The Biogeography of Ground Beetles of Mountains and Islands

GENERAL EDITORS

Dr. G.R. Noonan
Dr. G.E. Ball
Dr. N.E. Stork

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The High Altitude Fauna of South Siberian Mountains and its Origin (Coleoptera: Carabidae)

VICTOR G. SHILENKOV

The montane insects in the USSR have been studied repeatedly since the classical work of A.P. Semenov-Tian-Shanskij (1937), who treated theoretically the evolution of the alpine biota. The attention of many prominent zoogeographers to the mountain regions is not accidental. Speciation processes are most intensive there, and the mountain fauna contains elements of different ages, from ancient relicts to neoendemics. This provides a biogeographer with research material for faunal reconstructions.

The montane fauna of the Caucasus, Carpathians, Central Asia and partly of the Far East of the USSR have been the most investigated. Much less is known about the insects of South Siberian mountains. For fifteen years I have been studying Carabidae in extensive areas, which include the Altai-Sajan mountain system, the mountain ridges around Lake Baikal, and Transbaikal. This paper treats high altitude carabids of the South Siberian Mountains. Fig. 3.1 illustrates the mountain systems of this region. In different parts of mountain systems high altitude plant formations occur at various elevations (from 1300 to 2200 m, or higher), and include assorted types of subalpine and alpine meadows, alpine tundra, stone and mossy-lichen heaths, and periglacial zones. Maximal elevations occur in Central Altai, which has extensive modern glaciation (such as in Fig. 3.2) and the highest Siberian mountain, Belukha (4506 m).

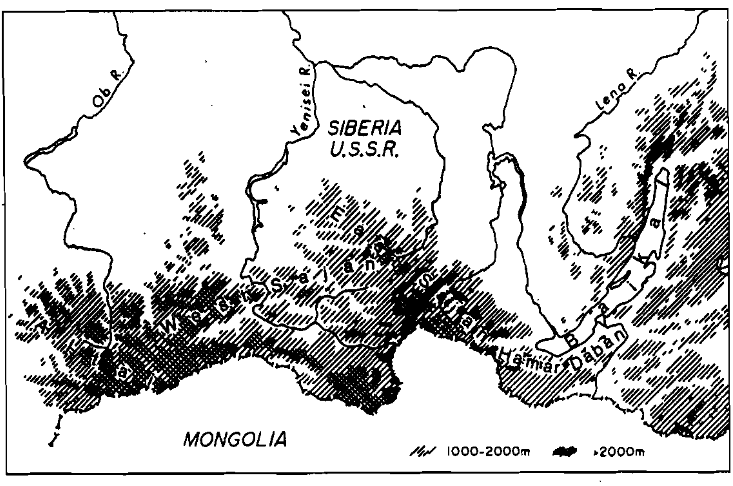

Figure 3.1: Hypsometric map of South Siberia showing Lake Baikal, major river systems, and mountain ranges

The amount of research on various parts of South Siberian mountains is generally inadequate, as indicated by discoveries of many new species of carabids in the past years. However, data are sufficient for drawing some interesting conclusions about the origin of high altitude carabids of this territory. Because of the lack of detailed information, I will discuss not specific mountain ridges, but large mountain systems that are natural geographic units, including Altai, West Sajan, East Sajan and Hamar-Daban (Fig. 3.1).

The inhabitants of the alpine zone are organized into three groups on the basis of their connections with this zone: 1, eualpine species, living only above timberline and occasionally extending (mainly along streams) to lower altitudes; 2, montane species, generally found in the forest zone, but sporadically or regularly ranging into the alpine zone and even occupying it; and 3, polyzonal species, widely spread in lowlands, but colonizing mountains easily, including high altitudes, often with the help of man.

