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The Ground Beetle Fauna (Coleoptera, Carabidae) of Southeastern Altai

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Abstract—Long-term studies of the ground beetle fauna of Southeastern Altai (SEA) revealed 33 genera and 185 species; 3 and 15 species are reported for the first time from Russia and SEA, respectively. The following genera are the most diverse: *Bembidion* (47 species), *Amara* and *Harpalus* (21 each), *Pterostichus* (14), and *Nebria* (13). The subarid (35%) and boreal (32%) species prevail in the arealogical spectrum, while the mountain endemics comprise 13% of the fauna. The carabid fauna of SEA is heterogeneous in composition and differs significantly from that of the Western and Central Altai. The boreal mountain component mostly comprises tundra species with circum-boreal or circum-arctic ranges, while the subarid component (typical Mongolian together with Ancient Mediterranean species) forms more than one-half of the species diversity in the mountain basins. The species diversity increases from the nival mountain belt (15 species, predominantly Altai-Sayan endemics) to moss-lichen tundras (40, mostly boreal, species). The variety of habitats and constant hydrothermal regimes in the intrazonal valley communities determine high taxonomic diversity of Carabidae, including both tundra or meadow-steppe species typical of the region and some forest ones. Under the condition of moisture deficiency, many steppe species also concentrate in river floodplains.

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The ground beetle fauna of Southern Siberia has been studied for over 180 years. The first data on the Siberian Carabidae were published by Fischer von Waldheim (1820–1822, 1821, 1823–1824, 1825–1828, 1832), Gebler (1830, 1847, 1848), Motschulsky (1844, 1850), and Morawitz (1862).

By now, relatively complete faunistic synopses have been compiled only for Tuva (Shilenkov, 1998; Sambyla and Dudko, 2004), Khakassia (Shilenkov and Korshunov, 1985), and some regions of the Transbaikalia (Shilenkov, 1974, 1979, 1994, 1995; Shilenkov et al., 1999). Information on the carabid fauna of most of the Altai-Sayan Mountains is fragmentary. In particular, data are available on the local faunas of some regions of the Central (Matalin, 1988; Kolesnikov, 1992; Matalin and Fedorenko, 1999), Western (Matalin, 1986), and Southeastern Altai (Kovrigin, 1984; Khmel'kov and Kovrigin, 1985; Sysoletina and Kovrigin, 1987; Dudko and Lomakin, 1996; Ivanov and Dudko, 2006), and also Kuznetsk Alatau and Gornaya Shoria (Eryshov and Trofimova, 1984; Dudko et al., 2002).

The carabid fauna of the Southeastern Altai has hardly been studied (Mordkovich, 1968; Dudko, 1998; Fedorenko and Matalin, 2002). However, this fauna is truly unique owing to its position in the mountain belt of Southern Siberia at the junction of the Central and Western Altai on the one hand, and the Southern and Mongolian Altai, on the other. It is not a mere coincidence that several new taxa of Carabidae have been recently described from this territory (Matalin, 1999; Hieke, 2000; Fedorenko, 2001; Kataev, 2001).

MATERIALS AND METHODS

In this communication, the Southeastern Altai (SEA) territory is delimited according to the previous geobotanical regionalization (Ogureeva, 1980). It includes the Chuya and Sayliughem steppes with their peripheral foothills, and also the eastern part of Ukok Plateau limited by the Kurai Range, Lake Dzhulukul, and the upper course of the Chulyshman River in the north, the Chikhachev Range in the east, the Sayliughem Range in the south, and the Dzhazator River valley in the west. The prevalent landscapes are al-

pine, with the mean altitude of 1700–2100 m above sea level.

The altitudinal zonality is distinct although the forest belt is absent. The vegetation of the foothills surrounding the Chuya and Sayliughem basins is represented by Mongolian-Chinese (Chuya-Tuva) mountain steppe formations: true dry sod-grass steppes, which in the basins proper are replaced by desertified steppes, often combined with various halophytic complexes. The surrounding mountain ranges are dominated by Altai-Sayan mountain tundra formations, represented by steppe-like variants of meadow tundras combined with moss-lichen dwarf birch thickets and elements of dwarf larch shrubs on the northern slopes. Above them, up to the nival zone, there are moss-lichen tundras with the dryas, lichen-gravelly, and other variants, as well as various open communities.

The material used in preparing this communication was collected by the authors and their colleague entomologists in 1996–2008, in 70 localities of SEA (Fig. 1). The material was collected in different seasons of the year, from early spring to mid-autumn. The main collection methods included manual collection, soil traps, and excavations.

According to their distribution, the ground beetles occurring in SEA were subdivided into 5 groups: polyzonal, boreal, subboreal (= temperate), subarid, and the group of regional, i.e., Altai-Sayan endemics (Gorodkov, 1984, 1985; Dudko, 1998). The ranges of the polyzonal species extend over several natural zones, from the tundra or northern taiga to semideserts or deserts. The boreal species are mostly associated with the taiga zone. The subboreal group unites the species occurring in Siberia within a narrow band between the southern taiga and the steppes. The subarid species are mostly associated with the steppe and semi-desert areas of the Ancient Mediterranean region. Finally, the group of regional endemics comprises the species distributed only in the Altai-Sayan mountain region, including the mountains of Northern Mongolia.

The term "specific (= local) fauna" is used in the interpretation proposed by Chernov (1975). The local faunas were compared using the Shimkevich-Simpson index: $K_S = c/a$ if $a < b$, or $K_S = c/b$ if $b < a$, where a and b are the number of species in the faunas to be compared, and c is the number of species shared by the two faunas. The similarity dendrogram was calculated using the UPGMA algorithm implemented in the STATSOFT Statistica 5.5a software package.

RESULTS AND DISCUSSION

Specific Features of the Carabid Species Composition in the Southeastern Altai

The presently known fauna of SEA comprises 185 species of ground beetles from 33 genera (Table 1). Three species, previously known from Mongolia and China, are reported for the first time for the fauna of Russia. In particular, *Nebria changaica*, described from Mongolia as a subspecies of *N. nivalis* (Horvatovich, 1973) and later synonymized with *N. rufescens* (Shilenkov, 1982) or *N. nivalis* (Farkač and Janata, 2003), is considered here as an independent species distributed not only in Hangai but also in Altai. This decision is based on the differences in the male genitalia and the presence of zones of sympatry with both *N. nivalis* and *N. rufescens*. The beetle *Bembidion davaai* (Jedlička, 1968), described from the Gobi-Altai, was found on the banks of Lake Uch-Telets in the Chuya Steppe and in the Ak-Alaha valley on Ukok Plateau. The species is also known from Northern Mongolia where it occurs on the banks of Lake Khuvsgul (20–23.07.1984, D. Fedorenko). The species *Bembidion roborovskii* (Mikhailov, 1988), distributed in Nanshan and Hangai, was recorded in the Mt. Chernaya area and in the upper course of the Kalguty in the Sayliughem Range. In both localities the species inhabits steppe-like meadow tundras, often reaching high abundance. The following 15 species are reported for the first time for the Altai fauna: *Diacheila polita*, *Blethisa tuberculata*, *Elaphrus sibiricus*, *Dyschiriodes chalceus*, *D. nigricornis*, *Bembidion paediscum*, *B. axillare*, *B. tenellum*, *B. consummatum*, *B. ovale*, *Platidiolus rufus*, *Pterostichus planicola*, *Amara irkutensis*, *A. hicksi*, and *Dicheirotrichus bradycelliformis*. In general, the faunistic list given in Table 1 appears to be almost complete; it may be insignificantly supplemented after the obscure northern and southeastern parts of the region have been examined (Fig. 1).

The taxonomic composition of ground beetles in SEA is quite specific. The most diverse genus is *Bembidion* Latr., represented here by 47 species (25% of the total species diversity, abbreviated below as SD). No other region of Siberia is characterized by such high values. In particular, in the adjacent territories of Northeastern and Western Altai as well as in Kuznetsk Alatau and Tuva the fraction of this genus does not exceed 17–20% (Dudko and Lomakin, 1996; Shilenkov, 1998; Dudko et al., 2002; Sambyla and Dudko, 2004; Ivanov and Dudko, 2006). The most significant in this respect is the group *B. lunatum*

(subgenus *Asioperyphus* Výsoký): its 7 species (*B. altestriatum*, *B. infuscatum*, *B*. sp. pr. *infuscatum*, *B. ovale*, *B. pamiricola*, *B. sajanum*, and *B. smirnovi*) concentrate in the Chuya basin and the middle course of the Tarkhata and Chuya rivers. The genera *Amara* Bon. and *Harpalus* Latr. are represented in the region by 21 species (11% of SD) each. The former genus shows similar parameters of SD (10–14%) in Tuva, Mongolia, and Northeastern and Western Altai (Schilenkov, 1998; Dudko and Lomakin, 1996; Sambyla and Dudko, 2004; Ivanov and Dudko, 2006). The fraction of the genus *Harpalus*, tending to prefer arid and semiarid regions, is smaller than in Tuva and Mongolia (14% of SD) but greater than in Kuznetsk Alatau and Gornaya Shoria (6%) (Dudko et al., 2002). The genus *Pterostichus* Bon. comprises 14 species (8% of SD), which is less than in most of the other mountain regions of Siberia. For example, the taxocenes of the Central and Western Altai and the Eastern Sayan include from 3 to 6 sympatric species of the subgenus *Petrophilus* Chaud., whereas in SEA the subgenus is represented by only one quite common species *P. seriatus*; another species of the subgenus, *P. magus mongolicus*, is known from a single record in Mt. Sayliughem. Even lower is the diversity of the genus *Nebria* Latr. (13 species, 7% of SD), which is largely distributed in the Holarctic mountain systems; 6 species belong to the subgenus *Boreonebria* Jeann. and 5, to the subgenus *Catonebria* Shil.

