Coleopterous Insects

The total amount of the beetle fauna revealed in the course of the present study numbers 1939 species. The species diversity of various landscape-coenotic complexes of the Northwest Caucasus differs appreciably (Fig. 14). The richest taxocenes are recorded for the zonal communities—deciduous forests and dry light forests (854 species), treeless coenoses of the upland part of the region (458), inundated and plain forests (433), the alpestrine and alpine belts (388), natural steppes and pastures of the steppe and forest-steppe zones (341), mixed and coniferous forests

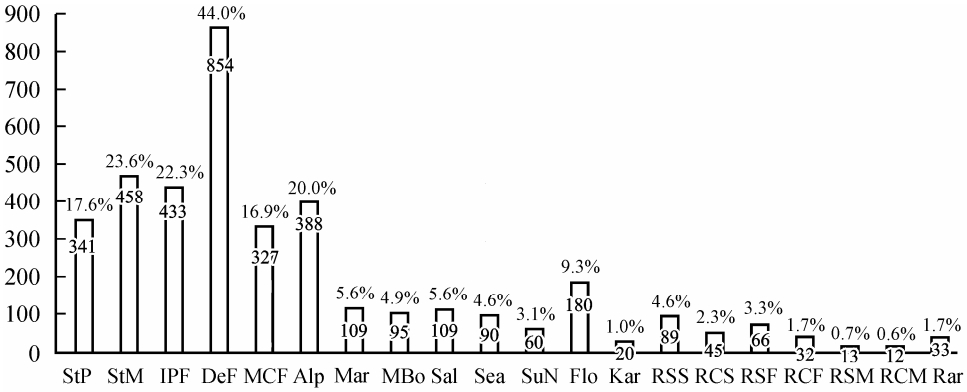


Fig. 14. Species diversity of the landscape-coenotic complexes of coleopterous insects of the Northwest Caucasus. For variants abbreviations, see text.

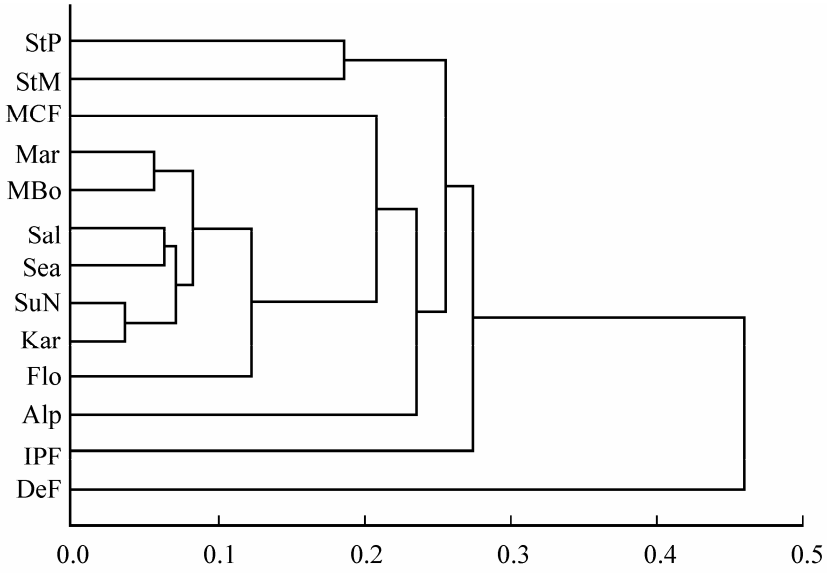


Fig. 15. Similarity of land landscape-coenotic complexes of coleopterous insects in the Northwest Caucasus. Scale indicates percent disagreement distance. For variants abbreviations, see text.

(327), and floodlands (bottomlands) (180). Species groupings (coenofaunas) of various land azonal communities total from 20 up to 109 species, and the fauna of water reservoirs numbers from 12 up to 89 species.

Similarity of species compositions contributes to the comprehension of regularities of formation of the regional coenofaunas of coleopterous insects. Similarity of the landscape-coenotic complexes based on Coleoptera as a whole is given in Fig. 15. The maximal similarity (computed using the percent disagreement distance) is observed in the pairs Mar and MBo, Sal and Sea, SuN and Kar, all the mentioned azonal communities types forming a uniform cluster with floodlands, and they all together, with mixed and coniferous forests. Another uniform cluster is formed by different types of steppes and the open treeless territories. The placement of inundated and plain forests and deciduous forests is not interpreted unambiguously. Differentiation of coenofaunas in various coleopterous taxa is note the same (similarity is computed on the basis of Jaccard similarity measure). All the studied groups of land beetles, except for chrysomelids (Figs. 16–20), manifest a significant similarity of the fauna of natural steppes and pastures of steppe and forest-steppe zones to the fauna of treeless coenoses of the upland part of the region; however this grouping of taxocenes of the open communities demonstrates a different affinity to taxocenes of the other types of landscapes. Whereas in ground beetles this grouping is closest to taxocenes of plain and dry low mountain forests, in Scarabaeoidea and Tenebrionoidea it most resembles the coenofauna of the Alpine belt, while in rove beetles and click beetles, the coeno-

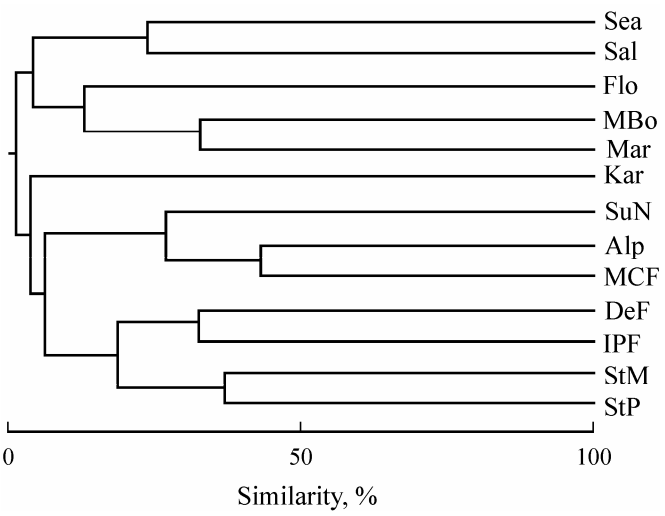


Fig. 16. Similarity of the landscape-coenotic complexes of the coleopterous family Carabidae in the Northwest Caucasus. For variants abbreviations, see text. In Figs. 16–22, scale indicates Jaccard similarity measure.

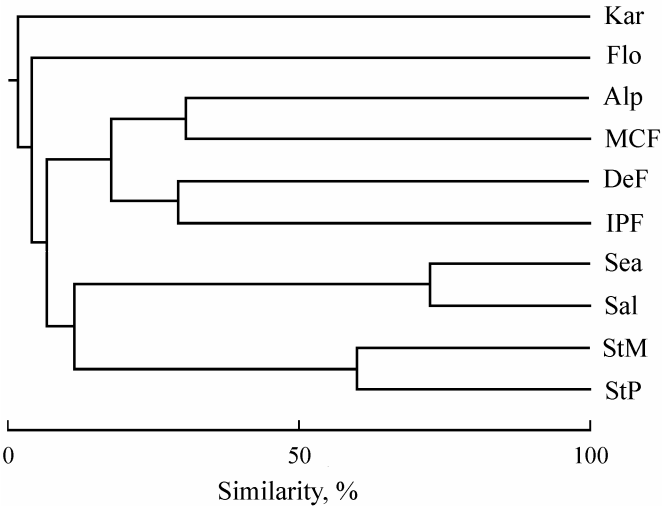


Fig. 17. Similarity of the landscape-coenotic complexes of the coleopterous family Staphylinidae in the Northwest Caucasus. For variants abbreviations, see text.

fauna of salinized habitats. Forest landscape-coenotic complexes are also positioned differently. In ground beetles and rove beetles the maximal similarity is established for taxocenes of deciduous forests and inundated and plain forests, while taxocenes of mixed and coniferous forests appear to be closer to the fauna of the alpine belt (besides in ground beetles the taxocene of mixed and coniferous forests shows obvious similarity to the taxocenes of the subnival belt, i.e. all mountainous fauna is characterized by significant integrity). In Elateridae and Tenebrionoidea, on the contrary, taxocenes of deciduous forests and ones of mixed and coniferous forests are closer to each other. In many groups, namely Scarabaeoidea, Elateridae, and Tenebrionoidea, all the forest communities constitute a uniform cluster, in Staphylinidae the dendrogram possesses a branch uniting the forest and alpine complexes. The dendrogram least informative for analysis of similarity of separate taxocenes is observed in chrysomelids (Fig. 21); however even it reveals a higher similarity of taxocenes of all zonal communities types to each other than each of them to different taxocenes of azonal types of communities. The most isolated position among the zonal chrysomelid coenofaunas occupies that of the natural steppes and pastures of the steppe and forest-steppe zones. Among aquatic beetle communities (Fig. 22) the complexes of stagnant reservoirs of the steppe and foothills compose a uniform cluster with artificial ones; another cluster is formed by steppe and foothill

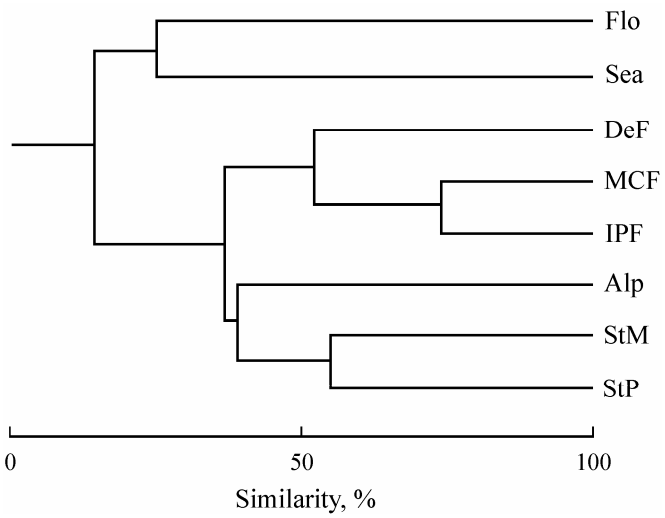


Fig. 18. Similarity of the landscape-coenotic complexes of the coleopterous superfamily Scarabaeoidea in the Northwest Caucasus. For variants abbreviations, see text.

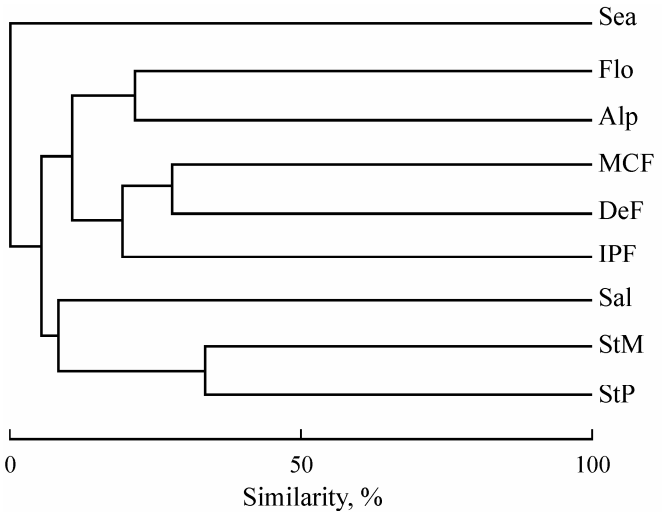


Fig. 19. Similarity of the landscape-coenotic complexes of the coleopterous family Elateridae in the Northwest Caucasus. For variant abbreviations, see text.

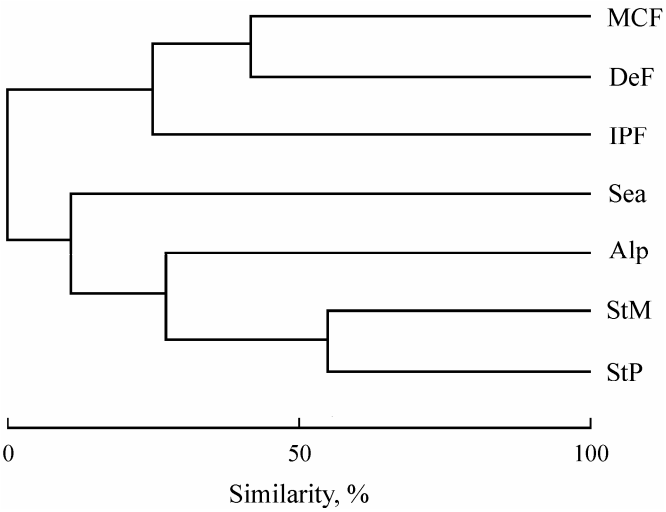


Fig. 20. Similarity of the landscape-coenotic complexes of the superfamily Tenebrionoidea in the Northwest Caucasus. For variants abbreviations, see text.

