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The Click-Beetles of North Ossetia, Caucasus: Fauna, Habitat Distribution, and Biogeography (Coleoptera: Elateridae)

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With 1 figure and 4 tables

Summary

The click-beetle fauna of North Ossetia, North Caucasus, is revised based both on extensive materials and a critical review of literature data. The fauna of North Ossetia comprises 82 species, 74 being present in our materials and 8 included from reliable literature sources. The occurrences of additional 4 species are doubtful and require confirmation. Further 8 species have erroneously been recorded for the fauna of North Ossetia. 16 species are new to the fauna of North Ossetia. The proportion of both European and Euro-Siberian species increases with altitude, whereas the Mediterranean (in wider sense) forms predominate in the northern lowland of the country. The species endemic/subendemic to the Caucasus constitute the bulk of the fauna of the middle-mountain forest belt. The endemics occupy almost all major habitat types of North Ossetia except for the alpine meadows and shingle beds along rivers; their proportion, however, is remarkably high in broadleaved mesophilous forests.

Zusammenfassung

Die Schnellkäferfauna Nord-Ossetiens (Nordkaukasus) wird auf Grund umfangreichen Materials und kritischer Literatursichtung revidiert. Insgesamt sind 82 Schnellkäferarten in Nord-Ossetien bekannt, davon liegen 74 Arten in unserem Material vor und 8 weitere basieren auf zuverlässigen Quellenangaben. Das Vorkommen von 4 weiteren Arten ist zweifelhaft und 8 Arten sind bislang irrtümlich gemeldet. Neu für die Fauna Nordossetiens sind 16 Arten. Der Anteil der europäischen und eurosibirischen Arten nimmt mit zunehmender Meereshöhe zu, während die mediterranen Arten in den nördlichen Ebenen des Landes überwiegen. Die für den Kaukasus endemischen/subendemischen Arten stellen den überwiegenden Anteil im mittleren Waldgürtel. Die endemischen Arten leben in fast allen Habitattypen mit Ausnahme alpiner Matten und der Kies- und Sandufer der Flüsse; ihr Anteil ist aber merklich höher in den mesophilen Laubwäldern des mittleren Gebirgsgürtels.

Contents

1. Introduction	3
2. Material	4
3. Habitat distribution and biogeography	9

3.1. Taxonomical composition	9
3.2. Zoogeographical structure	9
3.3. Range disjunctions and vicariance	10
3.4. Ecological structure of the click-beetle fauna	11
3.5. Distribution over major habitat types	12
4. Faunogenesis	14
5. Acknowledgments	17
6. References	17

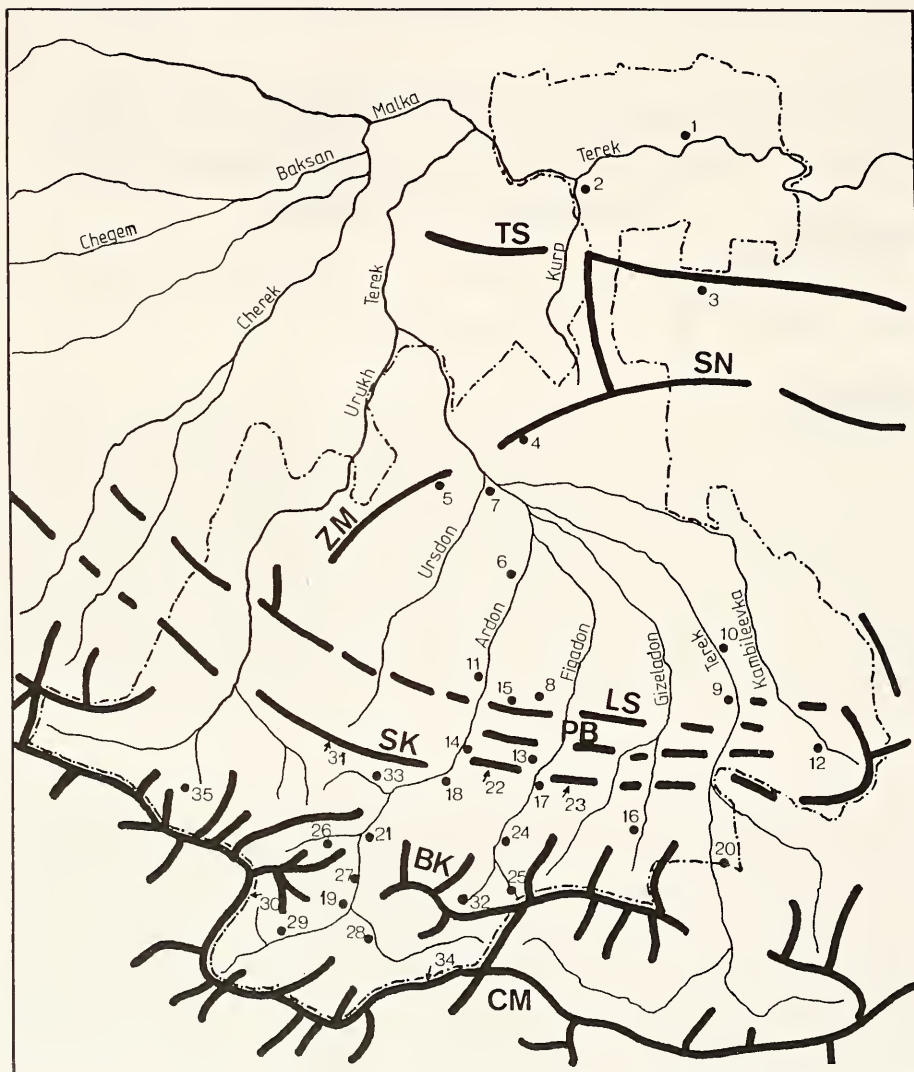


Fig. 1. Schematic map of North Ossetia and distribution of the study sites. For numbers identifications of the localities see Table 1. Mountain Ranges: *TS* = Terskiy; *ZM* = Zmeiskiye Gory („Snake Mountains“); *SN* = Sunzhenskiy; *LS* = Lesistyi („Woody“); *PB* = Pastbishnyi („Pasturable“); *SK* = Skalistyi („Rocky“); *BK* = Bokovoi („Lateral“); *CM* = Caucasus Major.

1. Introduction

North Ossetia is situated on the northern macroslope of the central Caucasus. This small country about 8,000 square km in area is characterized by exceedingly diverse natural conditions. It comprises all altitudinal belts of the central Caucasus ranging from the steppe zone around Mozdok (90–120 m a.s.l.) to the glaciers of the highest mountains. Five main mountain ranges form the relief of North Ossetia – Lesistyi („Wooded“), Pastbishnyi („Pasturable“), Skalistyi („Rocky“), Bokovoi („Lateral“), and Glavny („Major“) (Fig. 1). The highest mountain top is Uilpata (4,638 m) but there are many other peaks over 3,000 m supporting typically alpine habitats.