The genera *Carabus* L. and *Dyschiriodes* Jeann. comprise 8 species (4% of SD) each, *Agonum* Bon. and *Curtonotus* Steph., 6 species (3% of SD) each, and *Dicheirotrichus* Jacq. and *Cymindis* Latr., 5 species (2.5% of SD) each. The rest of the genera are represented in SEA by 1–3 species. A low impact of the genus *Agonum* should be noticed. This genus is much more diverse in other parts of the Altai, comprising up to 17 species in the Northeastern Altai only.

The most peculiar feature of the carabid fauna of SEA is a complete absence of the genus *Trechus* Clairv. Most species of this genus have local ranges and are very non-uniformly distributed in the mountains of Siberia. They have not been found in the northern part of Middle Siberia and in the entire Eastern Siberia (Shilenkov, 1994; Makarov et al., 2009). On the contrary, in the Altai-Sayan Mountains the genus is represented by no less than 40 species (some of them still undescribed), whereas the faunas of the different parts of Altai comprise up to 6–7 sympatric

Fig. 1. Map of the study region and the collection localities. **Ranges and mountain systems**: ***Shapshal Range***: *1*—Shapshal Pass (2550–2900 m); ***Chikhachev Range***: *2*—3 km SE of Mt. Chernaya (2500–3100 m); *3*—the Builyukem valley (2200 m); *4*—Buguzun Pass (2400–2600 m); *5*—the Buguzun valley, 5 km upstream of the Karagai outfall (2300 m); ***Mt. Sayliughem***: *6*—1 km NNW of Mt. Sayliughem (2200–2300 m); *7*—4 km NW of Mt. Sayliughem (2400–2700 m); *8*—6 km WNW of Mt. Sayliughem (2200 m); ***Southern Chuya Range***: *9*—the Taldura valley (2200–2400 m); *10*—the upper course of the Taldura (2600–2900 m); *11*—the Sebystei valley (2100–2200 m); *12*—the upper course of the Sebystei (2400–2600 m); *13*—the upper course of the Kokozek (2200–2400 m); *14*—the upper course of the Tara (2600–2950 m); *15*—the lower course of the Tara (2200–2400 m); *16*—S branch of Southern Chuya Range, near the Tara mouth (2600–2800 m); *17*—left tributary of the Tarkhata (2400–3100 m); ***Mt. Chernaya***: *18*—15 km NW of Mt. Kulunbazhi, right bank of the Tarkhata (2200 m); *19*—foot of Mt. Kulunbazhi (2600 m); *20*—near Mt. Chernaya (2500–3000 m); *21*—right tributary of the Kalanegir (2450 m); *22*—the lower course of the Kalanegir (2400 m); *23*—outfall of the Kalanegir (2200–2300 m); *24*—watershed of the Kalanegir and the Kuruk (2400–2700 m); ***Sayliughem Range (the upper course of the Zhumaly)***: *25–26*—the Zhumaly valley (2300–2500 m); *27*—left head of the Zhumaly (2600–2900 m); *28*—Teplyi Klyuch Pass (2800–2950 m); ***Sayliughem Range (the upper course of the Kalguty)***: *29*—8 km NW of Ulan-Daba beacon (2400 m); *30–31*—5 km SE of Argamdzhi (2300–2400 m); *32*—near Argamdzhi (2300 m); *33*—5 km NNE of Argamdzhi (2400 m); *34*—8–10 km NE of Argamdzhi (2400–2700 m); *35*—near Lake Gusinoe (2250 m); ***Mt. Maitobe***: *36*—8 km NE of Mt. Maitobe (2400–2500 m); *37*—near Mt. Maitobe (2600–2950 m); ***Ukok Plateau (the upper course of the Kaldzhin-Kul)***: *38*—near Lake Kaldzhin-Kul-Bas (2400–2550 m); *39*—5 km NW of Lake Kaldzhin-Kul-Bas (2600–3000 m); ***Southern Altai Range***: *40*—near Lake Muzdy-Bulak (2400–2500 m); *41*—2–4 km S of Lake Muzdy-Bulak (2700–3100 m). **Intermountain basins**: ***Chuya Steppe***: *42*—bank of the Chuya near Chagan-Uzun (1730 m); *43*—1 km N of Ortolyk (1800 m); *44*—2 km N of Kosh-Agach, Lake Uch-Telets (1750 m); *45*—2 km SW of Kosh-Agach (1750 m); *46*—3 km SE of Kosh-Agach, bank of the Chaganka (1750 m); *47*—6 km W of Kokorya, the Yustyt valley (1850 m); *48*—15–20 km SSW of Kosh-Agach (1850–1900 m); *49*—near Mt. Dzhalgiztobe (1900 m); *50*—20–25 km S of Kosh-Agach (1900 m); *51*—20–25 km SW of Mukhor-Tarkhata (1900 m); *52*—the Kokozek valley (2000 m); *53*—interfluve of the Chagan-Burgazy and Tarkhata (2000 m); *54*—the Chagan-Burgazy valley (2000 m); ***Sayliughem Steppe***: *55*—3 km E of Kokorya (1800 m); *56*—the Kyzyl-Shin valley (1900 m); *57*—10–12 km NE of Kokorya (2000 m); *58*—bank of the Buguzun (2050 m). **Valleys of large river and lakes**: ***Lake Dzhulukul***: *59*—E bank of Lake Dzhulukul (2200 m); ***Chuya Ruver***: *60*—the Kuiktanar mouth (1700 m); ***Tarkhata River***: *61*—the lower course of the Tarkhata (2100 m); *62*—the middle course of the Tarkhata (2200 m); ***Dzhazator River***: *63*—the Ildegem outfall, 17 km ESE of Belyashi (1630 m); *64*—3 km E of Chirubai ruins (2000 m); *65*—the Chikta outfall (2000 m); *66*—the Chikta (2200 m); *67*—2 km E of Chigur burial ground (2100 m); *68*—the Zhumaly valley, Kalguty ruins (2000 m); ***Ak-Alaha River***: *69*—the Akkol outfall (2200 m); *70*—10 km upstream from the Kalguty outfall (2150–2250 m).