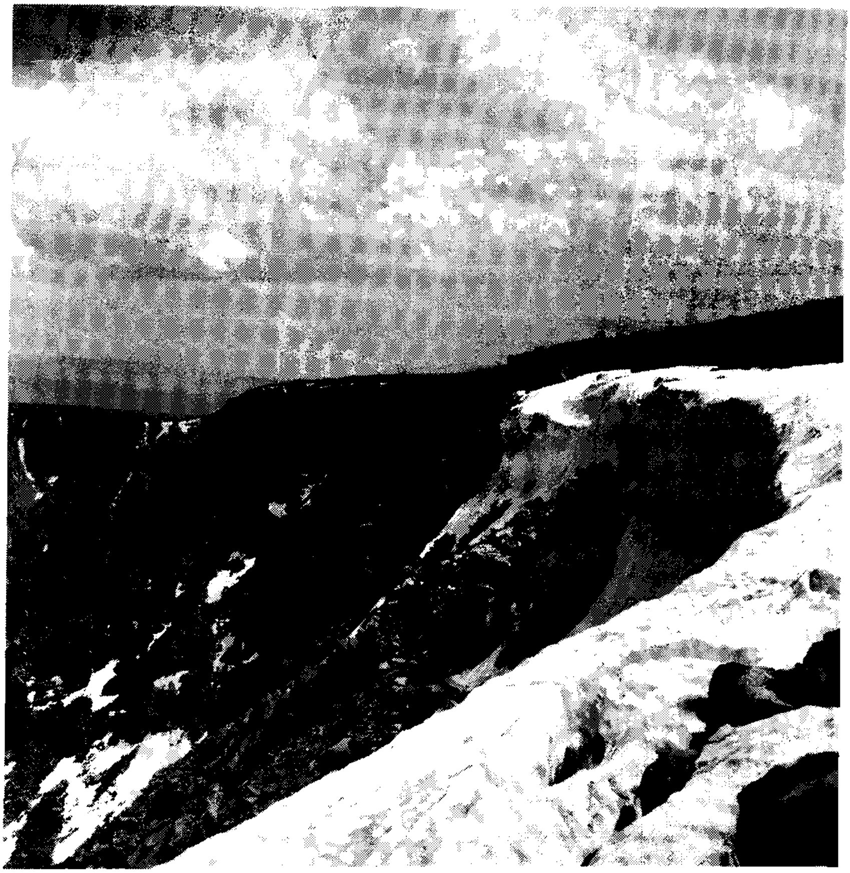

Figure 3.2: Central Altai, Seminskij mountain ridge, 2500 m above sea level, in July.

CURRENT KNOWLEDGE OF SOUTH SIBERIAN MONTANE CARABIDS

Until recently there have been no special works on the South Siberian montane carabid fauna. Some publications by previous authors have contained descriptions of new species from Siberia, including mountain regions (Fischer von Waldheim, 1822, 1823; Motschulsky, 1844; Gebler, 1833, 1843, 1847, 1848; Mannerheim, 1849; Chaudoir, 1850; Tschitschérine, 1894; Reitter, 1903; Poppius, 1906, 1907). In 1924 V. Lutshnik published his work on Carabidae of Minusinsk region (West Sajan), describing *Carabus* Linnaeus and *Nebria* Latreille. Some high altitude species were described later (Jedlička, 1959; Iablokoff-Khnzorian, 1971). Recently, I have investigated the South Siberian carabids: treating their classification in Shilenkov (1975, 1976, 1982a, 1982b, 1982c, 1983, and 1984); and Shilenkov and Sokolov, (1987); and studying their faunistic and altitudinal distributions in Shilenkov (1974, 1979, 1987a, and 1987b), Shilenkov and Kabokov (1978), and Shilenkov and Korshunov (1985).

Knowledge of the carabid fauna of such an extensive territory is preliminary. Many mountain ridges have not been investigated, and numerous new species need description.

Currently 81 species belonging to 16 genera are recorded in high altitudes of South Siberia (Table 3.1). These genera are quite characteristic for mountain regions of temperate zones. Noteworthy geographical distributions of genera and subgenera are as follows. Subgenera *Diocarabus* Reitter, *Aulonocarabus* Reitter, and *Hemicarabus* Géhin of the genus *Carabus* occur mainly in Siberia. *Catonebria* Shilenkov and *Reductonebria* Shilenkov of the genus *Nebria* are absent from Europe, but are richly represented in Siberia and North America. Most montane *Pterostichus* Bonelli, belong to subgenera *Euryperis* Motschulsky and *Cryobius* Chaudoir, as characteristic for mountain, taiga and tundra landscapes in Siberia and North America; few species of these subgenera occur in Europe. Subgenus *Plectes* Fischer von Waldheim is endemic to South Siberia. The geographical range of *Diacheila* Motschulsky in South Siberia is restricted to the mountains while in the north this holarctic genus inhabits tundra.