The territory of North Ossetia is divided into six geographical regions (NARDON-DETSKAYA, 1980; Tab. 1.). The northern lowland part along Terek River forms the Tersko-Kumskaya Plain recently converted from steppe biotops to agricultural land.

Table 1. Characteristics of localities. – *Abbreviations* (geographical regions): *TER* = Tersko-Kumskaya Plain, – *SUN* = Tersko-Sunzhenskiy region, – *NAK* = Naklonno-Osetinskaya Plain, – *MID* = Middle-mountain cuestas region, – *ARI* = Mountain arid basins, – *HIG* = High-mountain crystalline shifts.

No on map	Locality	Elevation (m.a.s.l.)	Region
1	Environs of Mozdok – Oktyabrskii, Komarovo, Kievskaya	90–140	TER
2	Sukhotskoye near confluence of rivers Kurp and Terek	100–135	TER
3	Voznesenskoye on Terskiy Mt. Range	350–500	SUN
4	Zek Mt., Sunzhenskiy Mt. Range, between Elkhotovo & Zamankul	450–780	SUN
5	Zmeiskiye Mts near villages Krasnogor and Zmeiskaya	450–680	SUN
6	Environs of Ardon near village Ramanovo	500–550	NAK
7	Bekan, mouth of Urs-don River	370–450	NAK
8	Khataldon village, middle flow of Khataldon River	600	NAK
9	Environs of Vladikavkaz (= Ordzhonikidze)	650–670	NAK
10	Mikhailovskoye 10 km N of Vladikavkaz	580–600	NAK
11	Alaghir	640–780	NAK
12	Tarskoye 10 km WSW Vladikavkaz	800–1000	MID
13	Kats in Kartsinskoye Valley, Pastbishchnyi Mt. Range	780–1000	MID
14	Shubi south of Tamisk	730–1100	MID
15	Suadagh, middle flow of Suadagh River	700–1000	MID
17	Environs of Fiagdon	900–1500	ARI
18	Environs of Zintzar and Mizur	900–1200	ARI
19	Environs of Zaramagh	1750–2850	ARI
20	Between Lars & Aramkhi, middle flow of Terek River	850–960	ARI
21	Buron, mouth of Tsei-don River	1300–1400	HIG
22	Kariu-khokh Mt., Skalistyi Mt. Range	2000–3200	MID
23	Tbau-khokh Mt., Skalistyi Mt. Range	2000–2600	MID
24	Kharisdzhin, middle stream of Fiagdon River	1500–1600	ARI
25	Dzamarash-kom Valley	2000–2500	HIG
26	Tsei Valley	1450–3200	HIG
27	Uiltsa, Kassarskoye Valley, between Zaramagh and Buron	1570–1700	HIG
28	Nar, Lya-kom Valley, above village Zaramagh	2000–2800	HIG
29	Upper reaches of Mamison-don River near Lisri and Kalaki	2200–3000	HIG
30	Mamisonskii Pass (northern slope)	2400–2850	HIG
31	Kion-khokh Mt., Skalistyi Mt. Range	2200–3200	HIG
32	Khilak, upper reaches of Bughilty-kom Valley	2300–3100	HIG
33	Sadon and Verkhni Zgit, Ardon River Basin	1500–2000	ARI
34	Rokskii Pass near village Zaki	2000–2900	HIG
35	Raiskiye Polyany, Karaugom Valley, upper reaches of Uruk	2400–3400	HIG

Two ridges situated immediately south of this plain are included in the Tersko-Sunzhenskii region and are characterized by a forest-steppe type of vegetation. A third region, the Naklonno-Osetinskaya Plain, is situated north of the Lesistyi Range along the middle flow of Terek River and its tributaries, Ursdon, Ardon and Fiagdon, between 400–700 m a.s.l. The mountainous parts of North Ossetia are shared by three regions – the middle-mountainous cuestas, high-mountainous crystalline shifts, and mountainous arid basins.

The natural vegetation of North Ossetia (AMIRKHANOV et alii, 1988; see also Tab. 1) is formed by lowland and mountainous steppes, mountainous xerophytic communities, floodland and foothill broad-leaved forests dominated by oak, middle-mountainous beech forests, mountainous pine and birch forests, subalpine and alpine *Rhododendron* elfin woods, subalpine and alpine meadows, petrophilous and periglacial vegetations. Remarkable is the absence of humid spruce forests characteristic of the northwestern Caucasus.

The beetle fauna of the Caucasus has long been known as the object of intensive investigations (SCHNEIDER & LEDER, 1878; RADDE, 1899). Concerning the click-beetles (Elateridae), comprehensive faunistic reviews exist, however, only for Transcaucasia, i. e. Armenia (MARDZHANIAN, 1987), Azerbaijan (AGAIEV, 1988), and partly Georgia (CHANTLADZE, 1983). The northern macroslope of the Caucasus seems to be less known despite the extensive collecting efforts which have mainly resulted in several scattered records and descriptions of new species.

The click-beetle fauna of the northwestern region of the Caucasus (Kuban) has been reviewed by STEPANOVA (1969) but the number of species (50) mentioned in that paper is certainly far lower than the real diversity to be expected. In a paper devoted to the click-beetle fauna of Kabarda-Balkaria, another central Caucasian republic, NEFEDOV (1961) recorded 39 species, of which 14 were clearly based on misidentifications.

The fauna of North Ossetia is somewhat better known in comparison with the adjacent northern Caucasian countries due to the work of CHOPIKASHVILI (1973) where 73 species have been recorded. Despite its doubtless importance, that paper, however, has some essential lapses: the geographical region from where her materials originated is not precisely defined, there are no localities for each species and, in addition, some species are recorded from doubtful or erroneous determinations.

Since 1982, one of us (SA) has started a thorough survey of land invertebrates covering almost all the territory of North Ossetia (Fig. 1, Tab. 1). The aim of this paper is to summarize new data on the species composition, habitat preferences and vertical distributions of the click-beetles in North Ossetia sampled during 9 collecting years.

2. Material

The present paper is based mostly on original materials although literature data and museum collections have also been taken into account. The majority of the materials were sampled by the authors and are mainly preserved in our collections, with a representative part shared with the collection of the Staatliches Museum für Naturkunde in Stuttgart. A comprehensive list of species is given in Table 2. The data on each species are ordered in Table 2 in the following way: (1) literature data on the distribution of the species in North Ossetia; (2) localities in North Ossetia where the species has been found according to our materials; (3) summary of the vertical distribution; (4) habitat preferences; (5) major type of distribution pattern and (6) general geographical distribution. The distributional data are taken mostly from GURJEVA (1979, 1989) and DOLIN (1982, 1988) as well as from numerous other literature sources.