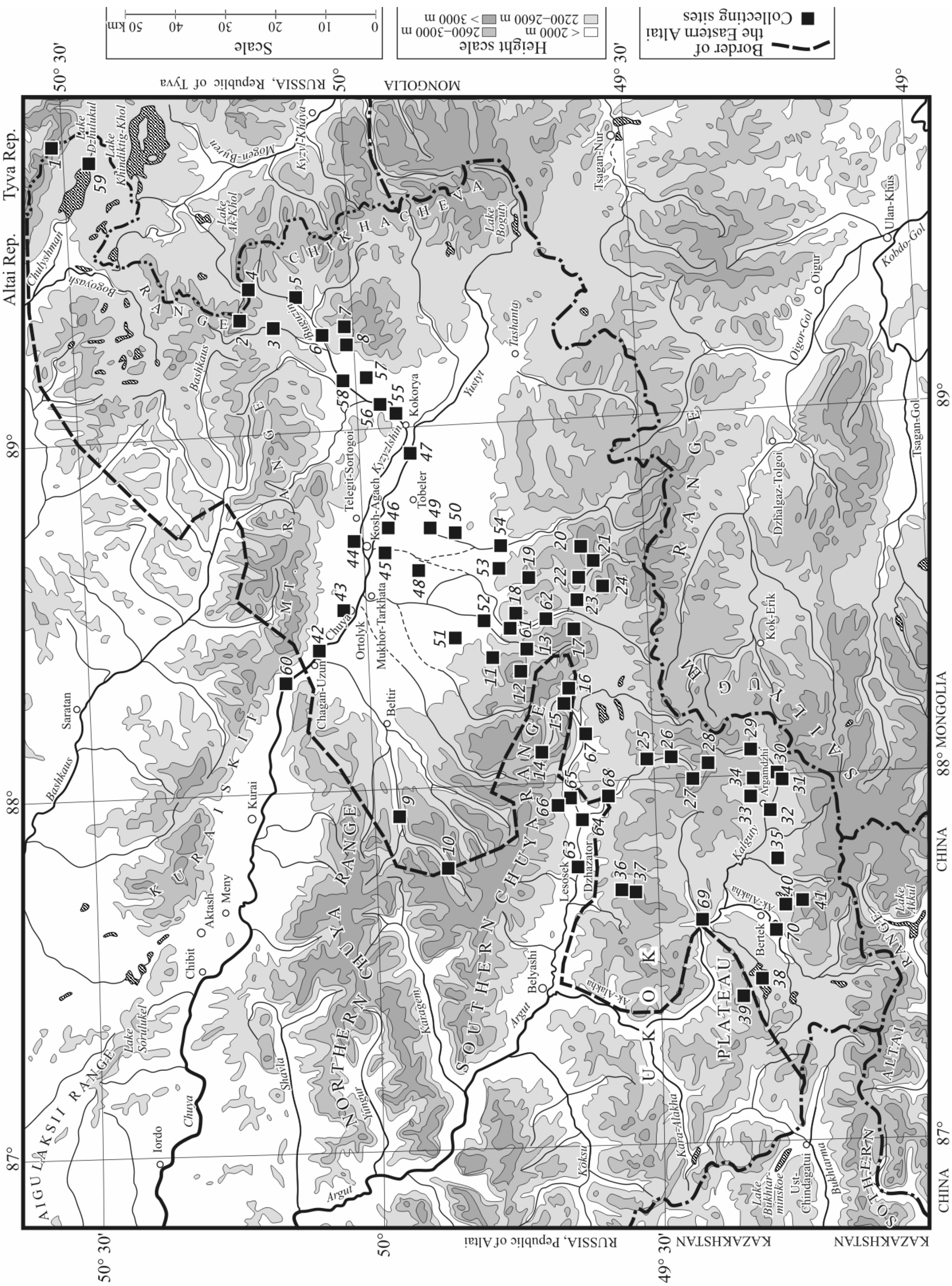
Border of
the Eastern Altai
Collecting sites
Height scale
< 2000 m
2200–2600 m
2600–3000 m
> 3000 m
Scale
0
10
20
30
40
50 km
Altai Rep.
Tyva Rep.
RUSSIA, Republic of Tyva
MONGOLIA
RUSSIA, Republic of Altai
KAZAKHSTAN
CHINA
88° MONGOLIA
50° 30′
50°
49° 30′
49°
87°
88°
89°
CHYKHACHEVA
RANGE
KURAISKII MT. RANGE
NORTHERN CHUYA RANGE
SOUTHERN CHUYA RANGE
AIGULAKSKII RANGE
UKOK PLATEAU
SAILYUGEM RANGE
SOUTHERN ALTAI RANGE
Lake Dzhulukul
Lake Khindiktig-Khol
Lake Ak-Khol
Lake Boguty
Lake Sorulukel
Lake Bukhtarminskoe
Lake Akkul
Chulyshman
Bogoyash
Bashkaus
Mogen-Buren
Kyzyl-Khaya
Tsagan-Nur
Ulan-Khus
Kobdo-Gol
Oigur
Oigor-Gol
Tsagan-Gol
Tashanta
Yustyt
Kokorya
Kyzylshin
Telegit-Sortogoi
Kosh-Agach
Tobeler
Dzhalgaz-Tolgoi
Kok-Erik
Ortolyk
Mukhor-Tarkhata
Chagan-Uzun
Chuya
Beltir
Saratan
Kurai
Aktash
Meny
Chibit
Iordo
Shavla
Yungur
Karagem
Argut
Belyashi
Lesosek
Dzhazator
Koksu
Ak-Alakha
Kara-Alakha
Kalguty
Argamdzhi
Bertek
Ust-Chindagatui
Bukhtarma

Table 1. Composition of local faunas of ground beetles (Coleoptera, Carabidae) of the Southeastern Altai

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
						Sayliughem Range		Ukok Plateau									
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Upper Zhumaly River	Upper Kalguty River	Mt. Maitobe	Upper Kaldzhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
1. *Cicindela* (s. str.) *altaica koschagachensis* Matalin											*6*			*6*			
2. *C.* (s. str.) *sylvatica sylvatica* L.																*e*	
3. *C.* (s. str.) *coerulea nitida* Licht.												*f*					
4. *Cylindera* (s. str.) *obliquefasciata descendens* F.-W.				*f*							*6 7, h*						
5. *Nebria* (*Boreonebria*) *changaica* Horvat.				*1 2, b*					*1 2*	*2*							
6. *N.* (*B.*) *kaszabi* Shil.	*7, a*			*1, a*													
7. *N.* (*B.*) *medvedevi* Shil.						*1*		*1, a*		*1*							
8. *N.* (*B.*) *nivalis* (Payk.)		*1 2*	*1 2 4*	*2*	*1 2 4*	*2 4*	*4*	*2*							*4*		*4*
9. *N.* (*B.*) *rufescens* (Str?m)		*4*	*4*		*4*	*4*					*6*	*6*				*6*	
10. *N.* (*B.*) *subdilatata* Motsch.											*6*				*4 6*	*6*	*4*
11. *N.* (*Catonebria*) *aenea aenea* Gebl.				*2 4*	*2 4*	*2 4*					*6*				*4 6*	*6*	
12. *N.* (*C.*) *baenningeri katunensis* Shil. et Dudko									*1*								
13. *N.* (*C.*) *fulgida* Gebl.	*2*	*2*	*2*														
14. *N.* (*C.*) *roddi* Shil. et Dudko									*1*								
15. *N.* (*C.*) *sajana sajana* Shil. et Dudko	*1*																
16. *N.* (*Eunebria*) *limbigera limbigera* Solsky											*6*						
17. *N.* (*Reductonebria*) *altaica* Gebl.		*2 4*									*6*	*6*				*6*	
18. *Notiophilus aquaticus* (L.)		*b*	*b e*	*b*	*5, b c d*	*5, a b d*	*5, b c*	*b, c*	*b*	*b*			*d*			*5, e*	*c*
19. *N. reitteri* Spaeth			*e*														
20. *Calosoma* (*Charmosta*) *investigator* Ill.	*b*																
21. *Carabus* (*Diocarabus*) *loschnikovi* F.-W.	*b*	*1, b c*	*e*	*b*								*5*	*d*				
22. *C.* (*D.*) *massagetus* Motsch.			*c e*	*b c*	*b c d*	*c d*	*c*	*c*	*3, b c d*	*b c*					*c*	*c e*	*c*
23. *C.* (*D.*) *slovtzovi mugurensis* Gott.		*b*		*b*	*b c*												
24. *C.* (*Eucarabus*) *arcensis conciliator* F.-W.			*c*								*5*						
25. *C.* (*Morphocarabus*) *aeruginosus aeruginosus* F.-W.			*e*										*d*				

Table 1 (Contd.)

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Sayliughem Range: Upper Zhumaly River	Sayliughem Range: Upper Kalguty River	Ukok Plateau: Mt. Maitobe	Ukok Plateau: Upper Kald-zhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
26. *C.* (*M.*) *mestscherjakovi teletzkianus* Shil.		*b*															
27. *C.* (*M.*) *spasskianus* F.-W.			*b*														
28. *C.* (*Scambocarabus*) *kruberi bungii* Gebler			*f*								5, *f*	*f*		*f*			
29. *Diacheila polita* (Fald.)									3								
30. *Blethisa tuberculata* Motsch.											6						
31. *Elaphrus* (*Arctelaphrus*) *lapponicus* Gyll.								3, *c d*	3	3							
32. *E.* (s. str.) *riparius* (L.)					4	4	4				6 7				4 6	6	4
33. *E.* (*Neoelaphrus*) *sibiricus* Motsch.											6 7						
34. *Loricera pilicornis* (F.)															6		
35. *Dyschiriodes* (*Eudyschirius*) *ferganensis ferganensis* (Zn.)											6 7						
36. *D.* (*E.*) *globosus* Herbst				4	4, *b c d*						6	6				6	
37. *D.* (s. str.) *chalceus* (Er.)											7						
38. *D.* (s. str.) *nigricornis* (Motsch.)															6		
39. *D.* (s. str.) *politus* (Dej.)															6	6	
40. *D.* (s. str.) *salinus striatopunctatus* (Putz.)											7						
41. *D.* (s. str.) *subarcticus altaicus* Fedor.				4							6	6			6		
42. *D.* (s. str.) *tristis* Steph.										4	6 7						
43. *Bembidion* (s. str.) *paediscum* Bat.											6					6	
44. *B.* (s. str.) *quadrimaculatum quadrimaculatum* (L.)														6			
45. *B.* (*Blepharoplataphus*) *hastii* C.R. Sahlb.	2	2 4	2 4	2 4	2 4	4	4	2		2 4					4 6	6	4
46. *B.* (*B.*) *davaai* Jedl.											6 7						4
47. *Bembidion* (*Bracteon*) *conicolle* Motsch.														6			
48. *B.* (*Chlorodium*) *almum protalmum* Net.											6				6		
49. *B.* (*Emphanes*) *axillare* (Motsch.)					4	4	*h*				6 7				6		4

Table 1 (Contd.)