Species of *Duvalius* Delarouzée are concentrated mainly in the mountain systems of the West Palaearctic region. Until recently, two species of this genus described by Jeannel (1962) from Tian-Shan have been considered as the most eastern. Moravec subsequently

Table 3.1: Distribution of High Altitude Carabids in the Mountain Systems of South Siberia

Taxa	HD	ES	WS	A	GRP	AD
Carabus (Morphocarabus) henningi F.-W.			+	+	S	M
C. (Morphocarabus) odoratus Motsch.	+	+			S	M
C. (Morphocarabus) regalis F.-W.				+	S	M
C. (Morphocarabus) putus Motsch.				+	S	M
C. (Morphocarabus) mestscherjakovi Lutsh.		+	+		WS	A
C. (Aulonocarabus) canaliculatus Ad.	+				S	M
C. (Diocarabus) loschnikovi F.-W.	+	+	+	+	S	M
C. (Diocarabus) slovtzovi Mnnh.	+	+			BS	A
C. (Megodontus) leachi F.-W.				+	A	M
C. (Megodontus) sajanus Breun.			+		WS	M
C. (Megodontus) schoenherri F.-W.	+		+		S	M
C. (Hemicarabus) macleayi Dej.	+				S	A
Nebria (Catonebria) fulgida Gebl.	+			+	AS	A
N. (Catonebria) aenea aenea Gebl.				+	A	A
N. (Catonebria) nitidula catenulata F.-W.	+				S	M
N. (Catonebria) mellyi Gebl.			+	+	AS	A
N. (Reductonebria) altaica Gebl.				+	AS	M
N. (Boreonebria) nivalis Payk.		+			H	M
N. (Boreonebria) rubrofemorata Shil.			+	+	AS	M
N. (Boreonebria) sajanica Bann.		+			ES	A
N. (Boreonebria) dabanensis Shil.	+				HD	A
Leistus frater Reitt.		+	+	+	AS	M
Notiophilus aquaticus L.			+	+	H	M
Diacheila polita Fald.	+	+			H	M
Duvalius baicalensis Shilenkov, n. sp.	+				HD	A
Trechus gebleri Shilenkov, n. sp.				+	A	A
T. korgonicus Shilenkov, n. sp.				+	A	A
T. irolensis Shilenkov, n. sp.	+				HD	M
T. eryshovi Shilenkov, n. sp.				+	A	M
T. mordkovitschi Shil.			+		WS	M
T. berlovi Shilenkov, n. sp.				+	A	M
T. holzun Shil. et Sok.				+	A	A
T. sokolovi Shilenkov, n. sp.				+	A	A
T. juliannae Shilenkov, n. sp.			+		WS	A
T. dubatolovi Shilenkov, n. sp.				+	A	A
T. katunensis Shilekov, n. sp.				+	A	A
T. alticola Khnz. (no. praeocc.)				+	A	A
T. almonius Reitter		+			ES	A
Bembidion (Plataphodes) difficile Motsch.	+				TP	M

Taxa	HD	ES	WS	A	GRP	AD
B. (Plataphodes) crenulatum R.F. Sahlb.		+			TP	A
B. (Plataphodes) aeruginosum Gebl.				+	A	A
B. (Testedium) bipunctatum L.				+	ES	A
B. (s.str.) quadrimaculatum L.				+	H	P
B. (Plataphus) gebleri Gebl.				+	H	M
B. (Plataphus) prasinum Duft.				+	TP	M
B. (Peryphus) scopulinum thermarum Motsch.				+	H	M
B. (Peryphus) yukonum Fall.				+	H	M
B. (Testediolum) seminskiensis Shilenkov, n. sp.				+	A	A
Amara (s.str.) famelica Zimm.				+	ES	M
A. (s.str.) erratica Duft.			+	+	H	M
A. (s.str.) nitida Sturm			+		TP	P
A. (Paracelia) quenseli Schoenh.			+	+	H	M
A. (Bradytus) apricaria Payk.				+	ES	P
A. (Bradytus) glacialis Mnnh.		+			H	A
A. (Leiocnemis) solskyi Heyd.				+	S	M
Curtonotus Shilenkovi Kryzhanovskij, n. sp.				+	A	A
Pterostichus (Euryperis) seriatus Chd.			+	+	AS	A
Pt. (Eryperis) lineiskiensis Shilenkov, n. sp.				+	A	A
Pt. (Euryperis) korgonieus Shilenkov, n. sp.				+	A	A
Pt. (Euryperis) seminskiensis Shilenkov, n. sp.				+	A	A
Pt. (Euryperis) subaeneus Chd.			+	+	AS	M
Pt. (Euryperis) tomensis Gebl.				+	A	M
Pt. (Euryperis) ehnbergi Popp.			+		WS	M
Pt. (Euryperis) monticola Gebl.			+	+	AS	M
Pt. (Euryperis) turanesis Jedl.		+			ES	A
Pt. (Euryperis) dilutipes Motsch.		+			S	M
Pt. (Euryperis) septentrionus Chd.	+				HD	M
Pt. (Cryobius) altaiensis Popp.				+	A	M
Pt. (Cryobius) sahlbergi Tschit.	+	+	+		BS	M
Pt. (Cryobius) lucidus Motsch.	+	+			BS	M
Pt. (Cryobius) homalonotus Tschit.		+	+		BS	M
Pt. (Cryobius) tunkinensis Shilenkov, n. sp.		+			ES	A
Pt. (Plectes) drescheri F.-W.				+	AS	M
Pt. (Steropus) maurusiacus Mnnh.			+		S	M
Agonum (Europhilus)? bellicum Lutshn.			+		?S	M
Calathus melanocephalus L.				+	ES	P
Harpalus fuliginosus Duft.				+	H	M
H. affinis Schrnk.				+	ES	P
Dromius agilis F.				+	ES	M
D. quadraticollis A. Mor.			+		S	M
Cymindis vaporariorum L.	+	+			TP	M