Table 2. Distribution over regions, habitat preferences and zoogeographical characteristics of click-beetle species of North Ossetia*). – *Literature sources* = sequential numbers of the publications where a certain species is mentioned from North Ossetia*); – *Localities* = sequential numbers of localities of the materials collected/checked by the authors; – *Vertical distribution* = species altitude range [m] based on the authors' materials alone; – *Habit. pref.* = habitat preference*); – *Distr. patt.* = major type of distribution pattern*); – *Geographical distribution* = detailed zoogeographical distribution*); – *) For explanation of the abbreviations see the legend below the table.

No	Literature sources	Localities (see Fig. 1, Tab. 1)	Vertical distribution	Habit. pref.	Distr. patt.	Geographical distribution
1.	<i>Agrypnus murinus</i> (L.)	3	–	EU	ES	Holarctic
2.	<i>Compsolacon crenicollis</i> (Mén.)	1, 3	350–1400	IZ	PT	EMed-Cauc
3.	<i>Lacon punctatus</i> (Hbst.)	3	–	FO	MD	Submed-Cauc
4.	<i>L. lepidopterus</i> (Panz.)	3	–	FO	EU	Eur-Cauc-W Sib
5.	<i>Drasterius bimaculatus</i> (Rossi)	3	90–450	EU	MD	Submed-Pont-MAsia
6.	<i>D. atricapillus</i> (Germ.)	1, 7	90–450	IZ	TU	EPont-MAsia
7.	<i>Aelosomus rossii</i> (Germ.)	3	90	EU	PT	EMed-Pont-MAsia
8.	<i>Aeloderma crucifer</i> (Rossi)	3	90	IZ	MD	Med-Pont-MAsia
9.	<i>Zorochros meridionalis</i> (Lap.)	3	350–750	IZ	EU	WEur-Cauc-Amin
10.	<i>Z. flavipes</i> (Aubé)	29	2450	IZ	EU	WEur-Cauc
–	<i>Z. dermestoides</i> (Hbst.)	3	–	IZ	EU	WEur
11.	<i>Z. quadriguttatus</i> (Lap.)	7, 26	350–2300	IZ	EU	WEur-Cauc
12.	<i>Z. ibericus</i> (Franz)	7	350–450	IZ	MD	SEur-Cauc
13.	<i>Z. murinus</i> (Rtt.)	7, 11	350–700	IZ	TU	Cauc-MAsia
14.	<i>Quasimus minutissimus</i> (Germ.)	19	2000	FO	EU	WEur-Cauc-Amin
15.	<i>Hypnoidus rivularius</i> (Gyll.)	22, 26, 32	200–3200	ME	ES	Eur-Sib-Cauc
16.	<i>Cidnopus minutus</i> (L.)	1, 4, 7, 8, 14, 17, 18, 19, 26, 27	–	–	–	–
17.	<i>Stenagostus rosti</i> (Schw.)	11, 14	90–2200	FO	EU	Eur-W Sib-Cauc-Amin
–	<i>Hemicrepidius carbonarius</i> (Step.)	3	600–850	FO	CA	Cauc
18.	<i>Atobis niger</i> (L.)	3	–	FO	CA	Cauc
19.	<i>A. kobchidzei</i> Dol. & Tchandt.	–	–	EU	EU	Eur-W Sib-Cauc-Amin
–	<i>A. vittatus</i> (F.)	3	600–850	FO	CA	Cauc
20.	<i>A. iristonius</i> Dol.	2	–	FO	EU	Eur-?Cauc-Amin
		5, 8, 11, 13, 14, 15, 17, 18, 21, 26, 27, 28	450–2800	EU	CA	Cauc

Table 2 (continued)

No	Literature sources	Localities (see Fig. 1, Tab. 1)	Vertical distribution	Habit. pref.	Dist. patt.	Geographical distribution
21.	<i>A. subfuscus</i> (Mull.)	3	19, 22, 26, 27, 28, 34	FO	EU	Eur-W Sib-Cauc-A Min
-	<i>A. uschderensis</i> Rtt.	3	-	?	CA	Cauc
22.	<i>A. circasicus</i> Rtt.	3	-	EU	CA	Cauc
23.	<i>Crepidophorus cavatus</i> (Cand.)	3	1, 3, 4, 5, 7, 11	FO	CA	Cauc-A Min
24.	<i>Aplotarsus angustulus</i> (Kiesw.)	-	23	ME	EU	WEur-Cauc
25.	<i>Hypoganus stephanovi</i> Den.	3	21, 26, 27	FO	CA	Cauc
26.	<i>Prosternon tessellatum</i> (L.)	3	1, 3, 4, 8, 11, 18, 19, 26, 28	FO	ES	Holarctic
27.	<i>Anostirus purpureus</i> (Poda)	3	16, 26	FO	EU	Eur-W Sib-Cauc
28.	<i>A. brevidis</i> Gur.	-	17	?	CA	Cauc
-	<i>Selatosomus aeneus</i> (L.)	3	-	EU	ES	Eur-Sib-A Min
29.	<i>S. caucasicus</i> (Mén.)	7	14, 18, 17, 19, 24, 26, 27, 19, 22, 26, 28, 29, 35	ME	CA	Cauc
30.	<i>S. melancholicus</i> (F.)	3	2400-3100	EU	ES	Eur-Sib-Cauc-M Asia
31.	<i>S. latus</i> (F.)	3	1, 2, 3, 4, 5, 7, 10, 18, 19	ST	SP	South-Palaeartic
32.	<i>S. alekseevi</i> Dol. & Pen.	6, 7	90-1800	ST	CA	Cauc
33.	<i>Denticollis flabellatus</i> (Rtt.)	3	900-2600	FO	CA	Cauc
34.	<i>D. parallelocollis</i> (Aubé)	3	600-900	FO	CA	Cauc-A Min
35.	<i>Megapenthes lugens</i> (Redt.)	3	600-1100	FO	EU	WEur-Cauc-NAfr
36.	<i>Procterus carinifrons</i> Desbr.	3, 5	650	FO	CA	Crim-Cauc
37.	<i>Ampedus melanotoides</i> (Rtt.)	3	500-650	FO	CA	Cauc
38.	<i>A. rufipennis</i> (Steph.)	3	100	FO	EU	WEur-Cauc
39.	<i>A. koenigi</i> Sem.	3	-	FO	CA	Cauc
40.	<i>A. hirticollis</i> (Sem.)	3	90-800	FO	CA	Cauc-A Min
-	<i>A. praestus</i> (F.)	3	400-1100	FO	ES	Eur-MSib-Cauc
41.	<i>A. ganglbaueri</i> (Rtt.)	3	-	FO	CA	Cauc
42.	<i>A. circasicus</i> (Rtt.)	3, 4	90-1000	FO	CA	Cauc
43.	<i>A. coenobita</i> (Costa)	-	90-1500	FO	PT	EMed
44.	<i>A. ochropierus</i> (Germ.)	3, 4	90-1500	FO	MD	SEur-Cauc-A Min
45.	<i>A. auranticulus</i> (Rtt.)	3	650-1000	FO	CA	Cauc
46.	<i>A. sanguinolentus</i> (Schrnk.)	3	90	FO	ES	Eur-Sib-Cauc