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
						Sayliughem Range		Ukok Plateau									
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Upper Zhumaly River	Upper Kalguty River	Mt. Maitobe	Upper Kald-zhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
50. *B.* (*E.*) *tenellum* Er.											*7*						
51. *B.* (*Eupetedromus*) *dentellum* (Thunb.)											*6 7*						
52. *B.* (*Notaphus*) *obliquum* Sturm											*6 7*				*6*		
53. *B.* (*N.*) *pedestre* (Motsch.)										*4*	*6 7*						
54. *B.* (*N.*) *semipunctatum* (Don.)											*6*						
55. *B.* (*N.*) *varium* (Ol.)											*6 7*			*6*			
56. *B.* (*Ocydromus*) *altestriatum* Net.														*6*		*6*	*4*
57. *B.* (*O.*) *bruxellense* Wesm.				*4*													
58. *B.* (*O.*) *captivorum* Net.											*6*						
59. *B.* (*O.*) *consummatum* Bat.											*6*			*6*			
60. *B.* (*O.*) *dauricum* (Motsch.)					*4 5*, *b*	*5*, *a b*		*b*			*7*				*5*	*c*	*4*
61. *B.* (*O.*) *femoratum femoratum* Sturm											*6*					*6*	
62. *B.* (*O.*) *infuscatum* Dej.		*4*	*4*		*4*	*4*					*6 7*	*6*	*4*	*6*	*6*	*6*	*4*
63. *B.* (*O.*) pr. *infuscatum* Dej.					*4 5*						*6 7*				*6*		
64. *B.* (*O.*) *insidiosum insidiosum* Sols.						*4*					*6*			*6*	*6*	*6*	
65. *B.* (*O.*) *obscurellum turanicum* Csiki					*4*						*6 7*			*6*	*6*	*6*	
66. *B.* (*O.*) *ovale* (Motsch.)															*6*	*6*	
67. *B.* (*O.*) *pamiricola* Lutshn.											*6*			*6*			
68. *B.* (*O.*) *petrosum* Gebl.		*4*		*4*							*6*	*6*		*6*	*6*	*6*	
69. *B.* (*O.*) *poppii* Net.			*4*								*6*	*6*		*6*	*6*	*6*	*4*
70. *B.* (*O.*) *sajanum* Shil.		*4*	*4*		*4*	*4*					*6*	*6*			*6*	*6*	*4*
71. *B.* (*O.*) *scopulinum* (Kirby)						*4*					*6 7*	*6*			*6*		
72. *B.* (*O.*) *smirnovi* Kryzh.											*6*	*6*					
73. *B.* (*O.*) *yukonum* Fall					*5*												

Table 1 (Contd.)

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
						Sayliughem Range		Ukok Plateau									
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Upper Zhumaly River	Upper Kalguty River	Mt. Maitobe	Upper Kald-zhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
74. *B.* (*Terminophanes*) *mckinleyi scandicum* Lindr.			*2 4*	*4*	*2 4*		*4*				*6*	*6*			*6*	*6*	*4*
75. *B.* (*Pamirium*) *roborovskii* Mikh.					*c*		*c*										
76. *B.* (*Plataphodes*) *aeruginosum* (Gebl.)	*1 2*	*1 2*		*1 2, a*	*1 2, a*	*1, a*		*1 2, a*	*1 2 4*								
77. *B.* (*P.*) *arcticum* Lindr.					*2 4*			*4*									
78. *B.* (*P.*) *difficile* (Motsch.)					*4*						*6*		*4*		*6*	*6*	
79. *B.* (*P.*) *fellmanni* (Mnnh.)	*2*	*1 2 4*	*2 4, a*	*1 2 4*	*1 2 4*	*4*	*4*			*2 4*					*4 6*	*6*	*4*
80. *B.* (*Melomalus*) *altaicum* (Gebl.)		*4*	*4*	*4*	*4*		*4*				*6*				*6*	*6*	
81. *B.* (*Plataphus*) *coelestinum* (Motsch.)			*2*	*4*	*2*	*2 4*	*4*										*4*
82. *B.* (*P.*) pr. *coelestinum* (Motsch.)											*6*	*6*		*6*	*4 6*	*6*	*4*
83. *B.* (*P.*) *gebleri gebleri* (Gebl.)																*6*	*4*
84. *B.* (*P.*) pr. *hyperboraeorum* Munst.					*4*				*4*						*6*		
85. *B.* (*P.*) pr. *prasinum* (Duft.)											*6*				*6*		
86. *B.* (*P.*) sp.				*4*													
87. *B.* (*Semicampa*) pr. *dormeyeri* Reitt.											*6 7*						
88. *B.* (*Testediolum*) *kokandicum* Sols.											*6*	*6*		*5*		*6*	
89. *B.* (*Testedium*) *bipunctatum bipunctatum* (L.)		*2 4*		*2*	*1 2 4, b c*	*2 4, b c*	*4*		*2 4*		*6*				*4*	*6*	
90. *Pogonus* (*Pogonoidius*) *meridionalis* Dej.											*7*						
91. *P.* (*P.*) *punctulatus* Dej.											*7*						
92. *Diplous depressus* (Gebl.)		*4*	*4*	*2*	*4*						*6*			*6*	*6*	*6*	*4*
93. *Patrobus septentrionis* Dej.				*d*				*b*	*3, d*				*3 4, d*			*c*	
94. *Platidiolus rufus* Chaud.														*6*			
95. *Poecilus* (*Derus*) *abditus* (Lutshn.)											+						
96. *P.* (*D.*) *major* (Motsch.)											*7, f*	*f*					
97. *P.* (*D.*) *peculiaris* (Tschitsch.)															*g*		
98. *Pterostichus* (*Bothriopterus*) *adstrictus* Eschsch.			*c*								*5*	*5*					

Table 1 (Contd.)

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
						Sayliughem Range		Ukok Plateau									
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Upper Zhumaly River	Upper Kalguty River	Mt. Maitobe	Upper Kald-zhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
99. *P.* (*Bothriopterus*) *oblongopunctatus oblongopunctatus* (F.)											*5*						
100. *P.* (*Cryobius*) *brevicornis* (Kirby)	*a b*																
101. *P.* (*C.*) *kuraicus* Shil.	*1, a b*	*1, a*		*a*				*1, a*	*1, a*								
102. *P.* (*C.*) *lucidus* (Motsch.)	*1, a*	*b*	*1, a b*														
103. *P.* (*C.*) sp.				*1, a*	*1, a d*	*1, a b d*	*b d*	*1, a*		*a*							
104. *P.* (*Petrophilus*) *magus mongolicus* (Motsch.)			*b*														
105. *P.* (*P.*) *seriatus* Chaud.	*a b*	*1 5, a b*	*1 5, a b e*	*1, a b c d*	*5, b c d*	*1, a b c d*	*b c d*	*1, a b c d*	*1 2 3, a b c d*	*b c*			*d*			*c*	
106. *P.* (*Phonias*) *diligens* (Sturm)						*3*										*6*	
107. *P.* (*Plectes*) *drescheri* (F.-W.)			*c e*														
108. *P.* (*Platysma*) *eschscholtzii* (Germ.)											*5*						
109. *P.* (*P.*) *planicola* (Tschitsch.)											*7*						
110. *P.* (*Pledarus*) *gibbicollis* (Motsch.)											*5*						
111. *P.* (*Steropus*) *maurusiacus* (Mnnh.)																*5*	
112. *Calathus* (*Neocalathus*) *melanocephalus* (L.)	*b*															*5*	
113. *Pseudotaphoxenus dauricus* (F.-W.)			*c f*		*c*	*c*	*c*	*c*		*c*	*g*	*f*			*c*	*c*	*f*
114. *Agonum* (s. str.) *chalconotum* Mén.											*6*			*6*	*5*	*6*	
115. *A.* (s. str.) *gracilipes* (Duft.)	*1*		*f*								*g*			*e*			
116. *A.* (s. str.) *impressum* (Panz.)											*6*				*6*		
117. *A.* (s. str.) *nitidum* Motsch.																*6*	
118. *A.* (s. str.) *quinquepunctatum* Motsch.				*d*	*5, b c d*	*b c d*		*3, c*	*3, c*				*3 4, d*				*4*
119. *A.* (s. str.) *sexpunctatum* (L.)																*6*	
120. *Sericoda quadripunctata* (Deg.)	*1*																

Table 1 (Contd.)

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
						Sayliughem Range		Ukok Plateau									
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Upper Zhumaly River	Upper Kalguty River	Mt. Maitobe	Upper Kald-zhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
121. *Amara* (s. str.) *aenea* (Deg.)														*6*			
122. *A.* (s. str.) *aeneola* Popp.		*c*	*5, b f*		*b c*	*b c*	*b c*			*c*		*5*					
123. *A.* (s. str.) *bamidunyae* Bat.		*b*	*c*	*c*							*5, g*		*d*			*5*	
124. *A.* (s. str.) *biarticulata* Motsch.	*1*											*5*					
125. *A.* (s. str.) *depressangula* Popp.		*5, f*	*5, b f*		*5, c*	*c*	*c*			*c*	*5, f g*				*5, c*	*c*	
126. *A.* (s. str.) *eurynota* (Panz.)																*c*	
127. *A.* (*Amathitis*) *microdera* (Chaud.)							*c*				*g*						
128. *A.* (*A.*) *abdominalis* (Motsch.)											*7*						
129. *A.* (*A.*) *silfverbergi* Hieke											*5 6 7*						
130. *A.* (*Bradytus*) *apricaria* (Payk.)					*5*											*5, f*	
131. *A.* (*B.*) *irkutensis* Baliani		*5*				*5*					*f*						
132. *A.* (*Amarocelia*) *erratica* (Duft.)				*1, b*	*c*	*1, a*	*c*				*5*					*5*	
133. *A.* (*Celia*) *brunnea* (Gyll.)				*b c d*	*c*			*d*									
134. *A.* (*C.*) *rupicola* Zimm.					*5, b c*	*b c*	*c*				*f g*	*f*			*5, c*	*5*	*f*
135. *A.* (*C.*) *mixaltaica* Hieke												*f*					
136. *A.* (*C.*) *praetermissa* (C.R. Sahlb.)	*b*																
137. *A.* (*C.*) *saginata vilis* Tschitsch.			*f*								*5, g*	*5*			*c*		
138. *A.* (*Paracelia*) *quenseli* (Schön.)	*b*	*5, b*	*b c e*	*b c d*	*5, b c d*	*b c d*	*c*	*b c*	*c*			*5*	*d*			*6, c*	
139. *A.* (*Percosia*) *infuscata* (Putz.)			*c*	*c*		*c*	*c*	*c*	*c*	*c*	*g*	*f*	*c*			*5*	*f*
140. *A.* (*Xenocelia*) *hicksi* Lindr.				*b*													
141. *A.* (*X.*) *solskyi* (Heyd.)				*b*									*d*				
142. *Curtonotus* (s. str.) *alpinus* (Payk.)		*b*	*b*	*b*	*5, b c d*	*a b c*	*b c*	*3, b c d*	*c*	*3, b*					*c*		*c*
143. *C.* (s. str.) *conoideus* (Putz.)					*c*							*5*			*c*		
144. *C.* (s. str.) *dauricus* (Motsch.)			*f*		*c*	*c*	*4, c*				*5, f g*	*5, f*			*5, c*		*4, f*

Table 1 (Contd.)