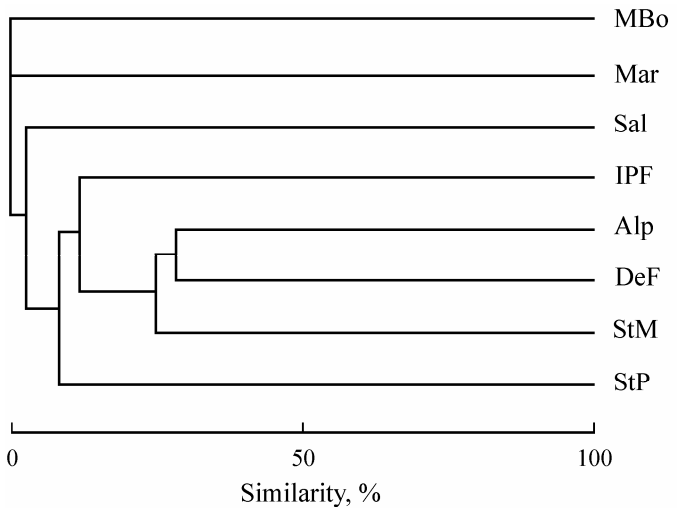


Fig. 21. Similarity of the landscape-coenotic complexes of the coleopterous family Chrysomelidae in the Northwest Caucasus. For variants abbreviations, see text.

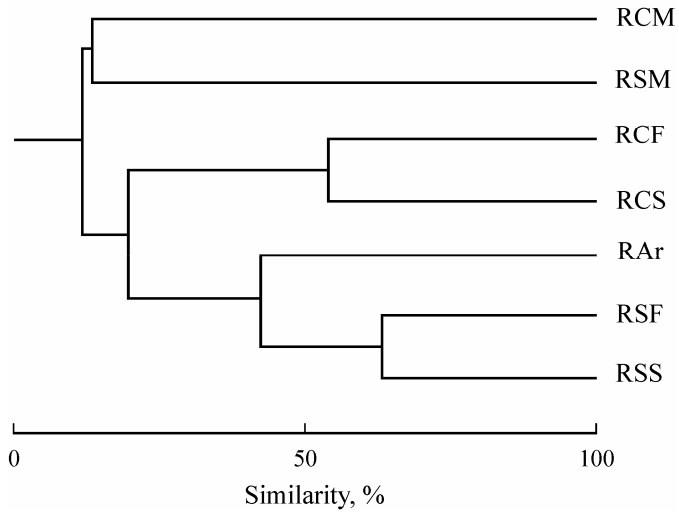


Fig. 22. Similarity of the landscape-coenotic complexes of aquatic beetles in the Northwest Caucasus. For variants abbreviations, see text.

running and circulating reservoirs, and the third one, by mountain and high-mountain reservoirs.

2. Comparative Arealogical Analysis of the Landscape-Coenotic Complexes of Coleopterous Insects

The ratio of different chorological complexes and types of ranges within the arealogical spectrum of the beetle fauna of the Northwest Caucasus as a whole is given in Fig. 23. About 35% of species of the Northwest Caucasus beetle fauna possess wide boreal ranges; a portion of species with the Forest European ranges is also rather large (11%), i.e., the total share of species with boreal ranges of different types approaches 50%. Species with the Caucasian ranges of various types seize about 25% of the beetle fauna, the remaining 25% of species possess ranges of the Ancient Mediterranean complex. The ratio of different types of ranges of separate landscape-coenotic beetle complexes and particular taxocenes is discussed below.

Land zonal communities. The beetle coenofauna of the natural steppes and pastures of the steppe and forest-steppe zones is nearly equally assembled by species with the Boreal and the Ancient Mediterranean ranges, species with the Caucasian ranges make up less than 5% of the coenofauna (Fig. 24). Differences in the arealogical composition between particular families are considerable. Thus in ground beetles and Tenebrionoidea (Table 1), the portion of species with

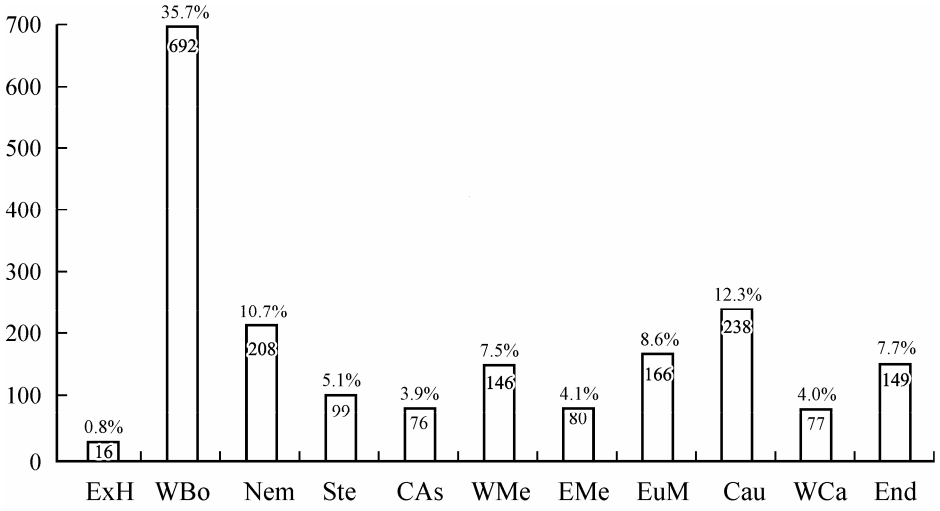


Fig. 23. Arealogical composition of the beetle fauna of the Northwest Caucasus. For variants abbreviations, see text.

the boreal ranges is rather low (19–40%), furthermore, species with the Steppe, the Wide Tethyan and the Euro-Mediterranean ranges prevail within the arealogical spectrum of the Ancient Mediterranean complex. A manifestative predominance of species with the ranges of the Boreal complex (usually wide ones) is observed in chrysomelids and rove beetles. Click beetles and Scarabaeoidea, possessing a rather small portion of species with the boreal ranges, include high percentage of the species of the Ancient Mediterranean complex, first of all those with the Wide Mediterranean ranges (18–29%). About the same proportions of species with the Boreal and the Ancient Mediterranean ranges, as in the complex of natural steppes and pastures of the steppe and forest-steppe zones, is observed in the complex of the treeless coenoses of the upland part of the region; however percentage of the Caucasian species is higher here and

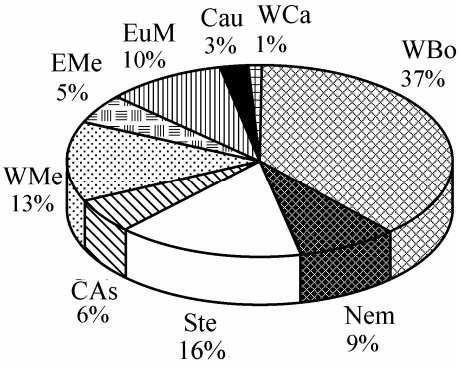


Fig. 24. Arealogical composition of the beetle fauna of natural steppes and pastures of the steppe and forest-steppe zones in the Northwest Caucasus. For the ranges abbreviations, see text.

makes up more than 10% (Fig. 25). Both in the ground beetles and Tenebrionoidea (see Table 1), similarly to the previous landscape-coenotic complex, the portion of species with the Boreal ranges is rather insignificant and varies from 22 to 42%, species possessing the Steppe, the Wide Tethyan, and the Euro-Mediterranean ranges similarly prevail in the Ancient Mediterranean complex. The pattern of the dominence of species with the Boreal complex ranges close to the plain steppes is also observed in chrysomelids and rove beetles. Species possessing the Wide Mediterranean ranges also prevail among click beetles and Scarabaeoidea. In general, spectra of the ranges of various Coleoptera taxa for all the open, not high-mountain landscapes of the Northwest Caucasus are very close.

The arealogical structure of the beetle taxocenes of different forest types is rather diverse. The beetle complex of inundated and plain forests is characterized by the dominance of species with boreal ranges (60%); among the species possessing the Ancient Mediterranean distribution type the ones with the Euro-Mediterranean ranges prevail (15%) (Fig. 26); the share of the Caucasian species is only 3%. Species with the Wide Boreal ranges in carabids, Tenebrionoidea, and chrysomelids (Table 2) constitute approximately 50–75% of taxocenes, while species with the Forest European ranges, 5–20%. The widest spectrum of ranges of different types of all the three abovementioned groups is recorded for ground beetles; in particular, carabidofauna includes a lot of species with ranges of the Euro-Mediterranean type. Rove beetles, click beetles, and Scarabaeoidea possess lower percentage of species with wide boreal ranges than

Table 1. Arealogical composition of the landscape-coenotic beetle complexes of woodless plain and low mountain landscapes of the Northwest Caucasus (%)

Taxon	Type of the range										
	ExH	WBo	Nem	Ste	CAs	WMe	EMe	EMe	Cau	WCa	End
Natural steppes and pastures of the steppe and forest-steppe zones											
Carabidae	0.00	34.97	4.90	23.78	7.69	4.20	3.50	18.18	2.10	0.70	0.00
Tenebrionoidea	0.00	12.50	6.25	50.00	25.00	0.00	6.25	0.00	0.00	0.00	0.00
Chrysomelidae	0.00	63.16	2.63	0.00	15.79	13.16	0.00	2.63	2.63	0.00	0.00
Staphylinidae	0.00	66.67	0.00	3.03	0.00	0.00	0.00	27.27	3.03	0.00	0.00
Elateridae	3.03	15.15	6.06	18.18	6.06	18.18	9.09	9.09	12.12	3.03	0.00
Scarabaeoidea	0.00	32.63	21.05	8.42	0.00	28.42	8.42	0.00	1.05	0.00	0.00
Steppe habitats, treeless mountain tops, glades, other meadow-steppe coenoses of the upland part of the region											
Carabidae	0.00	36.61	5.46	14.75	4.37	5.46	3.28	18.58	6.56	1.09	3.83
Tenebrionoidea	0.00	11.11	11.11	33.33	22.22	0.00	5.56	0.00	11.11	5.56	0.00
Chrysomelidae	0.00	60.00	7.27	0.00	10.91	10.91	2.73	0.00	7.27	0.91	0.00
Staphylinidae	0.00	66.67	4.76	2.38	0.00	0.00	2.38	21.43	2.38	0.00	0.00
Elateridae	0.00	12.50	12.50	8.33	0.00	16.67	12.5	4.17	12.5	8.33	12.50
Scarabaeoidea	0.00	34.31	20.59	2.94	0.00	24.51	9.80	0.00	5.88	1.96	0.00

Note. For abbreviations of the ranges, see text.

ground beetles, but the number of species with the Forest European, the Wide Mediterranean, and Euro-Mediterranean ranges grows. In the click-beetle taxocene of the inundated and plain forests, portion of species with the Caucasian types of ranges is maximal and reaches 37%.

The portion of species with boreal ranges in the beetle coenofauna of deciduous forests, as well as in the coenofaunas of the previous types, is large and makes up 50%; however there are more European species among them in comparison with the above landscape-coenotic complexes, the portion of species with ranges belonging to the Ancient Mediterranean complex, on the contrary, is considerably reduced, but that of species with the Caucasian types of ranges increases (up to 28%, Fig. 27). Two pairs of coleopterous taxa in the deciduous forest fauna possess a similar arealogical structure. The first pair unites ground beetles and rove beetles (see Table 2), among them species with the Wide Boreal, Forest European, Euro-Mediterranean, Wide Euxian, and West Caucasian types of ranges prevail. The second pair, comprising click beetles and Tenebrionoidea, possesses a higher portion of species with the Wide Mediterranean, the East Mediterranean, and the West Caucasian ranges. The "edges" of arealogical spectrum are occu-

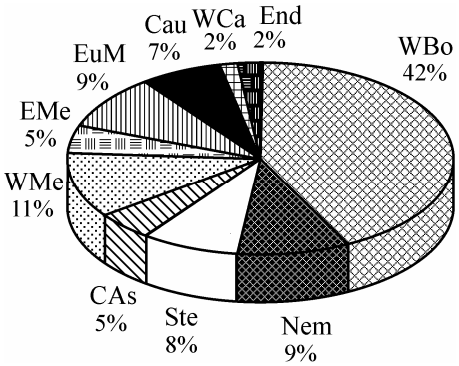


Fig. 25. Arealogical composition of the beetle fauna of meadow-steppe formations of the upland part of the Northwest Caucasus. For the ranges abbreviations, see text.