HD – Hamar-Daban, ES – East Sajan, WS – West Sajan, A – Altai, GRP – geographical range pattern (H – Holarctic, TP – Transpalaearctic, ES – Eurosiberian, S – Siberian, AS – Altai-Sajanian, BS – Baikal- Sajanian, A – Altaian, WS – West Sajanian, ES – East Sajanian, HD – Hamar-Dabanian), AD – altitudinal differentiation (A – eualpine, M – mountain, P – polyzonal).

(1986) described a new species from Kirgisian, moving eastward, the known range of *Duvalius*. In 1988 I found new species of *Duvalius* in alpine meadows of Hamar-Daban, the first record of the genus for Siberia. The evidently relict character of this find points to the ancient connections of the montane fauna through the Eurasian continent.

For comparison, a brief review of the data about high altitude carabids of other mountain systems of the USSR is offered.

In the alpine zone of the Ukrainian Carpathian Mountains, 41 species of carabids belonging to 15 genera have been recorded (Csiki, 1946; Ponomartshuk, 1963; Rizun, 1988). Most of these genera are the same as in Siberia, but some special elements are characteristic for the Carpathians – *Pseudanophthalmus* Jeannel, *Patrobus* Stephens, and *Deltomerus* Motschulsky.

For the eastern part of the Caucasus, Abdurakhmanov (1981) has recorded 69 species representing 16 genera. Probably, this list is not complete regarding the richness of this mountain system. Along with the genera common to all mountains some endemic species of *Pristonychus* Dejean and *Deltomerus* live in the high altitudes of the East Caucasus.

For the alpine zone of southeast Kazakhstan, Kryzhanovskij (1953, 1965) and Kabak (1985) have recorded more than 100 species belonging to 17 genera. Many endemic and hemiendemic subgenera are characteristic for this area: *Eotribax* Semenov-Tian-Shanskij, *Alipaster* Reitter, *Cratocarabus* Reitter, *Cechenotribax* Semenov & Znojko, and related groups of *Carabus*; *Pseudometallina* Netolitzky of *Bembidion* Latreille; and *Oreolyperus* Tschitschérine of *Pterostichus*. The endemic Central Asian genus *Colpostoma* Semenov-Tian-Shanskij penetrates here. It is interesting that representatives of some typically lowland genera inhabit the alpine zone: *Cicindela* Linnaeus, *Asaphidion* Gozis, *Taphoxenus* Motschulsky, and *Microlestes* Schmidt-Goebel. Many of these genera have evolved endemic alpine species.

The high altitude carabid fauna of the southeastern part of Central Asia is mostly diverse (Mikhailov, 1973, 1976, 1986; Mikhailov & Tshikatunov, 1987). About 120 species of 30 genera have been recorded, with numerous endemics or hemiendemics of subgeneric rank: for genus *Carabus*, subgenera *Ulocarabus* Reitter, *Cratophyrtus* Reitter, *Goniocarabus* Reitter; for *Pterostichus*, subgenus *Asioplatysma* Kryzhanovskij; for *Leistus*, subgenus *Chaetoleistus* Semenov-Tian-Shanskij; and for *Bembidion*, subgenus *Pamirium* Netolitzky. Some genera, such as *Neopangus* Tschitschérine and *Bronislavia* Semenov-Tian-Shanskij (tribe Harpalini) occur in the alpine zone of this region. The process of penetration of the high altitude zone by the typically lowland genera is much more prominent here than in Kasakhstan: *Cicindela* Linnaeus, *Calosoma* Weber, *Clivina* Latreille, *Tachyura* Motschulsky, *Trichocellus* Ganglbauer, *Ophonus* Stephens, *Lebia* Latreille, and other genera inhabit the alpine zone in southeastern Central Asia.