Table 2 (continued)

No	Literature sources	Localities (see Fig. 1, Tab. 1)	Vertical distribution	Habit. pref.	Distr. patt.	Geographical distribution
47. <i>A. pomonae</i> (Steph.)	3	1	90	FO	ES	Eur-Sib-Cauc
48. <i>A. pomorum</i> (Hbst.)	3	1, 3, 4, 5, 11	90-750	FO	ES	Eur-Sib-Cauc-Amin
49. <i>A. elongatulus</i> (F.)	3	1, 4	90-700	FO	EU	Eur-Cauc-Amin
50. <i>A. wachangii</i> Dol.	3, 4	11, 13	650-800	FO	CA	Cauc
51. <i>A. erythrogonus</i> (Mull.)	3	12, 13	800-900	FO	EU	Eur-Cauc
52. <i>Elater ferrugineus</i> L.	3	—	—	FO	EU	Eur-Cauc-Amin
53. <i>Melanotus castanipes</i> (Gyll.)	—	5, 11, 14, 26, 27	450-2000	FO	ES	Holarctic
54. <i>M. rufipes</i> (Hbst.)	3	11	650	FO	EU	Eur-Wsib-Cauc-Amin
55. <i>M. brunneipes</i> (Germ.)	3	1, 3, 4, 5, 7, 8, 10, 14, 17, 18, 21	90-1500	EU	EU	Eur-Cauc-Amin
56. <i>M. tenebrosus</i> (Er.)	—	18	1000	FO	EU	WEur-Cauc
57. <i>M. fusciceps</i> (Gyll.)	3	1, 2, 3	90-350	ST	MD	EMed-Pont-Cauc
58. <i>Synaptus filiformis</i> (F.)	3	1, 2, 7, 11, 18	90-1000	EU	SP	Eur-Med-Cauc-SSib
— <i>Adrastus limbatus</i> (F.)	3	—	—	ME	EU	WEur-Amin-?Cauc
59. <i>A. dolini</i> Welschm.	4	11, 13	600-800	ME	CA	Cauc
60. <i>A. longicornis</i> Gur.	—	1, 7, 8, 11, 27	90-1500	ME	CA	Cauc
61. <i>A. circassicus</i> Rtt.	3	11	650	?	CA	Cauc-Amin
62. <i>Idolus adrastoides</i> Rtt.	3	1, 2, 4, 5, 7, 8, 11, 14, 22	90-2600	FO	CA	Cauc-Amin
— <i>Agriotes reitteri</i> Schw.	3	—	—	EU	CA	Cauc
63. <i>A. gurgistanus</i> Fald.	3	4, 10	400-600	ST	PT	EMed-Pont
64. <i>A. starcki</i> Schw.	3	—	—	FO	CA	Cauc
65. <i>A. usulatus</i> (Schall.)	3	4, 10, 14	350-1100	ME	EU	Eur-Med-Cauc
66. <i>A. infuscatus</i> Desbr.	3, 4	1, 3, 4, 5, 7, 11, 13, 14, 15	90-1050	FO	PT	EMed-Cauc
67. <i>A. tauricus</i> Heyd.	3, 4	9, 10, 11	600-700	ME	CA	Crim-Cauc
68. <i>A. obscurus</i> (L.)	3	11, 14, 18, 25	600-2100	ME	ES	Eur-Sib-Cauc
69. <i>A. lineatus</i> (L.)	3	1, 8, 10, 11	100-600	ME	ES	Palaeartic
70. <i>A. incognitus</i> Schw.	3	1, 2, 10	90-700	ME	PT	SEur-Pont-NKazakh
71. <i>A. metalliculosus</i> Cand.	3	1, 2	90-120	ME	TU	MAsia-Mong-Cauc-Amin
72. <i>A. lapicida</i> Fald.	3	1, 2	90-120	ST	CA	Cauc
73. <i>A. sputator</i> (L.)	3	1, 4, 5, 7, 10, 17	90-900	ST	ES	Palaeartic

Table 2 (continued)

No	Literature sources	Localities (see Fig. 1, Tab. 1)	Vertical distribution	Habit. pref.	Distr. patt.	Geographical distribution
74.	<i>A. medvedevi</i> Dol.	1	90	ME	PT	Pann-NPont-Cauc
75.	<i>Cardiophorus discicollis</i> (Hbst.)	3	—	ST	PT	EMed-Pont-NKazakh
76.	<i>C. vestigialis</i> Er.	3	90	ST	MD	Eur-Med-Cauc
—	<i>C. rufipes</i> (Goeze)	3	—	ST	MD	WEur-Med
77.	<i>C. maritimus</i> Dol.	—	90–1100	ST	PT	Pan-NPont-Cauc
78.	<i>C. arnoldii</i> Dol.	1, 5, 10, 18	90–120	ST	PT	NPont-Cauc
79.	<i>C. kryzhanovskiyi</i> Dol. & Tchantl.	1, 2	90	ST	CA	Cauc
—	<i>C. nigropunctatus</i> Cand.	1	—	SD	TU	MAsia-?Cauc
80.	<i>C. cinereus</i> (Hbst.)	1, 3, 7	90–450	FO	EU	Eur-Wsib-Cauc-AMin
—	<i>C. rubripes</i> (Germ.)	3	—	ST	PT	SEur-Pont-NKazakh
81.	<i>C. decorus</i> Fald.	3	90–1100	EU	CA	Cauc-AMin
82.	<i>Paracardiophorus musculus</i> (Er.)	1, 2, 3, 4, 5, 7, 14, 18 1, 7	90–300	IZ	MD	Eur-Med-SSib

Explanations: No: Sequential numbers are given to species recorded on the basis of the authors' materials and/or reliable literature citations. Species without sequential numbers are considered as erroneously recorded in the fauna of North Ossetia. — *Literature sources*: 1. RADDE (1899); 2. DOLIN (1971); 3. CHOPIKASHVILI (1973); 4. GURJEVA (1979); 5. DOLIN (1988); 6. DOLIN & PENEV (1988); 7. GURJEVA (1989). — *Habitat preference*: EU = Eurytopic, FO = Forest, ME = Meadow, ST = Steppe, IZ = Intrazonal, SD = Semidesert. — *Distribution pattern*: ES = Euro-Siberian, EU = European, MD = Mediterranean, PT = Pontic, CA = Endemic and subendemic to the Caucasus, TU = Turanian. — *Geographical distribution*: C = central, E = eastern, W = western, N = northern, S = southern; AMin = Asia Minor, Cauc = Caucasus, Crim = Crimea, Eur = Europe, Kazakh = Kazakhstan, Med = Mediterranean, MAsia = Middle Asia, Pont = Pontic, Sib = Siberia, Submed = Submediterranean.