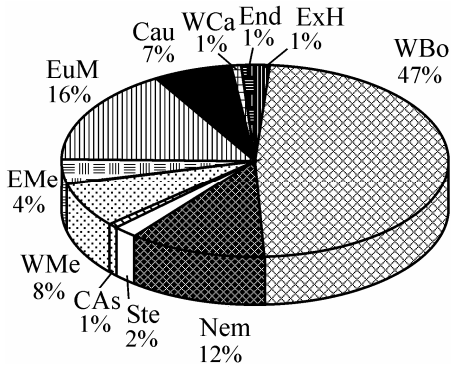


Fig. 26. Arealogical composition of the beetle fauna of inundated and plain forests in the Northwest Caucasus. For the ranges abbreviations, see text.

Table 2. Arealogical composition of the landscape-coenotic beetle complexes in the forests of the Northwest Caucasus (%)

Taxon	Type of the range										
	ExH	WBo	Nem	Ste	CAs	WMe	EMe	EMe	Cau	WCa	End
Inundated and plain forests											
Carabidae	2.56	47.86	5.13	3.42	0.85	5.98	5.98	18.8	5.98	1.71	1.71
Tenebrionoidea	18.18	45.45	18.18	0.00	9.09	9.09	0.00	0.00	0.00	0.00	0.00
Chrysomelidae	0.00	74.24	6.06	0.00	3.03	3.03	7.58	0.00	6.06	0.00	0.00
Staphylinidae	0.00	46.58	13.04	1.86	1.24	1.24	0.62	29.81	4.97	0.00	0.62
Elateridae	2.94	20.59	11.76	2.94	0.00	2.94	5.88	14.71	26.47	5.88	5.88
Scarabaeoidea	0.00	31.15	26.23	0.00	0.00	32.79	6.56	0.00	3.28	0.00	0.00
Deciduous forests of different types and dry light forests											
Carabidae	1.15	26.44	8.05	3.45	1.15	1.72	2.3	15.52	8.05	3.45	28.74
Tenebrionoidea	3.33	26.67	16.67	0.00	6.67	3.33	3.33	0.00	20.00	10.00	10.00
Chrysomelidae	0.00	54.26	10.11	0.00	9.57	9.04	2.66	1.60	12.23	0.53	0.00
Staphylinidae	0.00	33.57	17.86	1.07	0.00	0.71	1.07	15.36	20.00	3.93	6.43
Elateridae	4.60	19.54	14.94	0.00	0.00	2.30	4.60	10.34	21.84	13.79	8.05
Scarabaeoidea	0.00	26.45	24.79	0.83	0.00	29.75	6.61	0.00	7.44	4.13	0.00
Mixed and coniferous forests (including croocked forests)											
Carabidae	0.00	17.65	2.94	0.00	0.00	0.00	0.98	2.94	18.63	17.65	39.22
Tenebrionoidea	0.00	46.15	19.23	0.00	7.69	3.85	0.00	0.00	11.54	3.85	7.69
Staphylinidae	0.00	44.55	8.91	0.99	0.00	0.00	0.00	17.82	18.81	1.98	6.93
Elateridae	13.04	17.39	8.70	0.00	0.00	2.17	8.70	4.35	28.26	13.04	4.35
Scarabaeoidea	0.00	30.00	24.29	0.00	0.00	31.43	5.71	0.00	7.14	1.43	0.00

Note. For abbreviations of the ranges, see text.

pied by the taxocenes of chrysomelids, characterized by complete dominance of species with the Boreal ranges (54%), and Scarabaeoidea, with an enormous portion of the Wide Mediterranean ranges (30%).

The ranges of the beetle coenofauna of mixed and coniferous forests are nearly equally distributed between the Boreal, Ancient Mediterranean, and Caucasian complexes (Fig. 28). Scarabaeoidea and rove beetle taxocenes (see Table 2), possessing over 50% species with the Boreal ranges, also demonstrate a significant amount of species with the Mediterranean ranges, mainly the Euro-Mediterranean and Wide Mediterra-

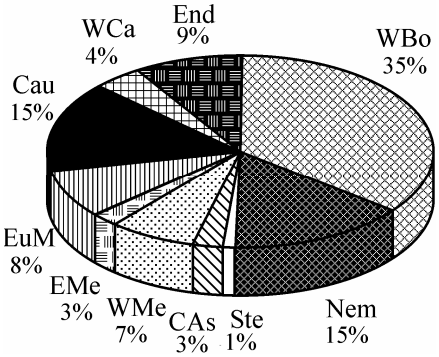


Fig. 27. Arealogical composition of the beetle fauna of deciduous and dry light forests in the Northwest Caucasus. For the ranges abbreviations, see text.

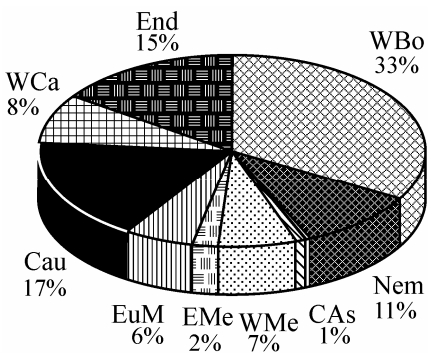


Fig. 28. Arealogical composition of the beetle fauna of mixed and coniferous forests in the Northwest Caucasus. For the ranges abbreviations, see text.

Table 3. Arealogical composition of the landscape-coenotic beetle complexes of alpestrine and alpine belts of the Northwest Caucasus (%)

Taxon	Type of the range										
	ExH	WBo	Nem	Ste	CAs	WMe	EMe	EMe	Cau	WCa	End
Carabidae	0.00	19.23	1.92	1.92	0.96	0.00	0.96	0.00	18.27	22.12	34.62
Tenebrionoidea	0.00	0.00	0.00	11.11	33.33	0.00	0.00	0.00	33.33	11.11	11.11
Chrysomelidae	0.00	67.12	6.16	0.00	8.90	2.74	3.42	0.00	9.59	1.37	0.68
Staphylinidae	0.00	35.19	5.56	0.00	0.00	1.85	0.00	9.26	27.78	1.85	18.52
Elateridae	9.09	13.64	4.55	0.00	0.00	4.55	9.09	4.55	31.82	13.64	9.09
Scarabaeoidea	0.00	26.76	19.72	0.00	0.00	26.76	5.63	0.00	12.68	8.45	0.00

Note. For abbreviations of the ranges, see text.

nean distribution. The Tenebrionoidea taxocene in the mixed and coniferous forests is characterized by the maximal percentage of the Boreal ranges (65%) among all the investigated Coleoptera groupings, the larger part of the rest of species belongs to the Caucasian complex (23%), species with the Ancient Mediterranean ranges constitute only 12% of the coenofauna. Click beetles and especially ground beetles manifest the dominance of species of the Caucasian complex, reaching 46% of the coenofauna in click beetles and 75%, in ground beetles

The percentage of species with ranges of the Ancient Mediterranean complex in the coenofauna of alpestrine and alpine belts is even lower than in the mountain forests (Fig. 29). Species with the Caucasian ranges prevail among ground beetles and Tenebrionoidea (Table 3); furthermore the ground beetle species possess the wide Boreal ranges, whereas species of Tenebrionoidea have the wide Tethyan ranges. In click beetles and rove beetles the Boreal and the Ancient Mediterranean species' ranges types are presented in approximately equal proportions. Whereas species with the East Mediterranean ranges prevail in the former family, species with the Euro-Mediterranean ones dominate in the latter taxonomic grouping. As well as in the respective groups' coenofaunas of the deciduous forests, leaf beetles demonstrate an overwhelming predominance of species with the Wide Boreal ranges, whereas the coenofauna of the Scarabaeoidea is characterized by the maximal percentage of the Mediterranean ranges, first of all, the Wide Mediterranean ones.

Land azonal communities. The beetle coenofauna of plain wetlands and temporarily flooded bottomlands (Fig. 30) comprises the overwhelming majority of species with the Wide Boreal and various Ancient Mediterranean ranges; the percentage of the ranges belonging to the Caucasian complex is low. Only two coleopterous families are recorded for this community type. The first one, ground beetles, differs in a rather complicated arealogical composition, whereas the second—chrysomelids, comprises only species with only wide boreal ranges (Table 4). The beetle coenofauna of the wetland, salinized and mineralized moun-

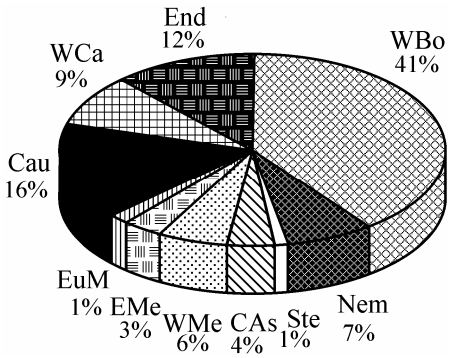


Fig. 29. Arealogical composition of the beetle fauna of alpestrine and alpine belts in the Northwest Caucasus. For the ranges abbreviations, see text.

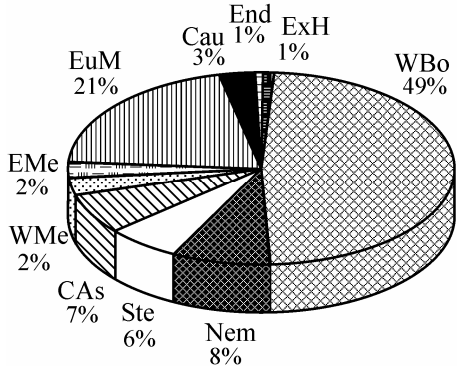


Fig. 30. Arealogical composition of the beetle fauna of wetlands and temporarily flooded bottomlands in the Northwest Caucasus. For the ranges abbreviations, see text.

Table 4. Arealogical composition of the landscape-coenotic beetle complexes of the wetland, temporarily flooded, salinized, and mineralized habitats of the Northwest Caucasus (%)

Taxon	Type of the range									
	ExH	WBo	Nem	Ste	CAs	WMe	EMe	EMe	Cau	End
Marshes, temporarily flooded bottomlands, and wetlands of the plain and seaside parts of the region										
Carabidae	0.93	47.66	8.41	6.54	7.48	1.87	1.87	21.5	2.8	0.93
Chrysomelidae	0.00	100	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wetland, salinized and mineralized habitats of the upland part of the region										
Carabidae	1.23	43.21	3.7	6.17	6.17	2.47	4.94	23.46	7.41	1.23
Chrysomelidae	0.00	92.86	7.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solonchaks and other salinized habitats										
Carabidae	0.00	22.22	0.00	30.16	14.29	11.11	4.76	14.29	3.17	0.00
Chrysomelidae	0.00	33.33	0.00	0.00	26.67	33.33	0.00	0.00	6.67	0.00
Staphylinidae	0.00	44.00	0.00	4.00	0.00	0.00	0.00	48.00	4.00	0.00
Elateridae	0.00	0.00	0.00	25.00	50.00	25.00	0.00	0.00	0.00	0.00

Note. For abbreviations of the ranges, see text.

tain habitats, consisting like the previous plain one only of carabids and chrysomelids only (Fig. 31), differs however in a higher percentage of species with the Caucasian ranges, reaching 8%. The ground beetle coenofauna is characterized by very high diversity of ranges (see Table 4), whereas the leaf beetles are represented only by species with the Wide Boreal and the Forest European ranges.

The coenofauna of salinized habitats (Fig. 32) is characterized by a rather low portion of the Boreal distributional ranges and nearly complete absence of the Caucasian ones. The bulk of species possesses various ranges of the Ancient Mediterranean complex. Whereas the families of leaf beetles and rove beetles (see Table 4) have a rather high percentage of species with the Boreal ranges, in ground beetles it is much lower, and in the click beetle species with such distributional ranges are completely missing. The beetle coenofauna of sea coasts and beaches (Fig. 33) has a similar ratio of different types of ranges with predominance of species with the Wide Mediterranean ones. The coenofauna of rove beetles and Scarabaeoidea (Table 5) is characterized by the maximal percentage of the Boreal ranges, their portion in carabids is smaller, whereas in the Tenebrionoidea and click-beetle taxocenes this type of the distributional ranges is missing.

The diagram of the chorological complexes and types of distributional ranges for the subnival belt is based on carabids only (represented there by petrophilous and hygrocryophilic forms) (Fig. 34). The Caucasian zoogeographical elements prevail, the portion of

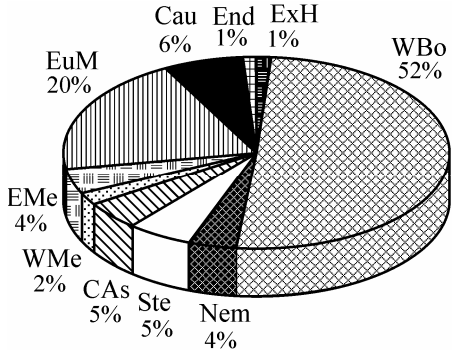


Fig. 31. Arealogical composition of the beetle fauna of the wetland, salinized and mineralized habitats of the upland part of the Northwest Caucasus. For the ranges abbreviations, see text.