Thus, the general diversity of the high altitude carabid fauna of South Siberia is quite comparable with that of such mountain areas as the Carpathians, the Caucasus, and East Tian-Shan, but it is evidently poorer than the diversity of species found in Gissaro-Darvaz and West Tian-Shan. The South Siberian region is not as rich in species as Central Asia and the Caucasus, but it is notably richer than the Carpathians.

Some genera play a predominant role in the formation of the high altitude carabid fauna in South Siberia. In *Pterostichus* 18 species are recorded, mostly belonging to subgenera *Euryperis* (eleven species) and *Cryobius* (five species). For other genera, the numbers of species recorded are: *Trechus* Putzeys – thirteen; *Carabus* – twelve; *Bembidion* - ten; *Amara* Bonelli – seven; and only one or two species for each of the remaining genera.

The number of species increases from east to west (Table 3.2). This increase is probably due to the number of species being dependent on the areas of different mountain systems, their altitudes and, consequently, on the history, climate, and degree of development of alpine landscapes, of each mountain fauna's formation.

Alpine zones of different mountain ridges and whole mountain systems are separated significantly now by the forest zone, as reflected in rather low coefficients of similarity that reach their lowest values between the most remote mountain systems (Table 3.4). The pronounced similarities between Altai and West Sajan and between East Sajan and Hamar-Daban (Fig. 3.3) point to a sharply defined zoogeographical boundary between West and East Sajan, reflecting different ways of formation of their mountain fauna and the presence of local centres of endemism.

GEOGRAPHICAL RANGE PATTERNS OF HIGH ALTITUDE CARABID FAUNA IN SOUTH SIBERIA

All species are arranged in two groups according to the type of geographical range pattern: species with wide distribution; and endemics of mountain systems of South Siberia. The first group is represented by four sub-groups:

Table 3.2 Number of species and percentage (in parentheses) of different geographical range patterns in mountain systems of South Siberia

Geographical Range Patterns	Hamar-Daban	East Sajan	West Sajan	Altai	Total
Holarctic	1(5.9)	3(16.7)	3(13.1)	8(16.7)	11(13.6)
Transpalaearctic	2(11.8)	2(11.1)	1(4.3)	1(2.1)	5(6.2)
Eurosiberian				6(12.5)	6(7.4)
Siberian	6(35.3)	3(16.7)	6(26.1)	5(10.4)	14(17.3)
Altai-Sajanian	1(5.9)	1(5.6)	6(26.1)	9(18.7)	9(11.1)
Baikal-Sajanian	3(17.6)	4(22.2)	2(8.7)		4(4.9)
Local endemics	4(23.5)	5(27.7)	5(21.7)	19(39.6)	32(39.5)
Total	17	18	23	48	81

Table 3.3: Frequency of eualpine, mountain and polyzonal species and their percentage (in parentheses) in different mountain systems of South Siberia

	Hamar-Daban	East Sajan	West Sajan	Altai
Eualpine	5(29.4)	8(44.4)	4(17.4)	18(37.5)
Mountain	12(70.6)	10(55.6)	18(78.3)	26(54.2)
Polyzonal			1(4.3)	4(8.3)

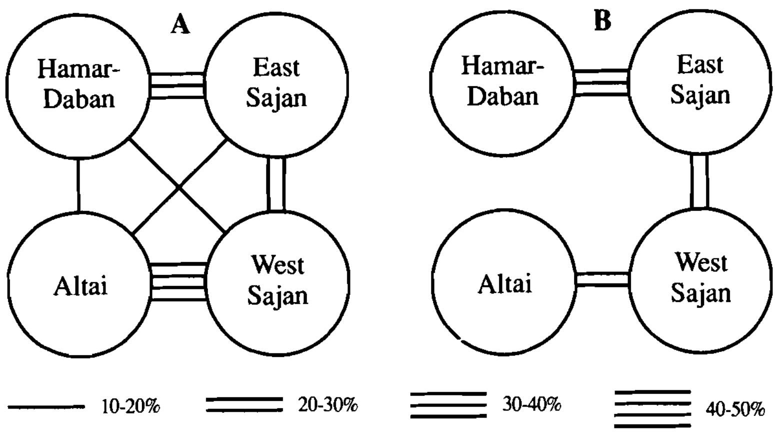

Figure 3.3:- Faunal connections between the high altitude Carabids of the mountain systems of South Siberia, on the base of similarity coefficients. A - Simpson coefficient, B - Jaccard coefficient.