3. Habitat distribution and biogeography

3.1. Taxonomical composition

The bulk of both fauna and endemic species belongs to the subfamilies Elaterinae and Athoinae constituting 48.8 and 24.4% of the species pool, respectively. Both subfamilies are known as younger phyletic branches within the Elateridae recorded since the Palaeogene (Baltic amber) (DOLIN, 1978). In contrast, the other three subfamilies, Agrypninae, Negastrinae and Cardiophorinae, are known as phylogenetically older, separated already since the late Jurassic.

Also, noticeable patterns appear when one looks at the distribution of the species diversity and the number of endemics over tribes. The most diverse tribes in North Ossetia appear to be the Ampedini (18.3% of the whole fauna and 25.0% of the endemics), Pomachiliini (15.8 and 14.3%, respectively) and Athoini (13.4 and 25.0%, respectively). All tribes which comprise the majority of the endemic species are characterized as predominantly Holarctic. For example, according to GURJEVA (1979), the tribe Ampedini consists of 305 described species and 8 genera; 218 species and 4 genera are restricted to the Holarctic region. The tribes Athoini, Ctenicerini and Pomachiliini can also be considered as chiefly Holarctic (DOLIN, 1982; GURJEVA, 1979, 1989). Furthermore, the species diversity of and adaptive radiation within the tribes demonstrating the highest percentages of endemic species (Ampedini and Athoini) are confined to the belt of temperate arboreal vegetation of the Holarctic.

3.2. Zoogeographical structure

The zoogeographical characteristics of the species given in Tab. 2 reflect the distribution of each species in due detail. For the purposes of a zoogeographical analysis, it seems necessary to join the numerous particular distributions into major chorological complexes on the basis of the majority of each species' range. Seven patterns of distribution have thus become delimited (Tab. 2). A group of species endemic and subendemic to the Caucasus (35.4%) prevail in the whole faunal composition followed by species with European (24.4%), Euro-Siberian (13.4%) and Ponto-Mediterranean (12.2%) distribution patterns. Further, the seven complexes can be split into three major groups with respect to the division of the Palearctic region into subregions: (1) species of the Euro-Siberian subregion, with the majority of the species ranges lying in Europe and/or Siberia, (2) species of the Ancient Mediterranean subregion, with the majority of the species ranges lying either within the Mediterranean and/or Middle Asia, and/or territories around the Black and Caspian seas, and (3) species endemic or subendemic to the Caucasus. The concept of the Ancient Mediterranean has been primarily developed in Russia (cf. POPOV, 1927; KRYZHANOVSKIY, 1965; LOPATIN, 1980) and assumes that the faunas of the Mediterranean, Middle Asia and the southernmost parts of European Russia can be joined into one major complex on the basis of common origin from the territories surrounding the ancient Tethys Sea. This concept seems useful since very often it is quite difficult to separate the great variety of species ranges occupying different parts of that huge region extending from the western Mediterranean coast to Middle Asia. The crucial point of this concept is, how to classify the Eurasian steppe species, either as Euro-Siberian or Mediterranean. According to their taxonomic relationships, habitat pre-

Table 3. Zoogeographical structure (%) of the click-beetle fauna of North Ossetia and its subregions. (For *abbreviations* of subregions see Tab. 1.)

	Total	TER	SUN	NAK	MID	ARI	HIG
Euro-Siberian	37.8	27.0	42.9	35.0	45.5	50.0	60.0
Ancient-Mediterranean	26.8	45.9	28.6	30.0	9.1	11.1	13.3
Caucasian	35.4	27.9	28.6	34.1	45.4	27.8	26.6

ferences and range structure, most of the Eurasian steppe click-beetle species display clear connections with the Mediterranean fauna. Yet, another reason to join the Eurasian steppe species with the Mediterranean ones is that there are a large number of species distributed both in southern Russian steppes and in the Mediterranean region.

The click-beetle fauna of North Ossetia consists mostly of Euro-Siberian and Caucasian elements (37.8 and 35.4% respectively) followed by species with an Ancient Mediterranean (in wider sense) distribution pattern (26.8%) (Tab. 3). The proportions of these three major zoogeographical groups in the regions of North Ossetia demonstrate different trends (Tab. 3). The relative importance of the Euro-Siberian elements is higher in the mountains of North Ossetia than in its lowland part, reaching to 60% of the fauna in the highest regions. Mediterranean elements prevail in the northernmost lowland steppe part of the country but their proportion in the mountains drops to 9–13%. The species endemic/subendemic to the Caucasus display the highest relative importance in the middle part of the altitudinal gradient, namely in the belt of middle-mountainous broadleaved forests and in habitats associated with them (meadows, forest clearings).

3.3. Range disjunctions and vicariance

Three main groups of disjunct ranges can be distinguished when one analyses the faunal connections of the North Caucasus. The first group is formed by northerly orientated disjunctions of European and Euro-Siberian species widely distributed on the Russian Plain but absent from its southern steppe regions. These are:

<i>Agrypnus murinus</i> ,	<i>Selatosomus melancholicus</i> ,
<i>Lacon lepidopterus</i> ,	<i>Anostirus purpureus</i> ,
<i>Hypnoidus rivularius</i> ,	<i>Ampedus erythrogonus</i> ,
<i>Cidnopus minutus</i> ,	<i>Elatер ferrugineus</i> ,
<i>Athous subfuscus</i> ,	<i>Melanotus castanipes</i> .
<i>Prosternon tessellatum</i> ,	

A related group encompasses the European and Euro-Siberian species which have vicariant forms in the Caucasus. For example *Selatosomus caucasicus*, widespread in North Ossetia, can be considered as a young, hardly discernable derivative of the Euro-Siberian species *Selatosomus aeneus*. Other examples of such Euro-Caucasian vicariant species pairs are *Athous kobachidzei* – *A. vittatus* and *Ampedus circassicus* – *Ampedus praeustus* (see also AGAEV, 1990). Range disjunctions of this pattern seem to be accounted for by ecological reasons since most of the above species are either forest- or meadow-dwellers for which the southern lowland steppes of the Russian Plain form a hardly surmountable barrier. Species of this group can be considered as northern, either taiga or nemoral, elements in the fauna of the Caucasus.