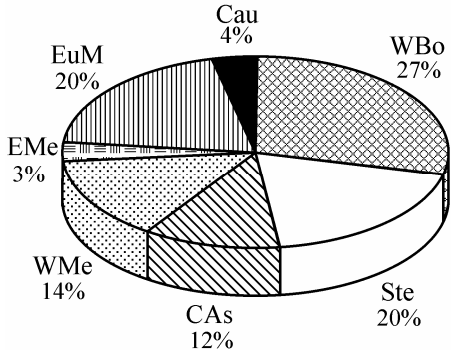


Fig. 32. Arealogical composition of the beetle fauna of solonchaks and other salinized habitats in the Northwest Caucasus. For the ranges abbreviations, see text.

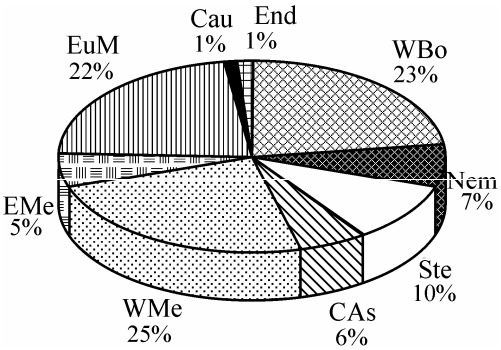


Fig. 33. Arealogical composition of the beetle fauna of sea coasts and beaches in the Northwest Caucasus. For the ranges abbreviations, see text.

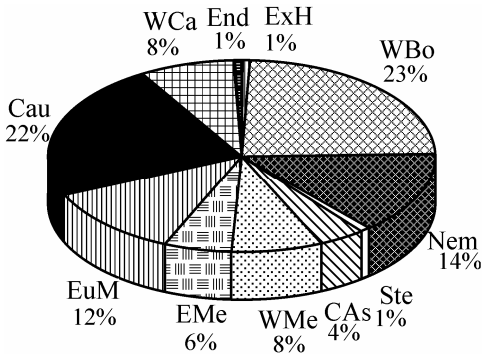


Fig. 35. Arealogical composition of the beetle fauna of floodlands of rivers and brooks in the Northwest Caucasus. For the ranges abbreviations, see text.

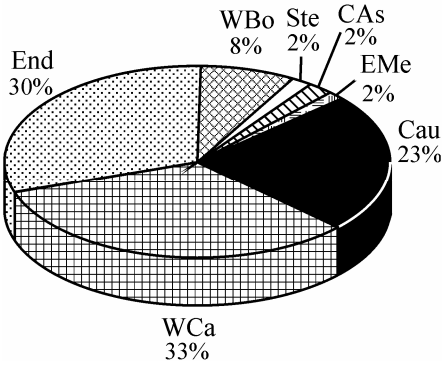


Fig. 34. Arealogical composition of the beetle fauna of subnival belt in the Northwest Caucasus. For the ranges abbreviations, see text.

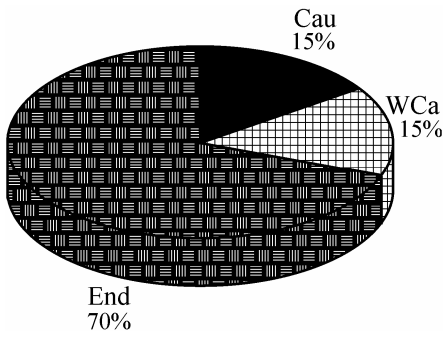


Fig. 36. Arealogical composition of the beetle fauna of the subterranean forms of karst in the Northwest Caucasus. For the ranges abbreviations, see text.

the West Caucasian species reaching 33%, and that of species endemic to the Northwest Caucasus, 30%.

The ranges of species representing the coenofauna of floodlands of the rivers and brooks (Fig. 35) are nearly equally shared between the Boreal, the Ancient Mediterranean, and the Caucasian complexes. Diagrams of chorological complexes and types of distributional ranges are rather similar for ground beetles and rove beetles (see Table 5) (manifesting predominance of the Caucasian and the Euro-Mediterranean distributional ranges) on the one side, and click beetles and Scarabaeoidea (with predominance of the Boreal and Ancient Mediterranean ranges), on the other.

The arealogical composition of coenofauna of the subterranean forms of karst (Fig. 36) is the closest to that of the subnival belt of all the abovementioned coenoses, but, however, differs in complete dominance of endemics of the Northwest Caucasus (70%), represented mainly by carabids.

Freshwater assemblages. All the water beetle complexes of steppe, stagnant foothill and artificial reservoirs, RSS, RCS, RSF, RAr (Table 6) are characterized by a very similar chorological structure with predominance of species with the Wide Boreal ranges. Mountain and high-mountain complexes, RCF, RSM and especially RCM (see Table 6), differ in a higher portion of species with different types of ranges, the maximal arealogical diversity being observed in the mountain running and circulating reservoirs.

The above data allow us to check possible similarity or coincidence of the chorological patterns (reflecting presumably historical conditions of formation of the regional beetle taxocenes) in different groups of coleopterous insects of the Northwest Caucasus. In this respect, Carabidae and Tenebrionoidea on the one hand, and Elateridae and Scarabaeoidea on the other, seem to be most similar (it concerns first of all the zonal taxocenes). Rove beetles reveal the greatest similarity to ground beetles in certain landscape-coenotic complexes, while in the others, with Scarabaeoidea or click beetles. Chrysomelids, a phytophilous group most distinct from the others in biological respect, strangely enough, sometimes shows the great-

Table 5. Arealogical composition of the landscape-coenotic beetle complexes of sea coasts and beaches, floodlands of the rivers and brooks of the Northwest Caucasus (%)

Taxon	Type of the range										
	ExH	WBo	Nem	Ste	CAs	WMe	EMe	EMe	Cau	WCa	End
Sea coasts and beaches											
Carabidae	0.00	14.29	0.00	14.29	19.05	9.52	4.76	38.10	0.00	0.00	0.00
Tenebrionoidea	0.00	0.00	0.00	20.00	20.00	40.00	10.00	0.00	0.00	0.00	10.00
Staphylinidae	0.00	36.00	0.00	0.00	0.00	4.00	0.00	56.00	4.00	0.00	0.00
Elateridae	0.00	20.00	0.00	40.00	0.00	20.00	0.00	20.00	0.00	0.00	0.00
Scarabaeoidea	0.00	25.64	17.95	7.69	0.00	41.03	7.69	0.00	0.00	0.00	0.00
Floodlands of the rivers and brooks											
Carabidae	1.03	21.65	6.19	0.00	7.22	1.03	6.19	17.53	23.71	6.19	9.28
Staphylinidae	0.00	32.26	12.90	0.00	0.00	0.00	0.00	12.90	29.03	9.68	3.23
Elateridae	6.06	9.09	24.24	3.03	6.06	12.12	3.03	3.03	12.12	12.12	9.09
Scarabaeoidea	0.00	20.83	25.00	0.00	0.00	25.00	12.50	0.00	12.50	4.17	0.00

Note. For abbreviations of the ranges, see text.

Table 6. Arealogical composition of coenofauna of water beetles of the Northwest Caucasus (%)

Type of reservoir	Type of the range						
	ExH	WBo	Nem	Ste	WMe	EMe	Cau
RSS	3.37	68.54	7.87	8.99	6.74	4.49	0.00
RCS	4.44	68.89	8.89	4.44	8.89	4.44	0.00
RSF	3.03	77.27	3.03	4.55	7.58	3.03	1.52
RCF	3.13	56.25	12.5	6.25	15.63	6.25	0.00
RSM	7.69	61.54	0.00	0.00	15.38	7.69	7.69
RCM	0.00	41.67	8.33	8.33	16.67	16.67	8.33
RAr	6.06	81.82	6.06	0.00	6.06	0.00	0.00

Note. For abbreviations of ranges and water reservoirs, see text.

Table 7. Share of different range types in formation of the zonal, azonal, and water beetle fauna of the Northwest Caucasus (%)

Complex of beetle communuties	Type of the range										
	ExH	WBo	Nem	Ste	CAs	WMe	EMe	EMe	Cau	WCa	End
Zonal	1.18	34.12	11.44	4.38	3.66	6.67	3.79	9.67	12.48	4.38	8.24
Azonal	0.36	26.45	6.16	7.97	7.97	9.42	4.71	11.59	14.13	3.26	7.97
Water	2.50	63.33	9.17	8.33	0.00	9.17	5.83	0.00	1.67	0.00	0.00

Note. For abbreviations of the ranges, see text.

est similarity to mainly ground or litter-dwelling predators, ground beetles and rove beetles.

The chorological structures of the beetle complexes of zonal, azonal and water communities as a whole, appreciably differ (Table 7). If the zonal beetle fauna of the Northwest Caucasus is composed mainly by species with the boreal ranges (about 47%), and the portion of the Ancient Mediterranean complex does not reach even 30%, the azonal fauna, on the contrary, is formed mainly by species with the Ancient Mediterranean ranges (about 42%), and the portion of species with the Boreal ranges makes less than 33%. Besides

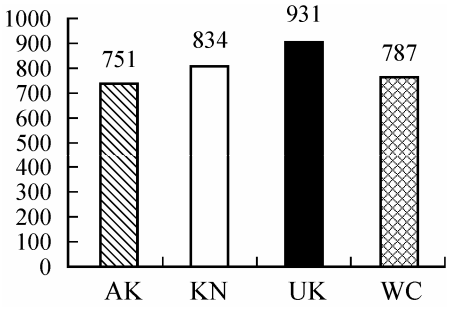


Fig. 37. Species diversity of zonal beetle taxocenes in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

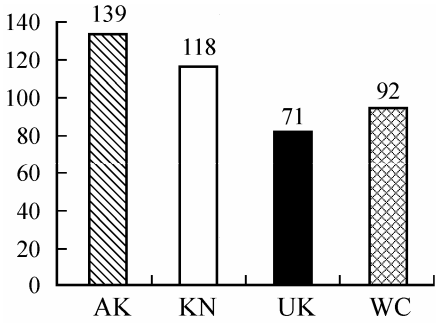


Fig. 38. Species diversity of azonal beetle taxocenes in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

the percentage of species with ranges of the Steppe and the Wide Tethyan types is noticeably higher in the azonal communities. The Caucasian complex in both types of assemblages comprises about a quarter of the fauna wholly and possesses rather a similar ratio of species with the concrete types of the Euxine ranges.

Allocation of species diversity among zonal (Fig. 37), azonal (Fig. 38), and water (Fig. 39) communities according to the regional biogeographical subdivisions is also fairly indicative. The diversity of inhabitants of the zonal communities is much higher in the mountain zoochorones and reaches the maximal value in the Upland Kuban Subprovince, and azonal ones, in the plain or low-mountain Azov-Kuban and Krymsk-Novorossisk Subprovinces, whereas their diversity in the Upland Kuban Subprovince is minimal.

Thus, the Boreal zoogeographical elements, constituting the numerical majority in a number of modern local coenofaunas, most probably have penetrated the terrain of the region or have widely populated it mainly during diffusion of the appropriate accommodating zonal communities to the mountain part of the region (though their species diversity is rather high even on the plain), while the Ancient Mediterranean ones did it mainly along with the development and progress of azonal communities in plain and low-mountain parts of the Northwest Caucasus. Evidently, it was in these parts of the region that the most notable refugia within its limits were situated [the Krymsk-Novorossisk Subprovince is known to house a series of obvious relicts, e.g. ground beetle *Nomius pygmaeus* (Dejean, 1831), etc.]. As it was already mentioned for separate taxocenes, the regional aquatic beetle fauna as a whole is characterized by complete dominance of the Boreal species (over 70%) and the lowest percentage of the Caucasian ones (2%). Furthermore, the maximal diversity of the freshwater taxocenes is observed in the Upland Kuban and the Azov-Kuban Subprovinces, and the minimal—in the West Caucasian province. All the biogeographical subdivisions of the region, except for Krymsk-Novorossisk Subprovince, appear to be by the substantially similar regularities of formation of the aquatic fauna (in the case of recruitment into analysis of some

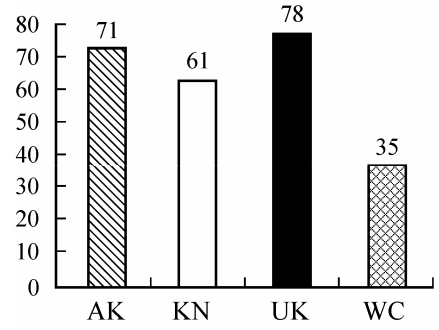


Fig. 39. Species diversity of water beetle taxocenes in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

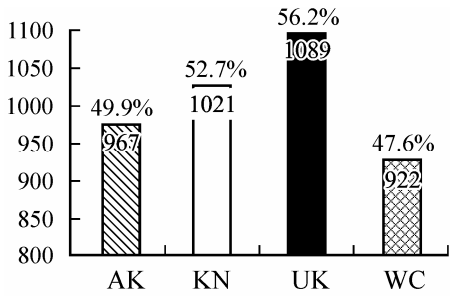


Fig. 40. Species diversity of beetles faunistic complexes in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

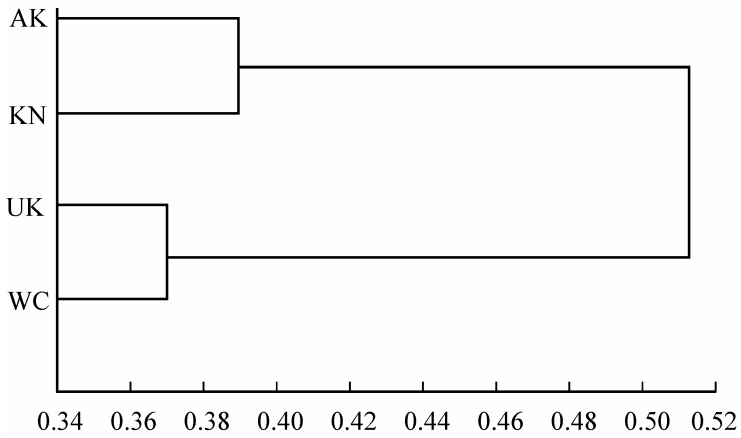


Fig. 41. Similarity of faunistic complexes of coleopterous insects in biogeographical subdivisions of the Northwest Caucasus. Scale indicates percent disagreement distance. For zoochorones abbreviations, see Fig. 13.

further groups of water beetles this treatment can be essentially corrected).