Widespread Species

1 Holarctic distributional pattern Eleven species with arcto-alpine distribution are included, two of them characteristic for the alpine zone (*Nebria nivalis* Paykull, and *Amara glacialis* Mannerheim). Others are regarded as montane species. Formation of this distribution pattern is attributed to the Bering Land, but Angara served as the primary centre of speciation. Most species have a circumpolar range, though some of them do not reach Europe (*Bembidion gebleri* Gebler, *B. scopulinum thermarum* Motschulsky), but are widely distributed in the Far East, including Primorie, Korea and Japan.

2 Transpalaearctic distributional pattern Four species with boreo-alpine distribution are included (*Bembidion difficile* Motschulsky., *B. crenulatum* R.F. Sahlberg, *B. prasinum* Duftschmid, *Cymindis vaporariorum* L.), and one widespread plyzonal species – *Amara* *nitida* Sturm. The first four species penetrated Europe at the time of maximal glaciation, but this migratory route was less significant than the one in the eastern direction with the formation of the Holarctic distribution pattern. The above mentioned species of *Bembidion* and *Cymindis* Latreille, as well as several Holarctic species, have, in Europe, relict distribution patterns with disjunctions, reflecting their wide expansion to the south in glacial time (Holdhaus and Lindroth, 1939). In Siberia, they are spread more uniformly, but are also attracted to mountains.

3 Eurosiberian distributional pattern This subgroup has six species, four of which are polyzonal. Two species (*Bembidion bipunctatum* L., and *Amara famelica* Zimmermann) have mainly an arcto-alpine distribution. None of these species penetrate to the east of Transbaikal.

4 Siberian distributional pattern This heterogeneous subgroup consists of 14 species with different routes of origin. Some species are widely distributed in Siberia from the Urals to the Pacific Ocean (*Carabus odoratus* Motschulsky); others are restricted by the eastern boundary of the Lena valley (*Carabus heningi* Fischer von Waldheim, *C. putus* Motschulsky, *Pterostichus maursiacus* Mannerheim); still others, beside their wide distribution in the mountains of South Siberia, occupy a secluded area in the Ural mountains (*Carabus loschnikovi* Fischer von Waldheim, *C. schoenherri* Fischer von Waldheim). Lastly, some species prevailing in the Far East do not penetrate to the west of Altai or even Baikal (*Nebria nitidula catenulata* Fischer von Waldheim, *Carabus macleayi* Dejean, *Amara solskyi* Heyden). Evidently, these differences in ranges depend on historical reasons, connected with different centres of origin of the Siberian fauna, but they are not analyzed here. All species of this group are montane.

Endemics of South Siberian Mountain Systems

All the following groups include endemics of South Siberian mountains and are restricted by one part or another of this mountain country.

1 Altai-Sajanian distributional pattern The connections between the Altai and the West Sajan are registered mainly because only two species out of nine belonging to this group, are in East Sajan, and one even in Hamar-Daban. Four species are alpine and five montane.

2 Altaian distributional pattern This is the most diverse group of high altitude carabids, including 19 species, of which five are montane, the others inhabiting only the alpine zone. This group consists mainly of local endemics of genera *Trechus* and *Pterostichus*, with most such endemic species not yet described.

3 West Sajanian distributional pattern Five species are restricted to the mountain ridges of the West Sajan, but one of them, *Carabus mestscherjakovi* Lutshnik, penetrates partly into the East Sajan. Only one species belongs to the eualpine group; the others are montane.

4 East Sajanian distributional pattern The four endemic species of the East Sajan are eualpine and known only from Tunkinskije Alpy mountain ridge. Their restricted geographical ranges are probably due to inadequate collecting in other parts of the East Sajan. All species are eualpine.

5 Baikal-Sajanian distributional pattern Four species more or less widely distributed in East Sajan and partly in West Sajan reach Hamar-Daban and other mountain ridges of Transbaikal. They are all eualpine, three of them belonging to the subgenus *Cryobius* of genus *Pterostichus*.

6 Hamar-Dabanian distributional pattern At present, only four endemics of Hamar-Daban are known, one of them being montane, the others eualpine.

Of 81 species recorded from high altitudes of South Siberia, 45 are endemics of this territory and about half of these inhabit the Altai Mountains. This shows the important role of the South Siberian mountains as important centres of speciation. A similar conclusion has been made for higher vascular plants (Malyshev, 1965; Malyshev and Peshkova, 1984). Endemism occurs mainly at the species level, although among *Trechus* the ranges of some morphologically sharply defined species groups hardly extend beyond the limits of the

Altai-Sajan mountain system. Quite peculiar is *Pterostichus (Plectes) drescheri* Fischer von Waldheim, occupying an isolated position among Siberian *Pterostichus*, and being related to Caucasian *Myosodus* Fischer von Waldheim. Probably, it is an ancient relict, along with *Duvalius baicalensis* (Shilenkov, in press).