Secondly, there are species with northwesterly orientated disjunct ranges, being present in Central and South Europe but absent from the central regions of European Russia west of the Dnieper:

Quasimus minutissimus,
Zorochros flavipes,
Z. quadriguttatus,
Aplotarsus angustulus (present also on the Crimea),
Megapenthes lugens,
Melanotus tenebrosus (a sister species is present on the Crimea).

This group is composed of species with varying habitat requirements ranging from inhabitants of shingle beds along rivers (*Zorochros* spp.) to meadow (*A. angustulus*) and typical forest species (*Megapenthes lugens*). An example of vicariant species group forming a Caucasian – West European – Crimean disjunction is the *Haplathous* Rtt. group of the genus *Athous* Esch. The widespread central- and south-east European *Athous austriacus* (Desbr.) is replaced, in the Caucasus, by *Athous circumductus* and, in North Ossetia, by the related species *A. iristonius*; on the Crimea, the *Haplathous* group is represented by *A. tauricus* and *A. tauricola* (DOLIN, 1982).

Finally, there are also species which are absent both from the Russian Plain and central Europe but occurring in South Europe, the Caucasus and, in most cases, in Asia Minor as well. Such species are:

Compsolacon crenicollis (present on the Crimea),
Lacon punctatus (present on the Crimea),
Zorochros ibericus (present on the Crimea),
Ampedus coenobita,
A. ochropterus (present on the Crimea),
Agriotes infuscatus.

All these species are confined to habitats which are largely isolated in South Europe, namely either shingle beds along rivers (*Compsolacon crenicollis*, *Zorochros ibericus*) or submediterranean broadleaved forests (all other species).

3.4. Ecological structure of the click-beetle fauna

The ecological structure of the click-beetle fauna of North Ossetia is shown on Tab. 4. In the whole species pool and within the group of endemics, forest-dwellers prevail, constituting 46.3% and 55.2%, respectively. The proportion of species associated with open habitats (meadows, steppes) is nearly the same in both groups compared. It can be concluded that the ecological structure within the group of endemic/subdendemic species reflects that of the whole species pool. In other words, endemism in click-beetles does not seem to be closely associated with a single habitat type, while endemic species are partitioned between habitats nearly in the same proportions as the whole fauna. An exception to this is a set of intrazonal species which are underrepresented within the endemic complex. Apparently, a low-level endemism noted for the habitat type of shingle beds along rivers can be accounted for by a relatively „old“ phylogenetic age of both systematic groups prevailing in such habitats, namely Agrypninae and Negastrinae known to be composed of well-established and discernable species in Europe (DOLIN, 1978, 1982).

Table 4. Ecological structure of the click-beetle fauna of North Ossetia.

Ecological groupings	Whole fauna		Endemic complex	
	No of species	%	No of species	%
Eurytopic	10	12.2	3	10.3
Forest	38	46.3	16	55.2
Meadow	12	14.6	4	13.8
Steppe	11	13.4	3	10.3
Intrazonal	9	11.0	1	3.4
Unclear	2	2.4	2	6.8

3.5. Distribution over major habitat types

Semiarid habitats of North Ossetia can be divided into two major groups, lowland steppes and mountainous xerophytic formations. Lowland steppes are inhabited by their own characteristic click-beetle species. For example, the following species are most abundant in steppe habitats around Mozdok:

Aelosomus rossii,
Drasterius bimaculatus,
Selatosomus latus,
*Agriotes lapicida**,
Melanotus fusciceps,
*Cardiophorus decorus**.

More rare, but also typical for such habitats, are *Agriotes sputator*, *A. gurgistanus*, *Cardiophorus maritimus*, *C. vestigialis*, *C. arnoldii*, *C. kryzhanovskii**. A similar but somewhat impoverished species composition can be observed in the mountainous xerophytic formation:

Selatosomus latus,
*S. alekseevi**,
Agriotes sputator,
Cardiophorus maritimus,
*C. decorus**.

In general, the click-beetle fauna of meadows exhibits some elements shared with steppes, e. g. *Agriotes sputator* and *Selatosomus latus*. However, meadows enjoy rich and diverse assemblages, and there are species confined mostly to this type of habitat:

*Athous iristonius**,
*Selatosomus caucasicus**,
*Adrastus longicornis**,
*A. dolini**,
Synaptus filiformis,
Agriotes ustulatus,
A. lineatus,
A. obscurus,
Melanotus brunnipes.

Subalpine and alpine habitats above the upper timber-line are largely represented by meadows of various types supporting petrophilous and subnival vegetations. Four elaterid species are characteristic of subalpine meadows:

Hypnoidus rivularius,
*Athous iristonius**,
*Selatosomus caucasicus**,
S. melancholicus.

Yet subalpine click-beetle assemblages are enriched by species recruited from the high-mountain forest belt, such as *Athous subfuscus*, *Prosternon tessellatum*, *Idolus*

* Species endemic/subendemic to the Caucasus.

*adrastoides**. Only two species have been captured in truly alpine habitats above 3,000 m in elevation, *H. rivularius* and *S. melancholicus*.

Floodland and foothill broadleaved forests in the northern part of the country are inhabited by:

<i>Cidnopus minutus</i> ,	<i>Agriotes infuscatus</i> ,
<i>Prosternon tessellatum</i> ,	<i>Melanotus brunnipes</i> ,
<i>Synaptus filiformis</i> ,	<i>Cardiophorus cinereus</i> .
<i>Idolus adrastoides</i> *	

Among dendrophilous xylobionts in this habitat type, *Crepidophorus cavatus**, *Ampedus melanotoides**, *A. circassicus**, *A. coenobita**, *A. ochropterus**, *A. sanguinolentus*, *A. pomonae*, *A. pomorum* are noteworthy. Mesophilous middle-mountainous broadleaved forests dominated either by beech or durmast oak form the main vegetation type of the middle-mountainous belt of North Ossetia. Larvae of the following species predominate in the litter and soil under the canopy of beech forests (ordered according to the relative abundance of species in the samples, coll. O. GVOZDEVA):

<i>Athous subfuscus</i> ,	<i>Athous iristonius</i> *
<i>Agriotes infuscatus</i> ,	<i>Idolus adrastoides</i> *

In addition, *Athous kobachidzei**, *Hypoganus stepanovi**, *Melanotus* cf. *rufipes* and *M. brunnipes* rarely occur there as well. *Prosternon tessellatum* is quite common in this belt but it prefers oak forests over beech ones. Dendrophilous click-beetle assemblages in broadleaved forests are represented by *Crepidophorus cavatus**, *Stenagostus rosti**, *Megapenthes lugens*, *Procaerus carinifrons*, *Ampedus hirticollis**, *A. coenobita**, *A. ochropterus**, *A. pomorum*, *A. elongatulus*, *A. wachtingi**, *A. erythrogonus* and some others. In comparison with deciduous forests, the fauna of coniferous stands is much poorer. The dominant species is *Athous subfuscus*. Also *Selatosomus caucasicus** is common in pitfall traps in light pine and pine-birch forests. In rotten pine trunks, *Ampedus hirticollis**, *A. auranticulus** and *Melanotus castanipes* occur.