Speciation in the region seems to proceed with the nearly equal intensity in both land zonal and azonal communities.

3. Faunistic Similarity and Chorological Pattern of Coleopterous Insect Taxocenes of the Regional Zoochorones

Correction of the sinperats of the biogeographical subdivisions of the Northwest Caucasus adopted below in comparison with the layout suggested by Shiffers (1953) has been discussed earlier (Zamotajlov, 1992b) and affects basically divisions of the Caucasian Area of Mountain Meadows and Forests. The most debatable question is delimitation of the Upland Kuban and the Elbrus Subprovinces. In the aforecited scheme (Fig. 13), the ranges of some characteristic Elbrus groups of the genus *Carabus* Linnaeus, 1758 are used as its markers, namely of the subgenus *Cechenochilus* Motschulsky, 1850, of the *kratkyi* species-group of the subgenus *Archiplectes* Gottwald, 1982, as well as one of the characteristic Kuban *prometheus* species-group of the subgenus *Archiplectes*. Consequently the border of the above subdivisions in the area of Skalstyi and Peredovoy Mt. Ranges appears to be shifted westwards, towards the valley of the Belaya River. However distribution of some other coleopterous species does not unequivocally correspond to this layout, therefore a classical phytogeographical division is used hereafter at calculations, and all species populating the southeast part of the North Caucasian Province within the limits of the region, are conventionally attributed to the Upland Kuban Subprovince. Distribution of numerous coleopterous species in the Northwest Caucasus coincides in general with the limits of the analyzed zoochorones; therefore such taxa can be used as indicators of the corresponding subdivisions. Thus, the following species can be indicated as characteristic of the Azov-Kuban Subprovince: *Blemus discus* (Fabricius 1792), all the species of the genus *Pogonus* Dejean, 1821 and *Pogonistes* Chaudoir, 1871, *Poecilus puncticollis* (Dejean, 1828), *Pterostichus elongatus* (Duftschmid, 1812), *Dicheirotrichus ustulatus* (Dejean, 1829), *Carterus angustipennis* (Chaudoir, 1852), *Ditomus calydonius* (Rossi, 1790) (Carabidae), *Pedinus volgensis* Mulsant et Rey, 1853, *Oodescelis polita* (Sturm, 1807), *Blaps halophila* Fischer von Waldheim, 1820, *Asida lutosa* Solier, 1836 (Tenebrionidae); as characteristic of the Krymsk-Novorossisk Subprovince: *Atranus ruficollis* (Gautier, 1858), *Amara fulva* (O. Müller, 1776), *Bradycellus harpalinus* (Serville, 1821), *Harpalus attenuatus* Stephens, 1828, *Microderes brachypus* (Steven, 1809), *Pangus scaritides* (Sturm, 1818), *Cymindis ovipennis* Motschulsky, 1844 (Carabidae), *Isomira murina* (Linnaeus, 1758), *Omophlus orientalis* Mulsant, 1856, *Corticeus longulus* (Gyllenhal, 1827), *Phaleria pontica* Semenov, 1901, *Trachyscelis aphodioides* Latreille, 1809, *Pedinus cimmerius caucasicus* G. Medvedev, 1968, *Ammobius rufus* (Lucas, 1846), *Leichenum pictum* (Fabricius, 1801), *Melanimon tibialis* (Fabricius, 1781) (Tenebrionoidea); as characteristic of the Upland Kuban Subprovince: *Cicindela desertorum* Dejean, 1825, *Nebria picicornis* (Fabricius, 1801), *N. tristicula* Reitter, 1888, *Dyschiriodes globosus* (Herbst, 1783), *Trechus alanicus* Belousov, 1990, *Patrobus atrorufus* (Ström, 1768), *Poecilus stenoderus* (Chaudoir, 1846),

Agonum sexpunctatum (Linnaeus, 1758), *Amara lunicollis* Schiödte, 1837 (Carabidae), *Laena starcki* Reitter, 1887, *Nalassus pharnaces* (Allard, 1876), *N. diteras* (Allard, 1876), *Platydema triste* Laporte et Brullé, 1831 (Tenebrionidae), *Mycetochara gracilicornis* Roubal, 1935 (Alleculidae); as characteristic of the West Caucasian Province: *Cicindela fischeri* (Adams, 1817), *Nebria jarrigei* Ledoux et Roux, 1991, *Elaphropus caraboides* Motschulsky, 1839, *Pterostichus tamsi* (Dejean, 1831), *Calathus femoralis* Chaudoir, 1846, *Harpalus alpivagus* Tschitschérine, 1899 (Carabidae), *Nalassus lineatus* (Allard, 1876), *Metaclisa azurea* (Waltl, 1838) (Tenebrionidae).

Allocation of the beetle fauna of the Northwest Caucasus among regional zoochorones is shown in Fig. 40. The maximal species diversity (1089) is observed in the fauna of the Upland Kuban Subprovince, followed by the Krymsk-Novorossisk (1021), Azov-Kuban Subprovinces (967), and the regional fragment of the West Caucasian Province (922). Faunistic similarity of the zoochorones, computed in the analysis based on a whole amount of the material studied (using the percent disagreement distance), is given in Fig. 41. Two clusters are distinguished, the first unites the Azov-Kuban and the Krymsk-Novorossisk Subprovinces, and the second, the Upland Kuban Subprovince and the West Caucasian Province. About the same structure of dendrograms (at different similarity level of the variants, computed on the basis of the Jaccard similarity measure) is obtained for ground beetles and rove beetles respectively (Figs. 42, 43). A close layout different in the more detached position of the Azov-Kuban Subprovince is noted for Scarabaeoidea, Elateridae, and Tenebrionoidea (Figs. 44–46). Leaf beetles, like three previous groups, demonstrate the minimal similarity of fauna of the Azov-Kuban Subprovince to the other subdivisions, but clustering of the mountain zoochorones is the opposite: higher similarity is found between the Krymsk-Novorossisk Subprovince and the West Caucasian province (Fig. 47). In the aquatic beetle fauna the West Caucasian Province (Fig. 48) appears to be the most detached from others. It is noteworthy that similarity of faunas of separate biogeographical subdivisions is rather low, in click beetles it does not exceed 46%, in ground beetles, 48%, in aquatic Coleoptera, 49%, in rove beetles, 54%, in Tenebrionoidea, 58%, reaching significant values only in chrysomelids and Scarabaeoidea (63 and 70%, respectively); however two latter groups do not make the majority of the analyzed fauna as a whole.

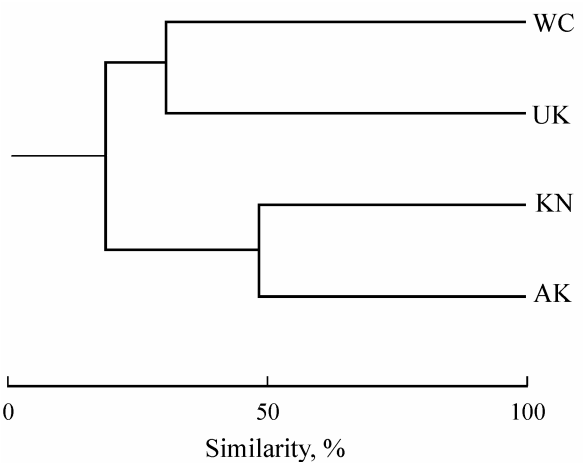


Fig. 42. Similarity of faunistic complexes of the coleopterous family Carabidae in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13. In Figs. 42–48 scale indicates Jaccard similarity measure.

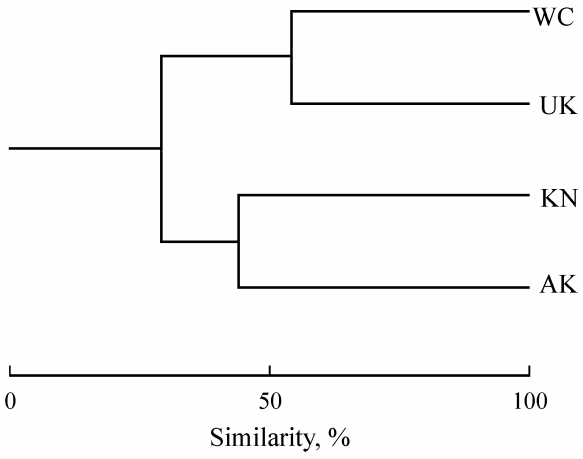


Fig. 43. Similarity of faunistic complexes of the coleopterous family Staphylinidae in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

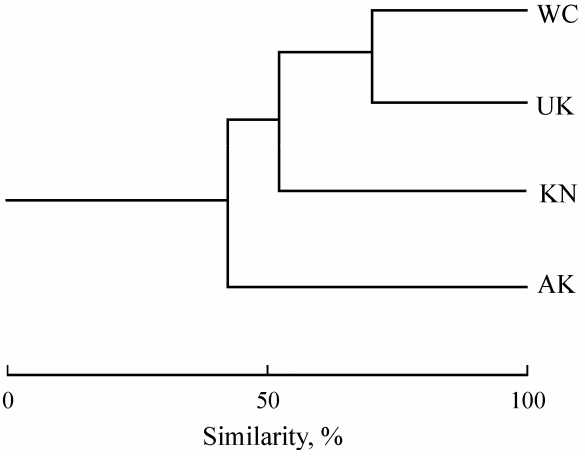


Fig. 44. Similarity of faunistic complexes of the coleopterous superfamily Scarabaeoidea in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

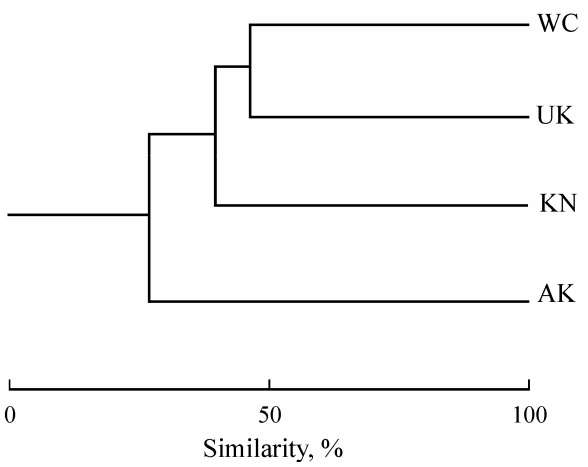


Fig. 45. Similarity of faunistic complexes of the coleopterous family Elateridae in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

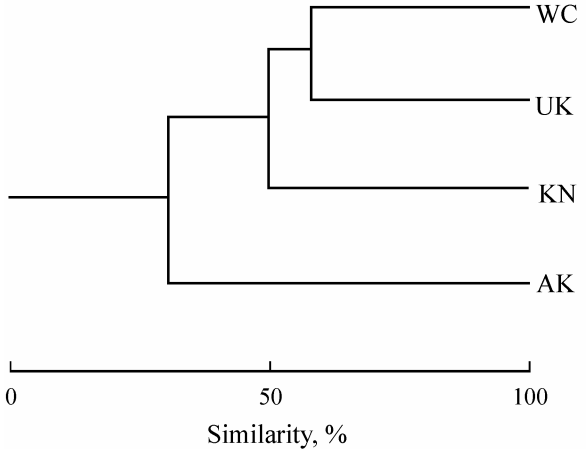


Fig. 46. Similarity of faunistic complexes of the coleopterous superfamily Tenebrionoidea in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