Species	Mountain ranges and systems										Basins		Valleys of large rivers and lakes				
						Sayliughem Range		Ukok Plateau									
	Shapshal Range	Chikhachev Range	Mt. Sayliughem	Southern Chuya Range	Mt. Chernaya	Upper Zhumaly River	Upper Kalguty River	Mt. Maitobe	Upper Kald-zhin-Kul River	Southern Altai Range	Chuya Steppe	Sayliughem Steppe	Lake Dzhulukul	Chuya River	Tarkhata River	Dzhazator River	Ak-Alaha River
168. *H. salinus klementzae* Kataev				*c*							*f g*	*f*			*c*		*f*
169. *H. solitaris* Dej.																*5*	
170. *H. torridoides* Reitt.		*b*	*b c*	*a*	*5, a c*						*5, g*	*5*			*c*		
171. *H. viridanus* Motsch.	*1*				*c*	*c*	*c*			*c*	*f g*	*f*			*c*	*5, c*	*f*
172. *H. vittatus vittatus* Gebl.		*c*	*f*		*c*	*5, c d f*	*c*				*5, f g*				*c*	*5*	*f*
173. *H. xanthopus xanthopus* Gemm. et Harold				*d*												*5*	
174. *Neophygas microcephalus* (Fald.)											*g*						
175. *Ophonus* (*Metophonus*) *hystrix altaiensis* Kataev											*g*	*f*			*c*		
176. *Corsyra fusula* (F.-W.)						*c*					*g*						
177. *Paradromius* (*Manodromius*) *ruficollis* (Motsch.)				*b*	*5, b c d*	*a b c d*							*d*				
178. *Cymindis* (*Chaetotarus*) *pilosissima dshungarica* Jedl.							*c*				*f g*	*f*			*c*		
179. *C.* (*Iscariotes*) *semenowi* Jak.											*h*						
180. *C.* (*Paracymindis*) *rostowtzowi rostowtzowi* Tschitsch.					*c*						*g*					*c*	
181. *C.* (*Tarsostinus*) *binotata* F.-W.		*c*	*5, c f*	*c*	*c*	*c*	*c*	*c*		*c*	*5, f g*	*5, f g*			*c*	*c f*	*f*
182. *C.* (*Tarulus*) *vaporariorum* (L.)		*c*	*b e*	*b*	*5, b c d*	*c*		*d*		*b*			*c*		*c*	*5*	
183. *Microlestes minutulus* (Goeze)											*5*			*f*			
184. *M. schroederi* Hold.											*g*						
185. *Apristis striatus* (Motsch.)			*4*											*6*			
Total number of species	23	32	46	48	59	44	38	26	18	24	98	42	17	26	58	67	37

Notes: Zonal plant communities: the nival belt (*a*), moss-lichen tundras (*b*), steppe-like meadow tundras (*c*), dwarf birch tundras (*d*), larch forests (*e*), dry sod-grass steppes (*f*), desertified steppes (*g*), and dry saline areas (*h*). Intrazonal plant communities: periphery of snowfields (1), banks of rivers and lakes in high mountain areas (2400–3000 m) (2), sedge-cottongrass bogs (3), banks of rivers and lakes in medium mountain areas (2000–2400 m) (4), valley series, i.e., shrub-meadow associations (5), banks of rivers and freshwater lakes in intermountain basins (1700–2000 m) (6), and banks of saline lakes in intermountain basins (1700–2000 m); + means that the species is cited by the original description only, without indication of a particular plant community.

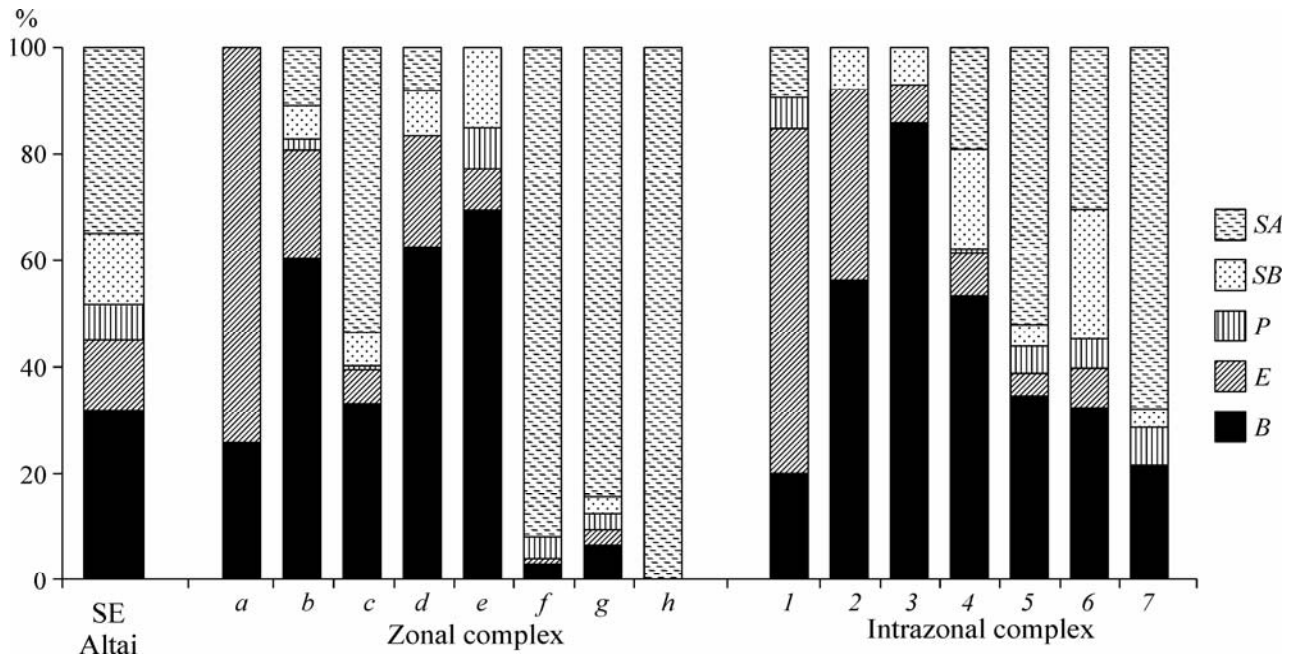

Fig. 2. An arealogical spectrum of ground beetles in the Southeastern Altai as a whole and in plant communities of the zonal (*a–h*) and intrazonal (*1–7*) series. Species groups: *SA*, subarid; *SB*, subboreal; *P*, polyzonal; *E*, Altai-Sayan endemics; *B*, boreal. The plant communities are designated as in Table 1.

species (Dudko et al., 2002; Ivanov and Dudko, 2006).

The Arealogical Composition

The carabid fauna of SEA is mostly formed by subarid (65 species, 35% of SD) and boreal (59 species, 32% of SD) elements. The impact of subboreal species and the Altai-Sayan mountain endemics is noticeably smaller: 24 species, 13% of SD each. The same is true of the polyzonal species: 13 species, 7% of SD (Fig. 2).

Most of the boreal species are characterized by very extensive distribution: 30 of them are circum-boreal (*Nebria rufescens*, *Notiophilus aquaticus*, *Diacheila polita*, *Elaphrus lapponicus*, *Patrobus septentrionis*, etc.). Only few species of this group are absent in the Western Palaearctic (*Bembidion arcticum*, *Amara hicksi*) or in the Eastern Nearctic (*Bembidion dauricum*, *Amara brunnea*). A considerable group of 16 species is characterized by broad Palaearctic distribution (*Cicindela sylvatica*, *Notiophilus reitteri*, *Elaphrus riparius*, *Amara praetermissa*, etc.). Among the rest of the Palaearctic species, 6 occur only in the Central Palaearctic (*Carabus loschnikovi*, *C. aeruginosus*, *C. mestscherjakovi*, *Pterostichus drescheri*, *P. maurusiacus*, and *Amara solskyi*), 4 in the Western and Central (*Bembidion bipunctatum*, *B. bruxellense*, *B. difficile*, *Pterostichus diligens*), and 3 in the Central and Eastern Palaearctic (*Bembidion conicolle*, *Platidiolus rufus*, and *Harpalus torridoides*). It should be noted that other parts of the Altai show a noticeably smaller fraction of circum-boreal species and a much greater fraction of Western Palaearctic ones (Kovrigin, 1984; Khmel'kov and Kovrigin, 1985; Dudko and Lomakin, 1996; Dudko et al., 2002; Ivanov and Dudko, 2006).