Analyses of degree of extension among eualpine, montane and polyzonal species provide interesting data. Among 31 eualpine species, 27 are endemics (87%), while among 45 montane species only 19 (42%) are endemics. All polyzonal species are widely distributed in the Palaearctic or Holarctic Regions. These figures suggest larger geographical ranges for montane species than for eualpine ones. Such larger ranges are probably due to montane groups being older than eualpine taxa. During the process of orogeny a montane group always develops before a eualpine group, and has more opportunity and time for distribution over large territory.

VICARIANCE AND SPECIATION AMONG HIGH ALTITUDE CARABIDS

Most eualpine species are neoendemics, as a rule slightly differentiated structurally. Many are parts of complexes of closely related species vicariated on different mountain ridges or even on different vertical zones of the same ridge. There are many *Trechus, Pterostichus,* and *Nebria*. Speciation among high altitude carabids is proceeding intensively at present. Many populations of one species from different mountain ridges have small but distinct differences, discoverable at the statistical level. But any discussion of microevolutionary process is beyond the scope of the present paper.

Small, brachypterous *Trechus* with slight capability for dispersal give a good example of "explosive" speciation under conditions of montane isolation. Speciation of large forms with capability of active dispersal, such as *Carabus*, develops differently. In high altitudes of South Siberia, 12 species of this genus have been recorded. Only four are endemics; others are more or less widely distributed in Siberia, but concentrated in mountain regions. They represent five subgenera, but five species belong to the structurally non-specialized *Morphocarabus*.

It should be noted that the number of *Carabus* species in South Siberia is smaller than those in the mountains of Central Asia and the Caucasus. This fact is explained by the more northern location of South Siberian mountains and their generally lower elevations.

In Altai, endemic *Carabus* are concentrated in the forest zone (only *C. leachi* Fischer von Waldheim reaches the alpine zone). The zone above the timberline is inhabited by Siberian species, with the most common taxa being *C. putus* Motschulsky and *C. loschnikovi* Fischer von Waldheim. For some species, a regular change of habitats in latitudinal direction has been recorded: *C. putus* Motschulsky, *C. henningi* Fisher von Waldheim, and *C. regalis* Fischer von Waldheim live in the alpine zone only in Altai, but to the east they are typically forest species. High altitude populations of these *Carabus* species possess some distinctive features, but such character states do not warrant subspecific recognition.

A somewhat different situation occurs in the alpine zone of the Sajan and Hamar-Daban, where, alongside quite common Siberian species of *Carabus*, live three endemics. One of them, *C. slovtzovi* Mannerheim, common to Hamar-Daban and East Sajan, is a typical neoendemic, an alpine derivative of *C. massagetus* Motshulsky, which lives in forests. The second species, *C. mestsherjakovi* Lutshnik, inhabits mainly alpine meadows in the West and East Sajan. It lacks close relatives in the mountains of South Siberia and must be regarded rather as an ancient element. The closest to it is *C. zherichini* Shilenkov (1990), with a large range in tundras from the Urals to Chuckchi Peninsula. The third species, a local endemic of the West Sajan, *C. sajanus* Breuning, is regarded as derivative from the widespread *C. schoenherri* Fischer von Waldheim, but it appears to be more common in the forest zone. Finally, *C. odoratus* Motschulsky, throughout its range including the mountains of South Siberia, has various subspecies, but they are not fully known.

The above examples show clearly a rather slight degree of alpine speciation in *Carabus* of South Siberia, in contrast to some carabid genera with species whose adults have smaller body sizes.

Table 3.4: Coefficients of similarity between mountain systems of South Siberia (above – Simpson coefficient, down – Jaccard coefficient)

	Hamar-Daban	East Sajan	West Sajan	Altai
Hamar-Daban	–	35.3	17.6	11.8
East Sajan	33.3	–	27.8	11.1
West Sajan	13.0	21.7	–	47.8
Altai	4.2	4.2	22.9	–

As in *Trechus,* alpine speciation is very apparent in *Pterostichus* and *Nebria.* Among alpine *Pterostichus* about half the species are clearly defined neoendemics, having sister species in different parts of mountain systems or in the forest zone. Practically all are brachypterous. Interesting examples of vicariance are given by *Nebria,* which is represented by pairs of sister species in different parts of mountain systems (Table 3.5).