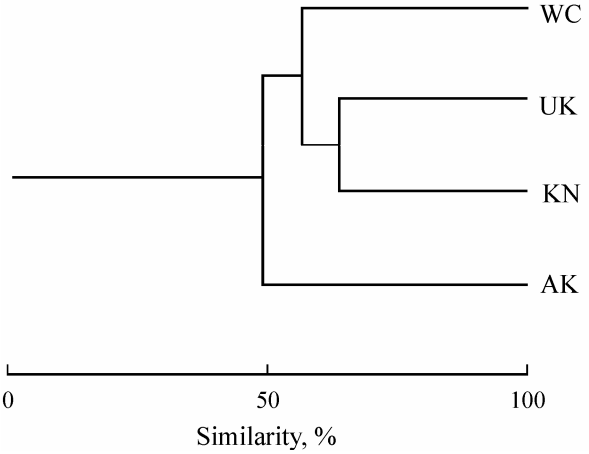


Fig. 47. Similarity of faunistic complexes of the coleopterous family Chrysomelidae in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

It seems interesting to compare the chorological pattern of particular beetle coenofaunas (landscape-coenotic complexes) in different zoochorones. The majority of the coenofaunas manifest striking uniformity of the pattern, even though the species compositions of coenofaunas differ rather strongly. This regularity is easily observed in several land zonal communities, namely, open treeless coenoses of the upland part of the region (Figs. 49–51), deciduous forests (Fig. 52–54), mixed and coniferous forests (Figs. 55–57) and the alpine belt (Figs. 58, 59). A similar rule is also observed in the azonal communities of the subnival belt (Figs. 60, 61) and floodlands (Figs. 62–64). The only exception recorded is coenofauna of the mountain moors and salinized habitats (Figs. 65–67), where the series UK → KN → WC manifests a gradual decrease of the number of the Boreal species and growing of number of species with the Ancient Mediterranean types of ranges, first of all with the Euro-Mediterranean ranges.

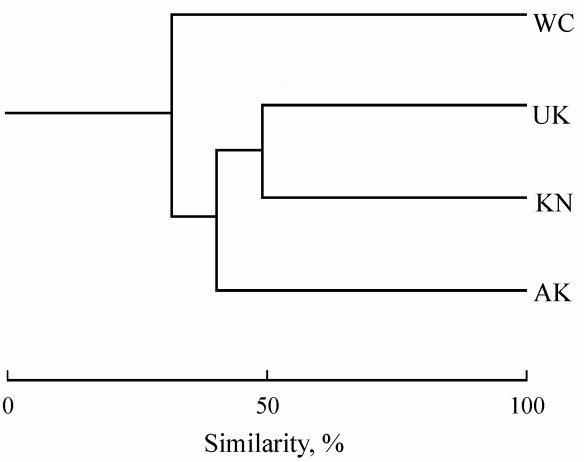
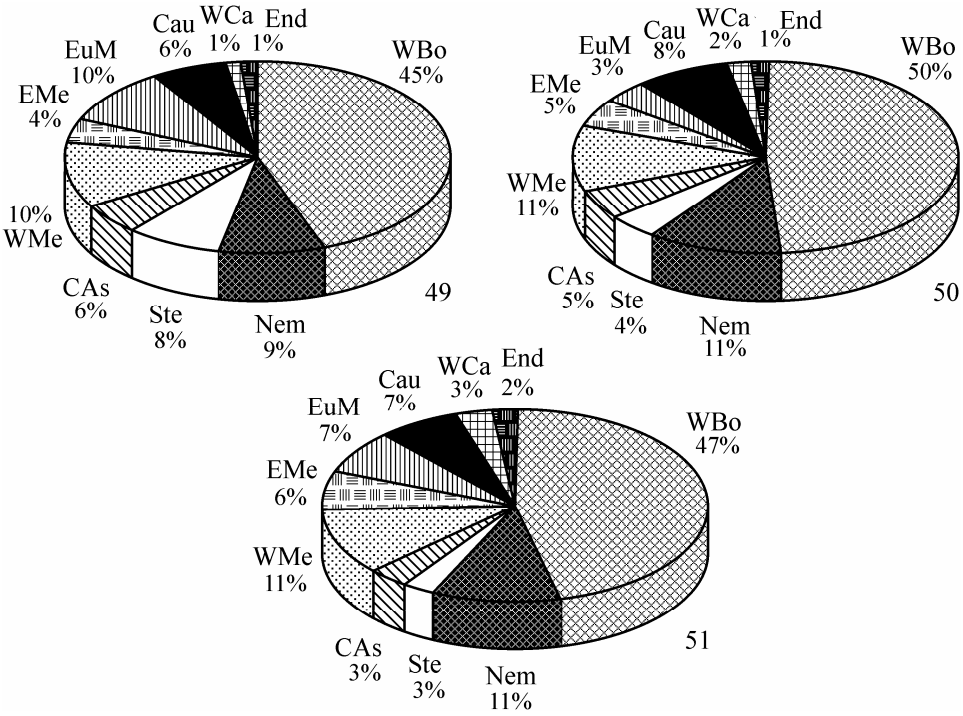
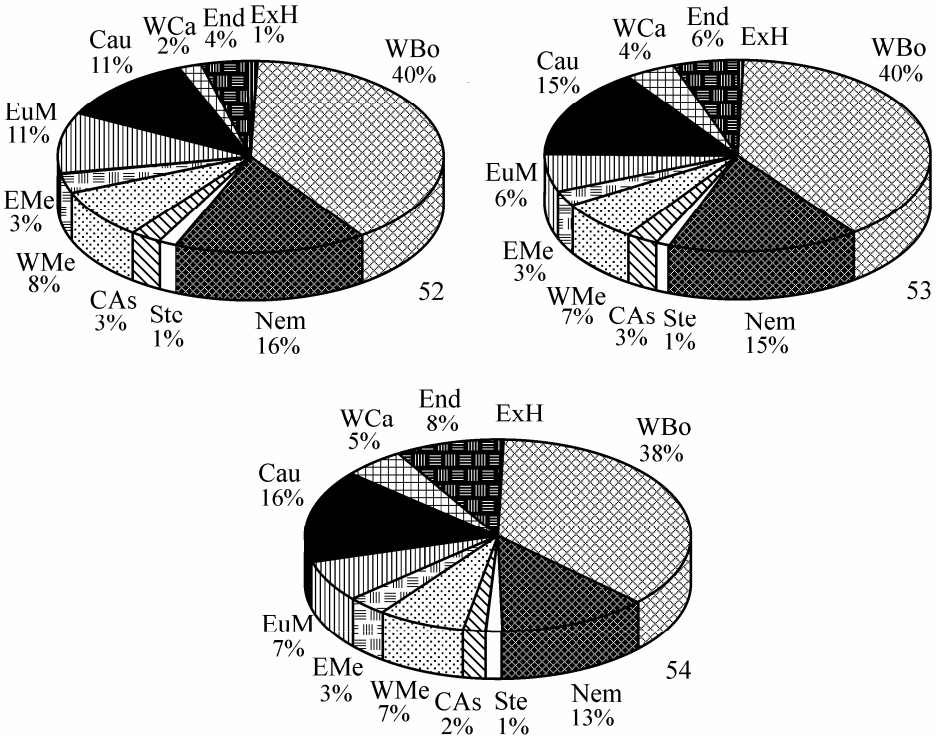


Fig. 48. Similarity of faunistic complexes of water beetles in biogeographical subdivisions of the Northwest Caucasus. For zoochorones abbreviations, see Fig. 13.

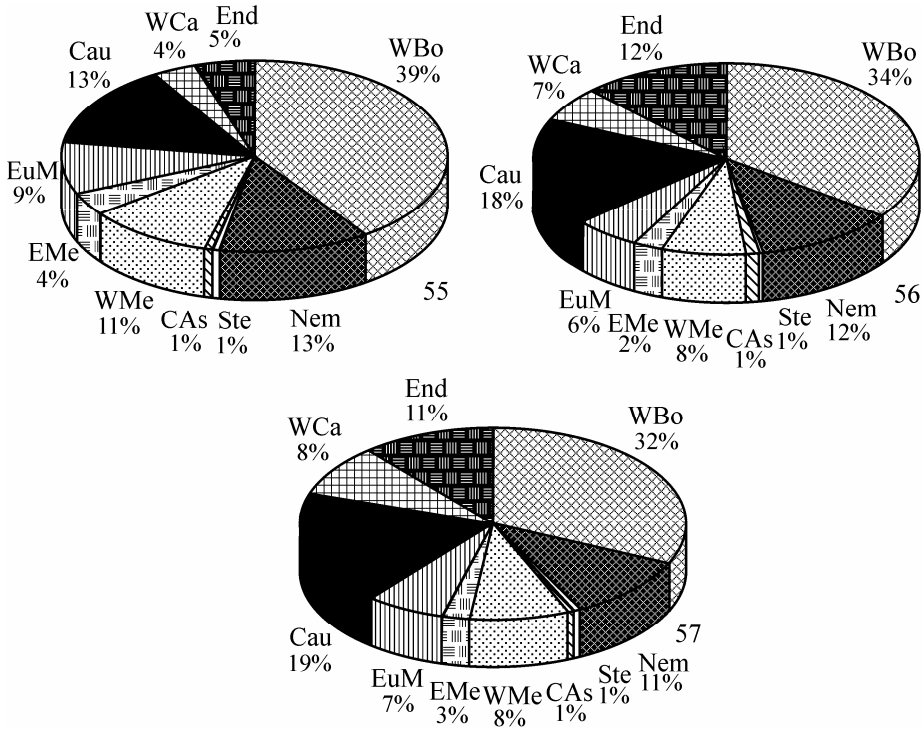
Thus, analysis of coleopterous insects allows us to assume that formation of the geographical structure of a particular coenofauna (first of all it concerns zonal coenofaunas) is determined by the historical factors governing the zoogeographical composition of the regional entomofauna as a whole rather than the zonal-territorial or microstational features of the accommodating landscapes. In certain coenofaunas some species can be substituted by others (examples of vicariation and allopatric speciation in the Caucasus are numerous enough), however general sources of formation of the appointed coenofauna remain invariable, leading to the close ratio of the arealogical groups.



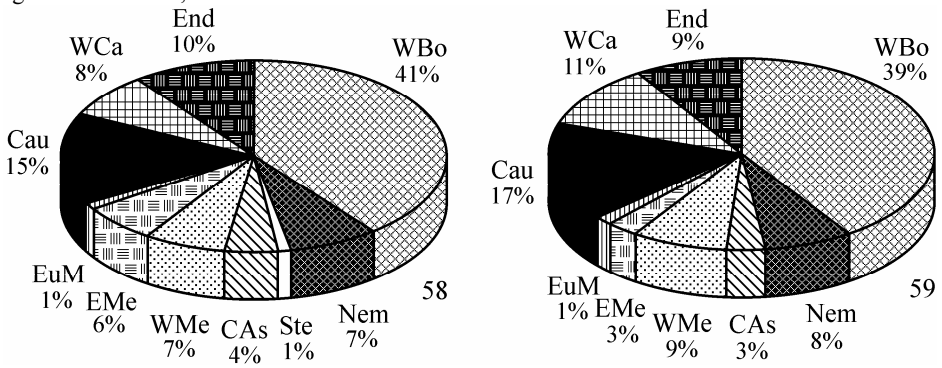
Figs. 49–51. Arealogical composition of the beetle coenofauna of meadow-steppe formations of the upland part in different biogeographical subdivisions of the Northwest Caucasus: (49) the Krymsk-Novorossisk Subprovince, (50) the Upland Kuban Subprovince, (51) the West Caucasian Province. For the ranges abbreviations, see text.



Figs. 52–54. Arealogical composition of the beetle coenofauna of deciduous forests in different biogeographical subdivisions of the Northwest Caucasus: (52) the Krymsk-Novorossisk Subprovince, (53) the Upland Kuban Subprovince, (54) the West Caucasian Province. For the ranges abbreviations, see text.