The subarid group is not uniform. More than half of its species (36) are the Mongolian faunistic elements (*Carabus kruberi*, *Bembidion pedestre*, *B. infuscatum*, *Dicheirotrichus roborowskii*, *Harpalus pusillus*, etc.). A somewhat smaller subgroup (21 species) unites the beetles with broad Ancient Mediterranean ranges (*Cylindera obliquefasciata*, *Dyschiriodes salinus*, *Bembidion petrosum*, *Pogonus meridionalis*, *P. punctulatus*, etc.). The ranges of 8 more species lie mostly in Central Asia, their eastern parts reaching the Altai, Tuva, Western Mongolia (*Nebria limbigera*, *Bembidion almum*, *B. insidiosum*, *B. pamiricola*, *B. kokandicum*, *Agonum chalconotum*, and *Amara bamidunyae*) and, less frequently, Eastern Siberia (*Dyschiriodes ferganensis*).

Most of the subboreal species (*Nebria subdilatata*, *Elaphrus sibiricus*, *Bembidion paediscum*, *B. semipunctatum*, *B. altestriatum*, *B. altaicum*, *B. coelestinum*, *Diplous depressus*, *Agonum impressum*, etc.)

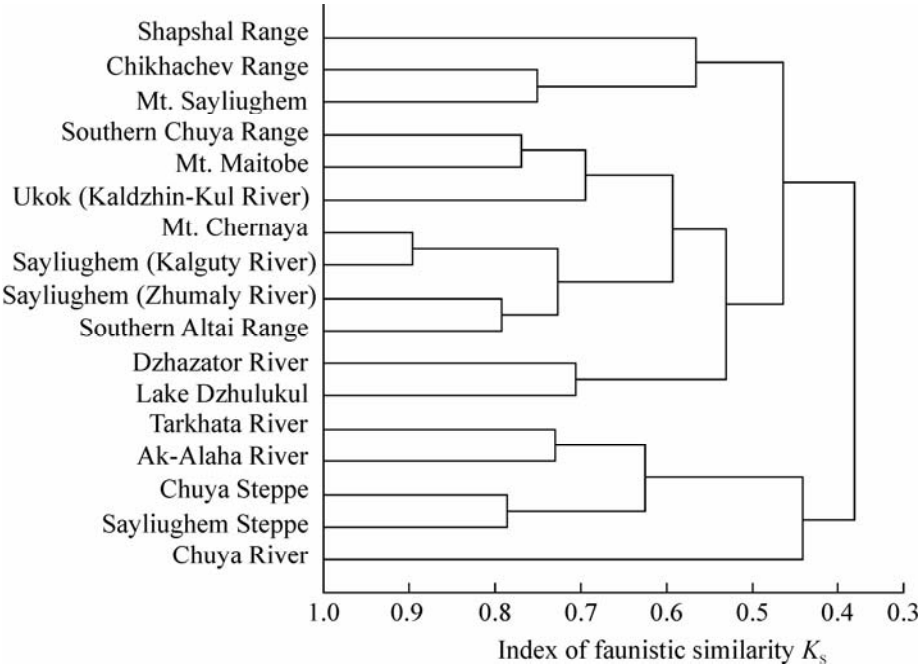

Fig. 3. Similarity dendrogram of the local carabid faunas in Southeastern Altai.

present in SEA are associated with banks of rivers and lakes. However, some species of this group (*Carabus massagetus*, *Pterostichus eschscholtzi*, *P. gibbicollis*, and *Amara microdera*) are more typical of the adjacent regions with a distinct forest-steppe belt. Three more species (*Calosoma investigator*, *Amara eurynota*, *Harpalus rubripes*), recorded only on the boundary of SEA, prefer more humid areas.

Only 13 polyzonal species have been recorded: *Dyschiriodes tristis*, *Bembidion quadrimaculatum*, *B. varium*, *B. femoratum*, *Calathus melanocephalus*, *Agonum gracilipes*, *A. sexpunctatum*, *Sericoda quadripunctata*, *Amara aenea*, *A. apricaria*, *Harpalus affinis*, *H. calceatus*, and *Microlestes minutulus*. Almost all of them are quite rare or have been found on the boundary of SEA (in the Chuya and Dzhazator valleys, and in the Shapshal Range).

Most of the 24 Altai-Sayan endemics occur in high and medium mountain areas. This group includes both local (*Nebria roddi*, *N. medvedevi*, *Pterostichus* (*Cryobius*) sp.) and relatively broadly distributed species (*Nebria changaica*, *N. kaszabi*, *N. aenea*, *N. baenningeri*, *N. fulgida*, *N. sajana*, *N. altaica*, *Carabus slovtzovi*, *C. spasskianus*, *Bembidion roborovskii*, *B. aeruginosum*, *B*. pr. *hyperboraeorum*, *Pterostichus kuraicus*, *P. lucidus*, and *P. seriatus*). Only *Bembidion smirnovi*, *Poecilus peculiaris*, *Amara mixaltaica*, *Cicindela altaica koschagachensis*, and *Ophonus hystrix altaiensis* inhabit low mountains and intermountain basins. The last two subspecies are endemic to the Chuya basin.

The Distribution of Species in the Region

In order to characterize the non-uniform distribution of species in the region, we have distinguished 17 carabid faunas, 10 of which correspond to the mountain ranges, 5 to the valleys of large rivers and lakes separating the ranges, and 2 to the Chuya and Sayliughem basins.

According to the results of cluster analysis, the faunas of the mountain ranges are quite similar and noticeably separated from those of the intermountain basins and river or lake valleys (Fig. 3).

The "mountain" cluster can be subdivided into two groups that correspond to the ranges surrounding the Chuya Basin in the south and in the northeast. The most similar are the local faunas of the Southern and Central Ukok (Southern Altai and Sayliughem Ranges, Mt. Maitobe), and the Chernaya mountain mass located to the north of Sayliughem Range. The complex of the Southern Chuya Range, one of the largest ranges of SEA characterized by considerable diversity of natural conditions, is somewhat more detached (Fig. 4, *1*). In particular, its western part, belonging to the Central Altai, is occupied by vast areas of larch forests. On the contrary, the eastern part has only isolated larch stands and dwarf larch thickets alternating with large fragments of alpine meadows. Owing to this

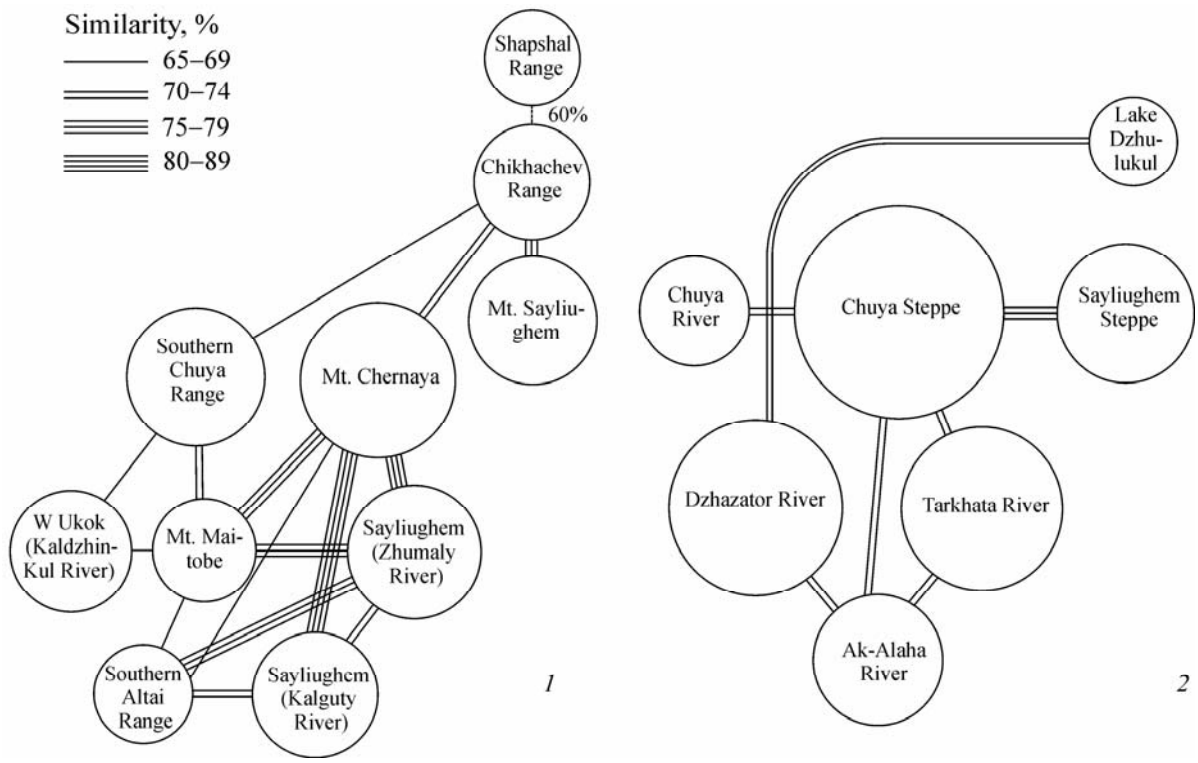

Fig. 4. Similarity graphs of the local carabid faunas of mountain ranges (*1*) and intermountain valleys (*2*) of Southeastern Altai. The area of the circles is proportional to the number of species in the corresponding local fauna; the similarities of less than 65% are not shown.

diversity, the fauna of the Southern Chuya Range includes some species that are absent or rare in most other localities: *Amara hicksi*, *A. solskyi*, *Harpalus nigritarsis*, *H. xanthopus*, *Paradromius ruficollis*, etc.