One of the most peculiar click-beetle assemblages is formed by species inhabiting intrazonal habitats along rivers and water bodies. There is some variation in species composition and diversity of the riparian habitats among mountainous belts. The riparian fauna of shingle beds along river midflows is the most diverse. Near Bekan (Ursdon River) and Alaghir (Ardon River), several species have been captured, most frequent of them being:

<i>Compsolacon crenicollis</i> ,	<i>Z. quadriguttatus</i> (rare),
<i>Zorochros meridionalis</i> ,	<i>Z. murinus</i> ,
<i>Z. ibericus</i> ,	<i>Drasterius bimaculatus</i> .

Intrazonal habitats both above and below the middle-mountainous belt are characterized by less diverse assemblages and a somewhat different species composition. In the high-mountainous belt, only one species has been found, *Zorochros quadriguttatus*. The very rare *Z. flavipes* seems also to be restricted to the upper flows of streams. Riverside habitats of the northern steppe part along the Terek River are populated by such widespread thermohygrophiles as *Aelosomus rossii*, *Drasterius bimaculatus*, *D. atricapillus*, as well as the rare *Aeloderma crucifer*.

Thus, as can be seen from this brief review, the Caucasian endemics are present in most major habitat types except for both shingle beds along rivers and alpine habitats. In all other habitats, endemics constitute about 30–40% of dominant species.

We interpret this phenomenon as evidence that, due to the long-term geographical isolation of the Caucasian fauna, active speciation processes have taken place in most habitat types. The highest proportion of endemics is observed in the belt of middle-mountainous broadleaved forests. In general, the Caucasian fauna can be considered to be well-balanced so far as the distribution of endemic forms over the habitats is concerned.

4. Faunogenesis

Without any doubt, the Caucasus can be regarded as one of the most complicated biogeographical regions lying at the border between Europe, Mediterranean, and Middle Asia. Being extremely diverse in ecological conditions, the Caucasus harbours species with rather different habitat requirements ranging from arid deserts to humid and mesophilous forests and alpine meadows. Each of these ecological groupings, however, is also quite distinct in age, place of origin, and pathways of penetration into the Caucasus. There are two major problems arising both from the complicated geological history and the diverse ecological conditions of the Caucasus. The first one concerns the age of different chronological „layers“ in the Caucasian biota and hence, the age of relict and endemic species. The second problem reflects various opinions existing on the routes and periods of colonization of the Caucasus by different floristic and faunistic elements.

The above distribution patterns of North Ossetian click-beetles reflect the complicated history and composition of the Caucasian fauna. Our finds have much in common with some well known biogeographical phenomena described for the Caucasian biota (cf. GROSSGEIM, 1936; MALEEV, 1940; KLEOPOV, 1940). For example, each type of range disjunctions noted above has its analog in other taxonomic groups, especially in such well-studied taxa as trees and shrubs. Several plant species are distributed around the Black Sea (Caucasus, Asia Minor, Balkans and, particularly, Crimea), being absent both from the Russian Plain and central Europe. Among the most popular examples are the eastern beech (*Fagus orientalis*), *Daphne ponticum*, *Rhododendron ponticum* (MALEEV, 1940; WULF, 1944; GROSSET, 1967). Other species have similar distribution but penetrate widely also central Europe and the western regions of the Russian Plain, e. g. *Quercus petraea*, *Acer pseudoplatanus*, *Hedera helix*, *Ilex aquifolium* and many others. Perhaps the best example of a disjunction pattern like Central Europe + Russian Plain – Caucasus is represented by the range of the English oak, *Quercus robur*. A boreo-montane distribution pattern is displayed by *Betula verrucosa*, *B. pubescens*, *Veratrum lobelianum*, *Lilium martagon* (KLEOPOV, 1940). Similar distributions demonstrated by species from various taxonomic groups require common explanations for the patterns observed. Such an explanation cannot be done without consideration of data, both distributional and paleontological/palynological, accumulated by modern phytogeography.

To find a suitable explanation for the recent composition of the North Caucasian click-beetle fauna, one ought to take into account that:

(1.) There are species which must have invaded the Caucasus from the north via Ciscaucasia. Such species are absent from Asia Minor but present both in the Carpathians and the Balkans. Some of them either inhabit the Crimea (*Aplotarsus incanus*) or have vicariant forms there (i. e. *Melanotus tenebrosus* – *M. tauricola* Dolin). It is remarkable that most of these species are either confined to forest, chiefly broadleaved, habitats (*Lacon lepidopterus*, *Anostirus purpureus*, *Ampedus rufipennis*,

A. sanguinolentus, *A. pomonae*, *A. erythrogonus*) or to subalpine meadows (*Hypnoidus rivularius*, *Selatosomus melancholicus*, *Aplotarsus incanus*, *Agriotes obscurus*). There is no logical evidence to suppose a period of invasion for most of such species earlier than the last, Mikulino Interglacial (= Riss/Würm), ca. 100,000 years ago, although the connection between the Caucasus and the South-Russian Platform has existed since the Cimmerian age of the Pliocene. Migrants from the north could have invaded the Caucasus earlier than the Mikulino Interglacial but this hypothesis can be neither proved nor disproved on the basis of recent species distributions alone.

During the phase of a climatic optimum of the Mikulino Interglacial, the recent steppe zone in the southern regions of European Russia was covered by meadow-steppes combined with European hornbeam-oak and oak forests in the west and east, respectively (GRICHUK, 1989). Later, in the Würm period, the level of the Black Sea was obviously about 40–60 m lower than at present, while the Azov Sea did not exist at all. The outline of the rivers flowing from the Balkans, Caucasus, Crimea, and Russian Plain must have been quite different from the recent one. That must have ensured repeated interchanges of species with different habitat requirements between the Caucasus, Crimea, Russian Plain, and Balkans via Ciscaucasia for a long time, at least from the Mikulino Interglacial up to the middle Holocene (GROSSET, 1967; GOLOVATCH, 1984).