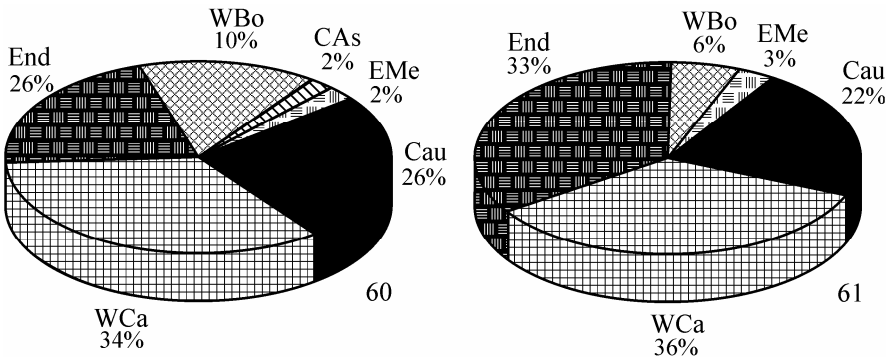
Figs. 55–57. Arealogical composition of the beetle coenofauna of mixed and coniferous forests in different biogeographical subdivisions of the Northwest Caucasus: (55) the Krymsk-Novorossisk Subprovince, (56) the Upland Kuban Subprovince, (57) the West Caucasian Province. For the ranges abbreviations, see text.



Figs. 58, 59. Arealogical composition of the beetle coenofauna of the alpestrine and alpine belts in different biogeographical subdivisions of the Northwest Caucasus: (58) the Upland Kuban Subprovince, (59) the West Caucasian Province. For the ranges abbreviations, see text.

4. Taxonomic Composition, Sources of Formation, and Arealogical Features of the Agrocoenotic Beetle Fauna

A considerable portion of the regional territory is occupied by agrarian landscapes, their beetle fauna being formed by faunistic elements inhabiting the surrounding wild landscapes; however, the agrarian landscapes themselves also exert an appreciable influence on the fauna of the natural coenoses. Coleopterous insects populating agrarian landscapes are rather numerous and, according to the authors, total 382 species. The overwhelming majority of them are ground beetles (229 species); however the diversity of chrysomelids (78) and Scarabaeoidea (30) is also rather impressive (Fig. 68). The similarity dendrogram of the natural landscape-coenotic complexes (Fig. 69) reveals the maximal resemblances of agrarian landscapes to the coenofaunas of the open, not high-mountain habitats and steppes of the steppe and forest-steppe zones and treeless coenoses of the upland part of the region. We have tried to reveal species belonging to the natural coenofaunas, which also occur in agrocnoses, and make a numeric estimation of the influence of the natural coenofaunas on the fauna of the agrarian land-



Figs. 60, 61. Arealogical composition of the beetle coenofauna of the subnival belt in different biogeographical subdivisions of the Northwest Caucasus: (60) the Upland Kuban Subprovince, (61) the West Caucasian Province. For the ranges abbreviations, see text.

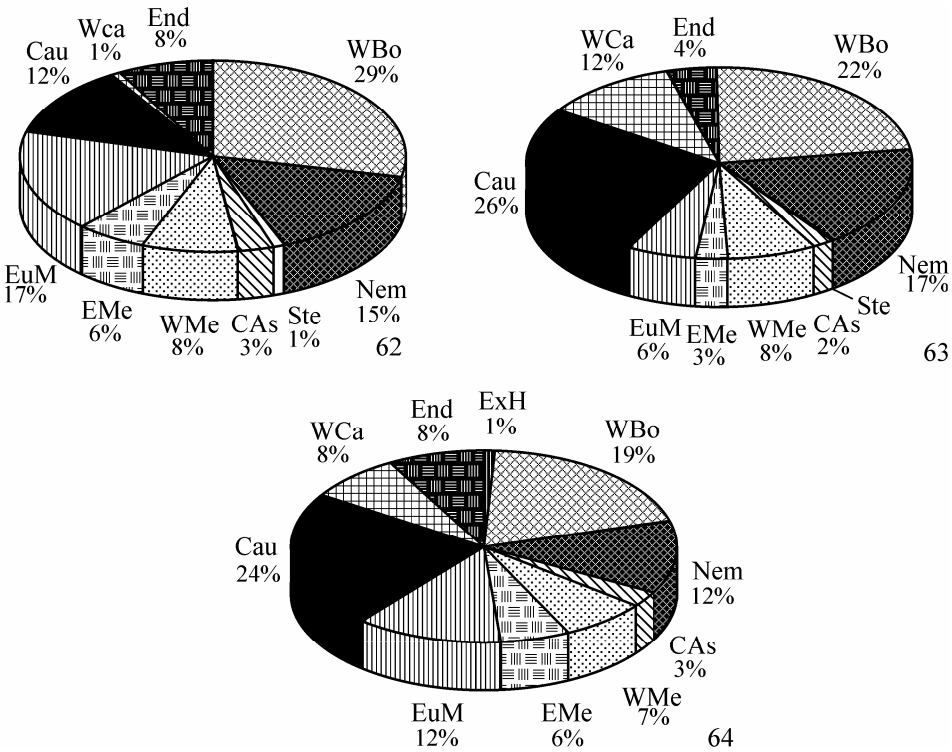
scapes (Fig. 70). The major role in the formation of the agrarian beetle fauna belongs to the predominant plain and foothill zonal communities: treeless coenoses of the upland part of the region, deciduous forests, the steppes of the steppe and forest-steppe zones, inundated and plain forests, which is supported by the example of various families of the analyzed insect group.

Participation of species with the ranges belonging to various chorological complexes and types in formation of the beetle fauna of agrarian landscapes is given in Fig. 71. The bulk of the species possesses the Wide Boreal ranges (almost 50%); portions of species with the Euro-Mediterranean (14%), the Wide Mediterranean (8%), the Steppe and the Forest European ranges (7% each) are rather substantial too.

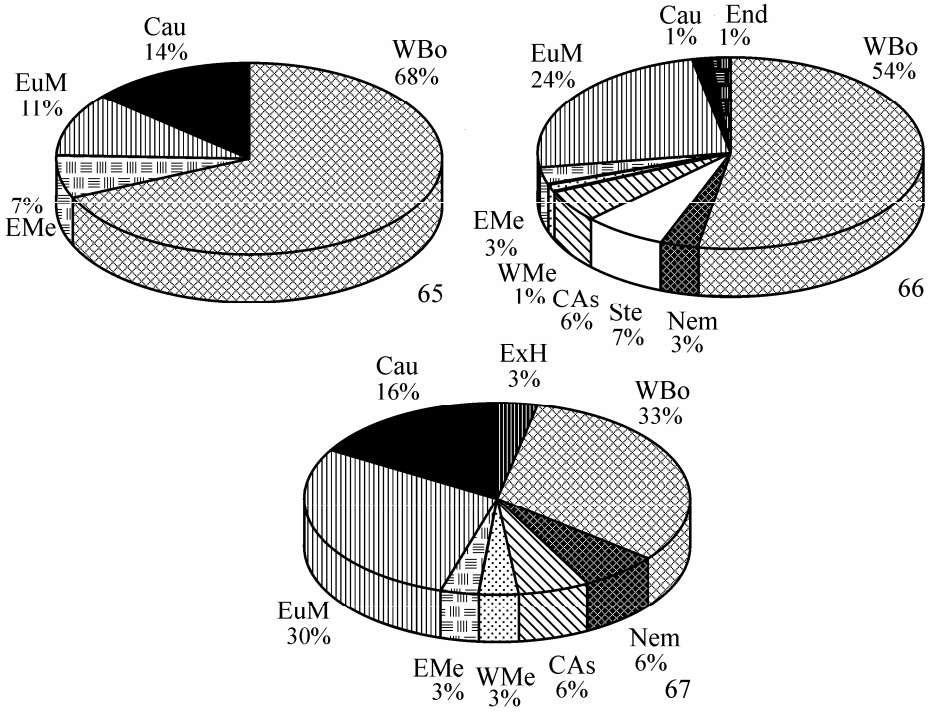
5. Some Features of Speciation in the Northwest Caucasus

The extent of endemism seems to be one of the major characteristics of the regional faunogenesis of any taxonomic group. Its study is an obligatory procedure for reconstruction of the scenario of the autochthonous speciation in the Northwest Caucasus. It is necessary to take into account, that the landscape complexes of the region rather essentially differ in the quantity of endemics, these differences being caused by the historical conditions of the genesis of the fauna. The ranges of regional endemics are also rather various; alongside with species populating separate types of communities (both zonal and azonal) and spread almost across whole terrain of the region or in all its biogeographical subdivisions (wide-areal, after Zernov, 2006); there are also taxa with a very restricted distribution, inhabiting separate mountain ranges, small karstic masses, valleys of small rivers and brooks or caves (narrow-areal, after Zernov, 2006). The quantity of endemics and subendemics of the region populating steppe landscapes is quite insignificant, and their ranges have been insufficiently investigated till now. There are relatively few coleopterous taxa of the generic or subgeneric level, endemic for the Northwest Caucasus. Considerably more taxa of the genus-group are distributed over the whole Caucasus or in the adjacent regions and represented in the region by congeners (consubgeners) endemic for the Northwest Caucasus. The study of the regional endemism and its peculiar features represents an independent problem beyond the scope of the present research in which we will touch upon it very briefly. Obviously faunogenetic reconstructions of the limited territory require using data on interfacing regions. Some regularities of the stage-by-stage formation of endemism can be outlined based on the authors' material from the Northwest Caucasus. The most convenient objects for reconstruction of regularities of the autochtonous speciation seem to be groups with numerous flightless (usually brachypterous) species or with the limited distributional ability, like ground beetles and Tenebrionoidea, mainly discussed below.

The percentage of endemics in the fauna of ground beetles of the Northwest Caucasus makes up about 17%, that in the Tenebrionoidea fauna, about 14%. The total percentage of endemics and subendemics (regional endems, after Grossheim, 1936), not exceeding the limits of the Caucasus (rarely partly distributed in adjacent territories), in the region makes up about 32% in ground beetles and about 28% in Tenebrionoidea. A significant portion of endemics belongs to the forest mesophillous forms, allied to the landscape-coenotic complexes of deciduous forests or mixed and coniferous forests. In the first complex portion of



Figs. 62–64. Arealogical composition of the beetle coenofauna of the floodlands of rivers and brooks in different biogeographical subdivisions of the Northwest Caucasus: (62) Krymsk-Novorossisk Subprovince, (63) Upland Kuban Subprovince, (64) West Caucasian Province. For the ranges abbreviations, see text.



Figs. 65–67. Arealogical composition of the beetle coenofauna of the wetland, salinized and mineralized habitats of the upland part of the region in biogeographical subdivisions of the Northwest Caucasus: (65) Upland Kuban Subprovince, (66) Krymsk-Novorossisk Subprovince, (67) West Caucasian Province. For the ranges abbreviations, see text.

endemics of the Northwest Caucasus compounds 30% in ground beetles and 10%, in Tenebrionoidea, taking into account West Caucasian and Wide Euxine endemics, it reaches 41 and 40% respectively. In the complex of mixed and coniferous forests these values make up 38 and 75% in ground beetles and 8 and 23%, in Tenebrionoidea. Endemism is fairly also developed in alpestrine and alpine belts where the portion of endemics of the Northwest Caucasus compounds 35% in ground beetles and 11%, in Tenebrionoidea, taking into account West Caucasian and Wide Euxine endemics it reaches 75 and 55% respectively. The amount of the Caucasian endemics in ground beetles is also high in the azonal assemblages of the subnival belt (86%), floodlands of the rivers and brooks (31%), and in caves (100%), where they are represented mainly by typical hypsobionts: petrophilous, hygrophilous and hygrocryophilous species. Such allocation is also substantially characteristic of click beetles and rove beetles. The aforesaid testifies, probably, to the common pathways of formation of Coleoptera faunas of the above specified landscape-coenotic complexes.

The geographical sources of the endemic groups and individual coleopterous species, populating the Northwest Caucasus, are treated differently by various authors, which seems to reflect the diversity and age variance of the ways of the penetration of beetles into this territory. Whereas Tenebrionoidea comprise a number of endemics belonging to the groups obviously possessing ancient tropical ranges and widely populating the forest zone, endemic ground beetles belong to the groupings with ranges mainly not exceeding the Palaearctics, their representatives populating not only zonal, but also various azonal communities developed during orogenesis. For example, it is supposed that penetration of the hypothetical ancestor forms of the spacious *Nannotrechus* genus-complex, comprising endogean species, from the Boreal Egeida (Jeannel, 1930; Belousov, 1998, 2008), while for the genus *Deltomerus* Motschulsky, 1850, including hygrophilous and hygrocryophilous species, from the Hyrcanian Provinces and the Toros Mountains (their fauna being derived, in its turn, from the West Himalayan ancestors) (Zamotajlov, 2005). Furthermore, at least two uneven-aged directions of invading the Caucasus are marked for each of the mentioned groups of carabids.