Among the ranges located to the northeast of the Chuya Basin, the most specific carabid fauna can be found in the northernmost Shapshal Range (Fig. 4, *1*). However, the isolated position of this fauna may be somewhat overestimated due to insufficient level of knowledge, since material from this area was collected only in late July. Moreover, some species not typical of high mountain areas (*Calosoma investigator*, *Calathus melanocephalus*, *Agonum gracilipes*, *Sericoda quadripunctata*, *Amara biarticulata*, *Harpalus optabilis*, *H. calceatus*, *H. amplicollis*, and *H. fuscipalpis*) were found in the Shapshal Range, the last 3 species being quite abundant up to 2900 m above sea level. These findings may be accounted for by mass migration from the habitats located far down the slope, facilitated by the ascending air currents; a similar phenomenon was reported for *Harpalus griseus* in China (Feng et al., 2007). In view of this, the above species may be regarded as "accidental" inhabitants of the alpine areas, in the terminology of Semenov-Tian-Shansky (1937).

Only few species associated with middle and high mountains have been found in all or nearly all the ranges of SEA. Among them, the Altai-Sayan endemic *Pterostichus seriatus* reaches considerable abundance in most variants of mountain tundras. Other common forms are the boreal species *Notiophilus aquaticus*, *Bembidion hastii*, *B. fellmanni*, *Amara quenseli*, *Curtonotus alpinus*, *Cymindis vaporariorum*, the subarid species *Carabus massagetus*, *Curtonotus fodinae*, *Harpalus pusillus*, *Cymindis binotata*, and the Altai-Sayan endemic *Bembidion aeruginosum*.

The intermountain basins and large river valleys form a single isolated cluster. Only the Dzhazator River valley and the Dzhulukul Lake basin belong to the cluster of the ranges and detached mountain areas, although being quite distinctly separated within the latter (Fig. 3).

The greatest diversity is characteristic of the carabid fauna of the Chuya Steppe, which comprises 98 species. It includes almost all the subarid species (57 out of 65), whereas the boreal forms are less numerous (17 species) and occur only in the intrazonal biotopes: along the banks of rivers and lakes. The fauna of the Sayliughem Steppe is very similar to that of the Chuya Steppe (Fig. 4, *2*) but comprises a noticeably smaller

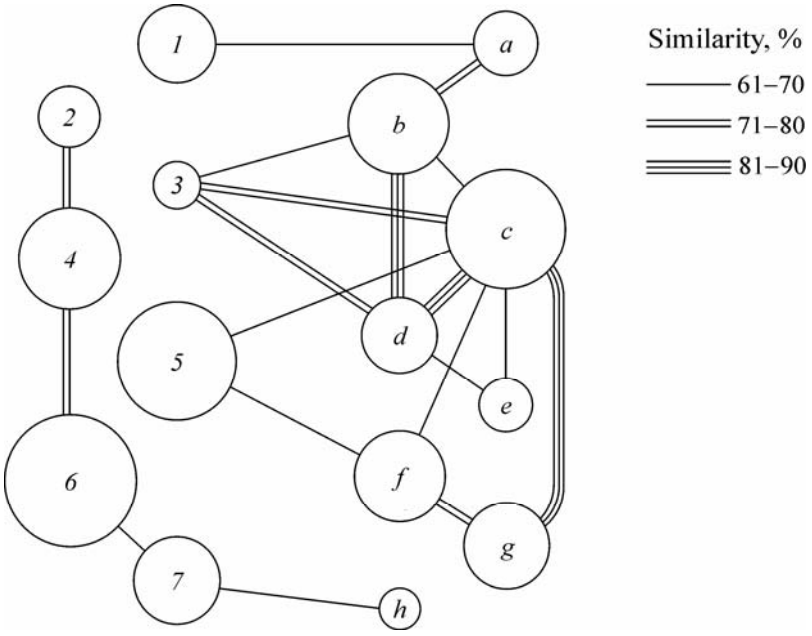

Fig. 5. Similarity graph of carabid assemblages of plant communities of the zonal (*a–h*) and intrazonal (*1–7*) series. The plant communities are designated as in Table 1. The area of the circles is proportional to the number of carabid species in the corresponding communities; the similarities of less than 61% are not shown.

number of species (42). The similar faunas of the Tarkhata and Ak-Alaha river valleys are clustered together with those of the Chuya and Sayliughem basins, even though their fractions of boreal species are almost twice as great as in the Chuya Steppe (Fig. 3).

The carabid fauna of the Chuya River valley is the most similar to that of the Chuya Steppe and clearly separated from other faunas. The faunas of the Dzhazator River and Lake Dzhulukul valleys are even more strongly separated from the "valley" cluster and grouped together with the "mountain" cluster (Fig. 3). Their specificity can be explained by their position on the boundary with the Central Altai and the presence of vast areas of larch forests. As a result, the faunas of these valleys include most of the forest species which are otherwise uncharacteristic of SEA (*Cicindela sylvatica*, *Bembidion paediscum*, *B. quadrimaculatum*, *B. conicolle*, *B. femoratum*, *Pterostichus diligens*, *P. maurusiacus*, *Calathus melanocephalus*, *Agonum nitidum*, *A. sexpunctatum*, *Amara aenea*, *A. eurynota*, *A. apricaria*, *Dicheirotrichus cognatus*, *Harpalus affinis*, *H. latus*, *H. oodioides*, *H. rubripes*, *H. solitaris*, and *H. xanthopus*).

The Landscape distribution

During analysis of the carabid fauna of SEA, we have considered both the zonal and the intrazonal complex (Table 1), even though this subdivision is largely conditional. Although the intrazonal complex consists mostly of the inhabitants of periaquatic stations, many meadow and field-meadow species can also be included into it, if the trans-zonal nature of their stations, determined by the similarity of conditions in different soil and climatic zones, is taken into account. This is even more true for the mountain areas, where the different altitudinal belts may be indistinctly separated in space. At the same time, many intrazonal species are associated with a particular zone or belt, though to a much lesser extent than the zonal species.

The Zonal Complex

The nival belt is characterized by the lowest diversity of the ground beetle fauna, which comprises only 15 species (Table 1), including 8 boreal ones and 7 endemic to the Altai-Sayan mountain system. However, most of the species typical of his belt are mountain endemics, comprising 74% of the average local fauna (Fig. 2*a*). Typical nival forms are species of the genus *Pterostichus*, subgenus *Cryobius*: *P. kuraicus* and *Pterostichus* sp., and also some species of the genus *Nebria*, such as *N. medvedevi* and *N. kaszabi*. Other inhabitants of the nival belt can also be found in moss-lichen (*Paradromius ruficollis*, *Pterostichus lucidus*) or true tundras (*Notiophilus aquaticus*, *Pterostichus brevicornis*), or occur in all or nearly all the tundra formations, including the mesophytic vari-

ants of steppe-like meadow tundras (*Bembidion dauricum*, *Pterostichus seriatus*, *Curtonotus alpinus*, *Amara erratica*, and *Harpalus torridoides*). Apart from the above species, two representatives of the genus *Bembidion* occur in the nival belt; one of them (*B. aeruginosum*) is a typical inhabitant of the banks of lentic reservoirs, whereas the other (*B. fellmanni*) occurs on the banks of rapid rivers and streams in the high and middle mountain areas.

The faunas of moss-lichen tundras are much richer in the species composition (40 species from 16 genera) and diversity (Table 1). The dominant groups are the boreal species (60% of SD) and the mountain endemics (20%). The combined fraction of the subboreal, polyzonal, and subarid species does not exceed 20% (Fig. 2*b*). The typical species of moss-lichen tundras are *Carabus loschnikovi*, *C. slovtzovi mugurensis*, *Pterostichus lucidus*, *P. seriatus*, *Amara solskyi*, *A. erratica*, *Curtonotus alpinus*, *Agonum quinquepunctatum*, and *Cymindis vaporariorum*. The dwarf larch communities, occupying considerable areas in some parts of the region, have a similar arealogical and species composition but are distinguished by a small number of species (21) and low density of the carabid population.

In the course of transition to the steppe-like variants of meadow tundras, the true tundra carabid species are quickly replaced by the meadow-steppe and mountain steppe ones. Species of the former group (*Pterostichus seriatus*, *Curtonotus alpinus*, *Carabus massagetus*, and *Dicheirotrichus mannerheimi*) are still present under relatively mesophytic conditions but quickly disappear as the soil becomes moisture deficient and the meadow tundra aspect changes for that of desertified steppes or even semi-deserts. On the contrary, the number of steppe species in the communities increases abruptly. Such species are many representatives of the genera *Amara*, *Curtonotus*, and *Harpalus*, first of all *A. rupicola*, *A. infuscata*, *A. microdera*, *C. fodinae*, *C. dauricus*, *C. conoideus*, *H. amariformis*, *H. viridanus*, *H. pusillus*, *H. macronotus*, *H. obtusus*, and also *Cymindis binotata* and *C. rostowtzowi*, a bothrobiont beetle *Pseudotaphoxenus dauricus* and a xerophilic species with some bothrobiont traits, *Bembidion roborowskii*. All these species except the last one occur in a very wide range of biotopes: from floodland areas with meadow-like vegetation to desertified steppes in the Chuya Basin. Some of them (*C. fodinae* and *H. pusillus*) extend into the moss-lichen tundras as well.