It must be emphasized, however, that such faunistic exchanges between the above territories must have not been restricted to the phases of climatic optima alone. On the contrary, during the maximal phase of the climatic optimum of the Mikulino Interglacial, Ciscaucasia is known to have been isolated from the adjacent South-Russian Platform by the so-called Upper-Khazar Basin, a strait that connected the present-day Caspian and Azov seas (GRICHUK, 1989). A reinforcing evidence for long-term interchanges seems to be the absence of click-beetle species occurring only on the opposite sides of the Black Sea, i. e. in the Caucasus and in the Balkans alone. This suggests that the opportunities for faunistic exchanges between both regions concerned have occurred more or less continuously at least since the middle Pleistocene. Biotic exchanges must have taken place mostly along river beds as well as through insular broadleaved forests that existed in phases of climatic optima within the present-day steppe zone and served as „stepping stones“ (GROSSET, 1967; GRICHUK, 1989). The occurrence of several click-beetle species (e. g. *Ampedus sanguinolentus*, *A. pomonae*, *A. coenobita*, *A. ochropterus*, *Agriotes infuscatus*) in floodland forests along the Terek River lying in the northern, lowland part of North Ossetia already suggests this most probable route of migration.

(2.) There are species quite similar in distribution to the previous ones but occurring in Asia Minor as well. This provides another logical explanation for their presence in the Caucasus, namely that they could have dispersed from the Balkans via Asia Minor. An additional evidence for such a pathway of dispersal is represented by species ranging from the Caucasus throughout Asia Minor up to the Balkans but absent both from the Crimea and the Russian Plain (i. e. *Agriotes turcicus*, *Agriotes infuscatus*). Yet there are also species present in Central Europe, the Balkans, Asia Minor, and Transcaucasia but missing both in Ciscaucasia and on the northern macroslope of the Caucasus Major (i. e. *Ampedus elegantulus*).

The „southern“ route of colonization of the Caucasus is a problem vigorously disputed by biogeographers. The question is, how important have been both pathways, the „southern“ (via Asia Minor) and the „northern“ (via Ciscaucasia), for the

formation of the modern Caucasian biota. The first point of view underestimates the chances for colonization from the north first due to water basins known to have isolated the Caucasus from the adjacent Russian Plain until the Sarmatian age of the Pliocene, and later by xerophytic steppes developed in their stead (cf. KULCZYNSKI, 1924). The second viewpoint implies a superior role of the „northern“ migration pathways which could have been realized since the middle Pleistocene (GROSSET, 1967) or even since the Neogene (GROSSGEIM, 1936; KLEOPOV, 1940, 1990). The composition of the North Ossetian click-beetle fauna clearly demonstrates the importance of the „northern“ pathway, for click-beetle groupings of different distribution patterns illustrate all hypothetical „stages“ of faunistic interchanges with the neighbouring areas.

(3.) The influence of the Caucasian fauna on the adjacent regions of the Russian Plain seems to be not so significant as the opposite penetrations of European/Euro-Siberian elements from the north (LAVRENKO, 1938; KLEOPOV, 1940; GOLOVATCH, 1984). Within several taxonomic groups, there are examples of purely Caucasian elements present in the biota of Middle Russia but such cases are exceptional, e. g. the herbs *Cerastium nemorale*, *Lysimachia verticillata*, *Veronica umbrosa* and some others (cf. LAVRENKO, 1938), the tree *Ulmus elliptica* (GROSSET, 1967), the earthworm *Dendrobaena schmidtii tellermanica* (PEREL, 1979), the centipede *Lithobius cronebergii* (ZALESSKAJA & GOLOVATCH, in litt.). Among the Elateridae, there is only one form of an obscure taxonomic status, *Cardiophorus (Dicronychus)* sp., closely related to the Caucasian *C. decorus*, that occurs in the steppes between the Dnieper and Volga. This can be expressed by the motto, often quoted in the Russian biogeographical literature (cf. GOLOVATCH, 1984), that the Caucasus has mostly gained but shared to a far lesser extent.

According to the opposite point of view, however, the Caucasian and Crimean refugia have served as source areas for recolonizations of the Russian Plain by mesophilous forest species after the last glaciation (GROSSET, 1967). This opinion cannot be easily proved or disproved on the basis of modern species distributions alone. Moreover, even if repopulations of the Russian Plain from the Caucasus did take place, the problem remains because they could have mostly occurred by the very same European/Euro-Siberian species and only rarely by Caucasian elements.

However, the Caucasus has served as a powerful migration route for reciprocal invasions of Mediterranean xerophilous species into the South-Russian steppes, on the one hand, and of Eurasian steppe species into the Mediterranean, on the other. Interchanging faunistic elements between the Mediterranean and Eurasian steppes can be illustrated by several click-beetle species occurring in xerophytic „Mediterranean-type“ habitats in the western parts of their ranges as well as in zonal steppe communities in more eastern regions (i. e. *Agriotes gurgistanus*, *Melanotus fusciceps*, *Cardiophorus maritimus*). Another group of species has a similar distribution pattern but it is confined to intrazonal, usually riverside, habitats (*Aelosomus rossii*, *Aeoloderma crucifer*, *Drasterius bimaculatus*, *Agriotes ponticus*). A variety of species distributions of the above pattern within several if not almost all taxonomic groups has formed a wide transitional area ranging from Mongolia to the Pyrenees, thus representing one of the basics of the concept of the Ancient Mediterranean (see above).

(4.) According to an old concept established in Russian phytogeography, the floras can be classified into three major groups: „relict“, „orthoselective“, and „migratory“ (KRASNOV, 1888: cited after LAVRENKO, 1938). „Relict“ floras have persisted

in situ since the Tertiary period, e. g. the floras of the Colchis, western Caucasus, and Hyrcania, eastern Caucasus. The floras developed in a certain region during a long period under one-way orientated changes in the environment, usually climate, can be termed as „orthoselective“, e. g. the floras of Middle Asia. Most of the floras in the temperate belt can be treated as „migratory“, that is composed of various floristic elements stemming from different regions.

KRASNOV's concept seems to be useful for zoogeography so far as one attempts to evaluate the degree of originality of a certain fauna. The click-beetle fauna of the northern macroslope of the Central Caucasus can be regarded as intermediate between „orthoselective“ and „migratory“. On the one hand, the high-level endemism in almost all habitat types and altitudinal belts suggests active autochthonous speciation. On the other, the presence of elements from neighbouring faunistic centers, namely the northern temperate, Mediterranean and even Middle Asian, implies a strong influence of biotic exchanges due mostly to the Pleistocene climatic perturbations.

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