The distributional pattern of the alpine beetle fauna of the Northwest Caucasus can be partly extrapolated from the history of formation of alpine fauna of the other groups of insects and invertebrates as a whole,

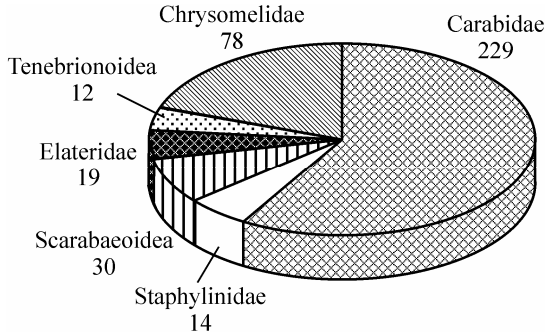


Fig. 68. Species diversity of different beetle taxonomic groups in agrarian landscapes of the Northwest Caucasus.

including land mollusks and planarias**.** The hypotheses seemed to be the best proved is the one, proposed by Kiyashko (2007) for formation of a complex of endemics of the land malacofauna of the Caucasus. Its essence is that raising of the crystal nucleus of the Caucasus Major during the Pliocene and the Early Pleistocene was accompanied by breaks, crushes and press back of the more ancient mountain surfaces constituted by sedimentary rocks. These stages of orogenesis coincided with glaciations in the Upper Pliocene–Late Pleistocene. Finally the high-mountain crystal ranges, the Main (Glavnyi), Peredovoy, and Bokovoy, appeared unsuitable for habitation of many invertebrates, including land mollusks and, apparently, many coleopterous insects during glaciations periods. On the contrary, the mountain masses composed by sedimentary rocks have played the role of the refugia rendering favorable microclimatic conditions for the Pliocene Epoch fauna during glaciations periods. In the latter case the optimum biotopic conditions have been caused by physical features of the limestone rocks (first of all by their temperature and moisture regime). Ranges built of sedimentary rocks even now differ in mainly higher humidity predetermining higher diversity of some adaptive types of beetles. The central, highest ranges of the Caucasus Major, built of crystal rocks, seem to have been invaded during interglacial periods from the upper forest belt. Perhaps the characteristic result of the postglacial (newest) stage of expansion of darkling beetles is the range of *Nalassus diteras*. This species is distributed within the entire alpine and alpestrine belts of the advanced ranges of the Caucasus Major and has an almost continuous range from the high mountains of Adygea up to Daghestan, with several isolated fragments of range in southern Georgia, eastern Armenia, and on the Stavropol Plateau. The presence of the isolated forest populations in the low mountains of southern Daghestan, in

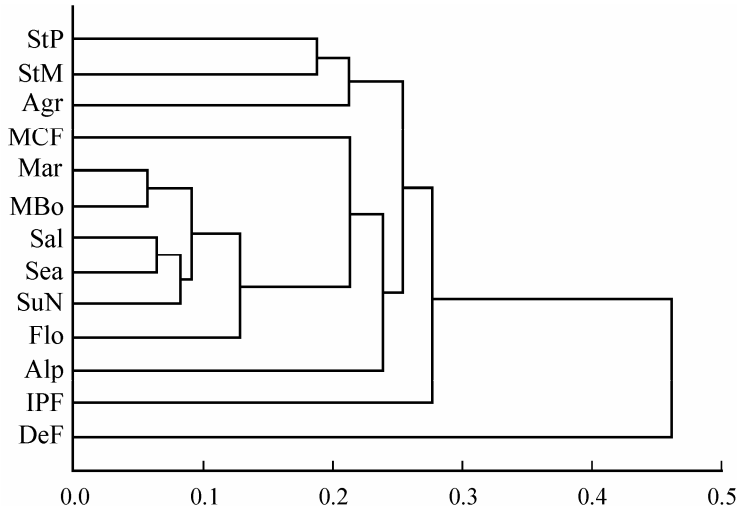


Fig. 69. Similarity of coleopterous insects fauna of agrarian landscapes to the faunas of natural land landscape-coenotic complexes of the Northwest Caucasus. Scale indicates percent disagreement distance. For variants abbreviations, see text.

the low and mid mountains of the Northwest Caucasus (Maikop, tops of cuesta masses near village Dakhovskaya), in the residual forest areas of the central Intramountain Daghestan and on the Stavropol Plateau seems to testify to the forest origin of *N. diteras*. Many species of the genera *Carabus*, *Pterostichus* Bon. and other ground beetles must have been distributed a similar way. Other Tenebrionoidea, endemic for the alpine belt of the Caucasus Major, possess isolated ranges at the mountain ranges, constituted by sedimentary rocks. One of the characteristic representatives of the Pliocene Epoch endemics *Pedinus circassicus* (Reitter, 1887) can be pointed out, whose range is limited by sedimentary high-mountain systems of the Northwest Caucasus. There are a lot of endemic taxa in ground beetles, populating exclusively limestone (seldom gypseous) karstic masses.

Two distinct stages of formation of the regional fauna of the forest mesophilic darkling beetles can be traced: Late Palaeogene—Neogene and Pleistocene. Autochthonous speciation of the forest mesophilic representatives of Tenebrionidae can be probably dated to Neogene (in particular, Early Miocene), though formation of some taxa (tribe Laenini and some taxa of the tribe Helopini) may be attributed to Paleogene. *Laena starcki*, *L. lederi* Wse., *Nalassus lineatus*, *Metaclisa azurea*, *Helops caeruleus steveni* Kryn. can be regarded as Paleogene elements. The present-day distribution of *Laena* Latr., *Nalassus* Muls., *Metaclisa* Duv., *Helops* F. and related genera covers, besides the Holarctic, the tropical regions of the Globe, where they reach the highest diversity. Recent endemics belonging to the abovementioned genera could emerge as a result of adaptive radiation

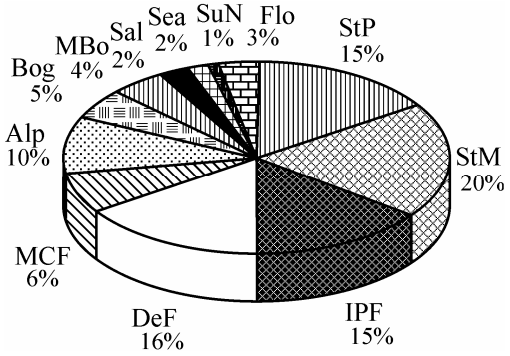


Fig. 70. Share of the natural landscape-coenotic beetle complexes in formation of the fauna of agrarian landscapes of the Northwest Caucasus (percentage of agrocenoses-dwelling species in natural coenofaunas). For complexes' abbreviations, see text.

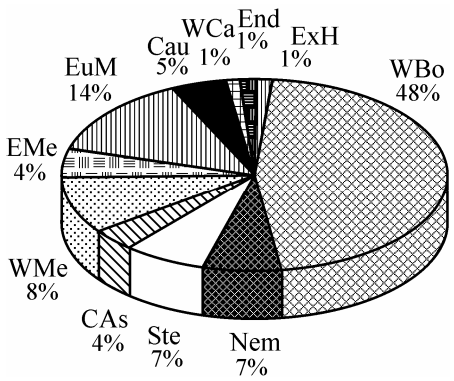


Fig. 71. Arealogical composition of the beetle fauna of agrarian landscapes of the Northwest Caucasus. For the ranges abbreviations, see text.

in Early Neogene. The formation of the present ranges of the majority of forest ground beetles could have taken place during the Upper Quaternary Period, Pleistocene and Holocene. Pulsings of the ranges in the interglacial refugia, described by Schweiger (1966, 1969), may also have contributed to formation of the observable diversity of the forest endemics. Events of the Atlantic Time and "Xerothermic Epoch" may have played the main role in fragmentation of the ranges of some species, first of all more hygrophilous and cryophilic. Complex faunistic analysis unambiqously restricts the presence of the forest-dwelling mesophilic endemic beetles to two landscape-coenotic complexes—deciduous forests and mixed and coniferous forests, while distribution of the Pleistocene boreal elements also covers inundated and plain forests and agrarian landscapes.

The overwhelming majority of the Caucasian groups of ground beetles typically possess the so-called "Elbrus" distribution. Their migration from the western part of the East Caucasus or from the Central Caucasus, territories considered sometimes as the center of formation of the Caucasian endemic beetle fauna as a whole, is supposed (Abdurakhmanov, 1985). The major direction of expansions from this center is northwest, which was in particular demonstrated by the examples of the genus *Lindrothius* Kurnakov, 1961 (Kurnakov, 1961), subgenus *Archiplectes* of the genus *Carabus* (see Gottwald, 1985), the Caucasian groups of the genus *Deltomerus* (see Zamotajlov, 1992a) and some groups of the *Nannotrechus*-complex (see Belousov, 1998). The two former authors date the initial stage of expansion of the abovementioned groups (penetration to the Caucasus Major) to the Upper Miocene. Thus endemic species of some Caucasian groups of the Northwest Caucasus appear to be the youngest. The individual polymorphism, high ecological flexibility, species diversity, abundance of geographical and ecological forms, extended ranges and concordance of their borders with the valleys of the large rivers, constraining interpopulation exchange, confirm this point of view. The process of the differentiation of the local forms and fragmentation of their ranges caused by the global factors in such groups seems to be proceeding until now.

ACKNOWLEDGMENTS

The authors are greatly indebted to the stuff and curators of the collections of the institutions, who provided us with material for study: the late Dr. G.S. Medvedev, Dr. B.A. Korotyaev, Dr. B.M. Kataev, Dr. A.V. Frolov, and V.N. Prasolov (the Zoological Institute of the Russian Academy of Sciences, St. Petersburg), Drs N.B. Nikitsky and A.A. Gusakov (Zoological Museum of the Moscow State University), Dr. K.V. Makarov (Moscow Pedagogical State University), Dr. V.Yu. Savitsky (Department of Entomology of Moscow State University), Dr. V.A. Minoransky (South Federal University, Rostov-on-Don), Dr. G.M. Abdurakhmanov (Institute for Applied Ecology of Republic Daghestan, Makhachkala), the late Dr. V.G. Dolin and Dr. A.V. Putchkov (Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev), Dr. A.F. Bartenev (Kharkov State University), Dr. A.N. Drogvalenko (Museum of Nature of the Kharkov State University), the late Dr. A.V. Zakharenko (Kharkov Entomological Society), Drs V.A. Lobkov, Yu.V. Suvorov, and S.L. Duz' (Odessa National University), Dr. M.Yu. Kalashian (Institute of Zoology of the National Academy of Sciences of Armenia, Yerevan), Drs M.A. Musaev and S.V. Aliev (Institute of Zoology of the National Academy of Sciences of Azerbaijan, Baku), the late Dr. M.Ya. Dzhambazishvili (Institute of Zoology of the National Academy of Sciences of Georgia, Tbilisi), Dr. O. Merkl (Hungarian Natural History Museum, Budapest), Dr. L. Zerche (Deutsches Entomologisches Institut, Müncheberg), Dr. M. Baehr (Zoologische Staatssammlung München), Dr. W. Schawaller (Staatliches Museum für Naturkunde, Stuttgart), Dr. Th. Deuve (Muséum National d'Histoire Naturelle, Paris).

The authors also express their sincere gratitude to Dr. V.V. Neimorovets (St. Petersburg) and Dr. Yu.G. Arzanov (Rostov-on-Don) for constructive discussion of the methods of the present study and other helpful comments, Yu.B. Liman for his help in the organization of the field researches, A.K. Makaov (Maikop), D.A. Zamotajlova and A.S. Bondarenko (both Krasnodar) for their help in calculations and technical preparation of the manuscript, and also to all the coleopterists contributing to this work by providing material collected in the region or various valuable information and advice, first of all, Drs I.A. Belousov, A.G. Koval, D.A. Dubovikov, P.V. Kiyashko (St. Petersburg), Drs D.G. Kasatkin, G.B. Bakhtadze, P.P. Ivliev (Rostov-on-Don), Dr. A.I. Miroshnikov, Dr. V.I. Shchurov, A.E. Abramov (Krasnodar), Dr. V.V. Martynov (Donetsk), Drs E.V. Komarov, O.G. Brekhov (Volgograd), and Dr. E.V. Iljina (Makhachkala).

This study was partially supported by grants from the Russian Foundation for Basic Research and ad-

ministration of Krasnodar Territory (project no. 09-04-96554) and the target program "Development of scientific potential of the higher school (2009–2010)" conducted by Federal Agency of Education of the Russian Federation (project no. 2.1.1/2996). Some investigations were carried out within the framework of the program of basic research, the Branch of Geology, Geophysics, Geochemistry and Mining Sciences of the Russian Academy of Sciences "The State of Environment and the Forecast of Its Dynamics under Influence of the Rapid Global and Regional Connatural, Social and Economic Changes," subprogram "Modern Transformations of Habitat and a Biota of Arid and Semiarid Zones of South Russia under Conditions of Climate Fluctuation" (state registration no. 01200850107), and the program of the Presidium of the Russian Academy of Sciences "The Fundamental Problems of Regional Development of the Russian Federation: Interdisciplinary Synthesis," project "Evaluation of the State of Pascual Ecosystems."

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