The steppe-like meadow tundras also noticeably differ from moss-lichen ones in arealogical composition. The subarid species clearly prevail (53% of SD) but the boreal ones retain their influence (33% of SD) (Fig. 2*c*). The steppe-like meadow tundras of SEA may be regarded as a kind of a buffer zone between the different habitats. However, even though these plant communities are characterized by the maximum species diversity of ground beetles, they have almost no typical species of their own. In general, the steppe-like variants of meadow tundras show high similarity with all the adjacent communities of the zonal complex and even with some intrazonal habitats (Fig. 5).

A considerable contribution to the carabid fauna of SEA is made by the dry desertified steppes of the Chuya Basin and the foothills of the mountain ranges surrounding it. The xerophilic beetles *Carabus kruberi*, *Poecilus peculiaris*, *Harpalus fuscipalpis*, *H. salinus klementzae*, *Amara saginata*, *A. abdominalis*, *A. silfverbergi*, *Ophonus hystrix altaiensis*, *Neophygas microcephalus*, *Corsyra fusula*, *Cymindis pilosissima* and the halophilic species *Cymindis semenovi* and *Poecilus major* were found only in these localities. The beetles *Cicindela coerulea nitida* and *C. altaica koshagachensis*, typical of the steppe zone, should be added to the above list. The desertified steppes are generally dominated by subarid species, comprising from 85 to 100% (Fig. 2*f*–2*h*).

The forest belt is completely absent in SEA. Small areas of larch stands occur only on Mt. Sayliughem and the territories bordering the Central Altai. The fauna of ground beetles is very poor in these areas (as contrasted to other regions of the Altai and Sayan Mountains where the forest belt is sufficiently well developed). It includes only 11 species with mostly boreal distribution, 4 of which (*Cicindela sylvatica*, *Notiophilus reitteri*, *Carabus aeruginosus*, and *Pterostichus drescheri*) are typical taiga-dwelling forms.

The Intrazonal Complex

The fauna of the banks of high mountain lakes and rivers is quite poor, including only 14 species. However, half of these species (*Nebria fulgida*, *N. changaica*, *N. nivalis*, *Bembidion aeruginosum*, *B. bipunctatum*, *B. coelestinum*, and *B. fellmanni*) are typical of these particular habitats, while some of them (most *Nebria* species and *B. aeruginosum*) also occur near the permanent and temporary snowfields. A much greater number of species can be found on the banks of reservoirs located below the alpine belts, down to

the bottom of the Chuya Basin. Such transregional forms are *Nebria aenea*, *N. altaica*, *Bembidion mckinleyi scandicum*, *B. fellmanni*, *B. hastii*, *Diplous depressus*, etc. The arealogical spectrum includes only three groups: the boreal, subboreal, and Altai-Sayan endemic (Fig. 2, *2*).

The species diversity of periaquatic ground beetles increases down the slope. As the altitude is reduced, the subarid (*Blethisa tuberculata*, *Bembidion consummatum*, *B. axillare*, *B. pedestre*, *B. infuscatum*, etc.) and subboreal species (*Nebria subdilatata*, *Elaphrus sibiricus*, *Bembidion poppii*, *B. asiaticum*) appear and steadily increase their impact. The fraction of mountain endemics decreases abruptly, comprising only 8% of SD already in the middle mountain areas. The boreal species remain quite numerous at these altitudes (53% of SD), whereas in the intermountain basins their fraction does not exceed 35% (Fig. 2, *4*, *6*).

The fauna of the banks of saline lakes is quite specific due to a typical set of halophilic species: *Dyschiriodes chalceus*, *D. salinus*, *Bembidion tenellum*, *Pogonus meridionalis*, *P. punctulatus*, *Poecilus major*, *Pterostichus planicola*, *Amara abdominalis*, and *Dicheirotrichus abdominalis* (Fig. 5). At the same time, these communities include many low-mountain hygrophilic species resistant to salification.

A number of stenotopic species, mostly of the genera *Nebria* and *Pterostichus*, are associated with permanent and temporary snowfields typical of the upper altitudinal belts. Apart from them, the snowfield communities include the cryophilic species of the genus *Bembidion* (which occur near all the available sources of moisture in the alpine areas), and also *Pterostichus seriatus* and *Amara erratica*, typical of the various kinds of mountain tundras. Since all the stenotopic ground beetle species occurring near the snowfields in SEA belong to the group of mountain endemics, this group prevails in the arealogical spectrum (Fig. 2, *1*). The snowfield ecotones are similar to the nival belt in the species composition and clearly isolated from all the remaining habitats (Fig. 5).

A poor but specific fauna is characteristic of sedge-cottongrass bogs, one of the commonest type of plant communities in the middle and high mountains of SEA. It includes only 8 species of ground beetles, 6 of which represent the boreal group (Fig. 2, *3*), including 5 species with circum-Arctic ranges (*Diacheila polita*, *Elaphrus lapponicus*, *Patrobus septentrionis*, *Agonum quinquepunctatum*, and *Curtonotus alpinus*). In the species composition of Carabidae, the sedge-cottongrass bogs are clustered together with the zonal tundra variants and distinctly isolated from the intrazonal habitats (Fig. 5).

A special position among the intrazonal complexes is occupied by the floodland shrub and meadow stations, also termed the valley series (Ogureeva, 1980). They provide favorable conditions for many species, from the tundra and steppe ones, generally typical of the region, to the meadow-steppe (*Amara apricaria*, *Curtonotus harpaloides*) and even forest ones (*Pterostichus adstrictus*). In general, the valley series are characterized by a high species diversity of ground beetles (55 species), especially those of the Ancient Mediterranean origin (Fig. 2, *5*). It should be noted that under the conditions of moisture deficiency, many steppe species also concentrate in river floodlands, where they may become even more abundant than in the zonal communities.

CONCLUSION

In its composition and aspect, the ground beetle fauna of SEA distinctly contrasts with the faunas of the adjacent Western and Central Altai, differing from them in a number of specific features. The difference is largely determined by an almost complete absence of the forest belt with many of its typical species. Even though the fauna as a whole has a steppe aspect, it includes few true steppe, forest-steppe, or meadow-steppe species. Species of the genus *Trechus*, quite common and diverse in the rest of the Altai region as well as the West Sayan (Dudko, 1998), are completely absent in the region in question. At the same time, SEA reveals a rich and specific complex of periaquatic ground beetles, mostly of the genus *Bembidion*. In particular, the group of *B. lunatum* is the most fully represented in SEA were it comprises seven sympatric species.

The arealogical spectrum is characterized by the prevalence of the subarid and boreal species groups. The polyzonal species are few in number and quite scarce. The subboreal group is noticeably impoverished as compared to other parts of the Altai-Sayan mountain system and mostly includes the periaquatic species. The specificity of the regional carabid fauna is enhanced by a moderate fraction of mountain endemics (13% of SD). Their impact is especially large (up to 80% of SD) in such extreme habitats as the nival belt and the periphery of snowfields.

In general, the ground beetle fauna of SEA can be clearly subdivided into two components: the fauna of the Chuya Basin and that of the surrounding mountain ranges.

The mountain fauna is boreal by origin. Its core mostly consists of the species associated with the tundra belt, many of which have circum-boreal or circum-Arctic ranges. The replacement of true meadow tundras with the various steppe-like variants, imparting a steppe or semi-desert aspect to the middle mountain landscapes, has allowed many steppe species to expand into these stations and to replace, partly or completely, the tundra-dwelling forms. The faunas of the southern and northeastern mountain ranges are generally similar, the former having a smaller fraction of boreal faunistic elements and a larger fraction of subarid (including Mongolian and steppe) ones. This difference may be partly accounted for by the presence of some boreal forms in the northeastern mountain areas, which are absent in the south. The local faunas of some ranges are made more specific by the presence of alpine species (mostly of the genus *Nebria*) with a mosaic distribution on the peaks.

On the contrary, the fauna of the Chuya and the adjacent Sayliughem basins has an Ancient Mediterranean, Mongolian origin. It includes relatively few boreal forms even in the intrazonal communities. The core of the fauna is formed by the typical Mongolian species and those broadly distributed in the Ancient Mediterranean region, their combined impact being 50% of the species diversity.

Thus, SEA is a heterogeneous region from the zoogeographical viewpoint. This conclusion agrees with the opinions of most researchers (Tulikova, 1982; Malkov et al., 1996; Bondarenko et al., 1999; Dolgovykh et al., 2001; Dolgovykh, 2005). However, the problem of delimitation of specific biogeographic subdivisions, or chorons, remains open. For example, in the regionalization scheme based on plant geography (Ogureeva, 1980), the entire territory of SEA, including the ranges surrounding the Chuya Basin, was assigned to the Mongolian Province of the Ancient Mediterranean Region. In the scheme based on entomological material (mostly Coleoptera – Kryzhanovskiy, 2002), only the Chuya Basin proper was assigned to this province; this variant is more consistent with our data.

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