The list of examples could be continued, using material from the whole of Siberia. It is worthy of note that alpine speciation is accompanied by reduction of hind wings, as reported for North American *Nebria* (Kavanaugh, 1985).

Thus, in high altitudes, where processes of fragmentation and isolation of populations prevail over the migration process, grounds for quick speciation are established. Careful taxonomic investigations help elucidate the relationships and phylogeny of species groups and postulate different stages of speciation, from small differences of local populations to subspecies and species.

Table 3.5: Examples of vicariance among sister species of *Nebria.*

N. nitidula catenulata F.-W. South Siberian, montane (in forest zone), winged.	*N. fulgida* Gebler Kuznetzk Alatau, Sajan, Hamar- Daban, eualpine, brachypterous.
N. subdilatata Motschulsky East Siberian, montane (in forest zone), winged.	*N. rubrofemorata* Shilenkov Altai-Sajanian, mainly alpine, but penetrating into forest zone, brachypterous.
N. sajanica Bänninger East Sajanian, eualpine, brachypterous.	*N. dabanensis* Shilenkov Hamar-Dabanian, eualpine, brachypterous.

SOURCES AND FORMATION OF THE HIGH ALTITUDE CARABID FAUNA OF SOUTH SIBERIA

The history of formation of the high altitude fauna of South Siberia is closely connected with the history of relief, climate and vegetation of this area.

Findings of the relicts of Palaeogene time in the alpine zone seem very unlikely, because that period was marked by continental subtropical climate over the territory of South Siberia (Kulkova *et al,* 1975), and relief was less with ridges of low elevations (Sinitzin, 1965). In the upper Oligocene under colder and drier conditions, the so-called Arcto-Tertiary (according to Engler) or Turgai (Kryshtofovitsh, 1958) Flora was formed. This flora was then closely allied to recent forests in southeastern Asia (China, Japan, and Primorie). During the upper Oligocene, the main elements of the Turgai Flora formed, and the Flora assumed its widest extent.

In the Middle Neogene, the orogeny process in Asia gathered great momentum. The largest mountain formations were created, extending in an uninterrupted band from northeastern Siberia to Tian-Shan (the so-called Great Transasian Mountain Way). Simultaneously with orogeny, the climate, slowly but steadily, became increasingly colder and drier. In mountain regions, suitable conditions developed for boreal community formations, such as taiga (Tolmatschow, 1943). At first, the areas occupied by these communities was not large, but in the Pleistocene, when the climate cooled, they became widespread. Along with the orogenic processes, the evolution of the biota's initial elements of montane communities took place, the latter having taken shape generally before the Quaternary (Tolmatschow, 1948).

The high altitude carabid fauna probably was formed first in the northeast and east of Eurasia, where clearly defined mountain landscapes existed since as long ago as Palaeogene. Newly elevated mountains of Siberia were occupied by species from more ancient systems, and simultaneously, autochthonous speciation took place.

The Pleistocene glaciations resulted in formation of an ice-sheet in the north of Siberia, while mountain glaciation expanded remarkably and caused an abrupt drop of the timberline level. In this period, intensive migratory processes between mountain systems and zonal tundra took place, in which the Great Transasian Mountain Way played the principal role. Through the Pleistocene time, the widest ranges were formed: Holarctic, Transpalaearctic, and Eurasian, wherein migration in an easterly direction was predominant. The origin of most mountain and tundra carabids of North America, for instance *Cryobius* (Ball, 1966), is undoubtedly Asian. Practically all North American *Nebria* are members of the three phylogenetic branches (Kavanaugh, 1985) that correspond to the three Asian subgenera: *Boreonebria* Jeannel, *Reductonebria* and *Catonebria* (Shilenkov, 1975).

Successive alternation of glaciations and warm interglacial periods led to repeated mergings and subsequent fragmentations of alpine landscapes. Periods of intense faunistic exchanges were followed by periods of isolation, when speciation was most active. Alpine biota are now in the stage of isolation, with active speciation occurring.

Modern civilization also makes a contribution within its powers to the formation of high altitude fauna. By cutting and burning down forests, building roads and vistas, man assists in the penetration of some species from intrazonal and ruderal biotypes into the mountains.

SUMMARY

The mountains of South Siberia are an important centre of speciation. Montane and especially high altitude carabid faunas have formed because of continued autochthonous processes, and comprise endemics of different ages, including ancient relicts. Migratory processes were much less significant for the formation of this fauna. The uniqueness of the alpine biota, and lack of adequate data, indicate the necessity of its further investigation. The growing destructive interference of man demands energetic protective efforts in mountain regions.

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