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Ground Beetles (Coleoptera, Carabidae) of the Ola Plateau Highlands, Kolyma Uplands

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Abstract—The ground beetle fauna was studied in 12 biotopes of the tundra belt on Ola Plateau, 130 km NW of Magadan. In all, 16 species were found above timber line (900–1220 m), which is comparable with the diversity in the mountain tundras of the upper reaches of the Kolyma (Berman et al., 1984; Bukhkalo, 1997), but the faunistic similarity of these regions is low (Jaccard's coefficient 22–29%). Besides the widespread species, a group of ground beetles with limited ranges is present; it includes *Carabus kolymensis* Lafer, 1989 occurring in the East Siberian mountain tundras, the Siberian-Nearctic, mainly arctic *Pterostichus agonus* G. Horn, 1880, and the East Siberian *Pterostichus eximius* A. Mor., 1862. The use of the term "arctic species" in arealogical and ecological studies is discussed.

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The category "arctic species" is used in the literature in rather different ways (see Chernov and Matveyeva, 2002), and its geographic (arealogical) and landscape-zonal (reflecting the environmental "optimum" for the species) aspects are often confused. It seems that this category should never be used without special explanation. Difficulties arise even in characterizing the boundaries of species ranges, since a number of "mainly arctic species," "arctic species in a broad sense" (Chernov and Matveyeva, 2002), and "species of the arctic fraction" (Sekretareva, 2004) are actually present not only in zonal tundras and metaarctic mountain systems, such as the Khibiny, Polar Urals, Putorana, Verkhoyansk Range, etc., but also in much more southern areas, such as the south Siberian and Mongolian mountains (see, e.g., Kuznetsov, 1938; Shtegman, 1938; Gorodkov, 1979, 1992; Konstantinova, 2000; Sekretareva, 2004; Dudko and Sambyla, 2005; Chernov and Tatarinov, 2006; Marusik and Eskov, 2009). For a long time, the ranges of species inhabiting the Arctic could not be analyzed due to the poor state of knowledge of the insects and arachnids of South and East Siberia and Northeast Asia. The modern state of knowledge allows us to discuss this problem.

Data on the ground beetle fauna of the Ola Plateau, situated on the Okhotsk macroslope of Northeast Asia, may be used in the study of this problem. The well-studied flora of the vascular plants of this region includes many species that are mainly distributed in the zonal and mountain metaarctic tundras but absent in other districts of the Kolyma Uplands (Khokhryakov and Yurtsev, 1974; Yurtsev and Khokhryakov, 1975; Khokhryakov, 1985). The Ola Plateau was characterized as a some kind of "refuge" of relict arctic plant species (Khokhryakov, 1989). In view of this, arealogical analysis of other taxa, in particular the relatively well-known ground beetles, seems promising.

The order Coleoptera, the largest order of animals (Zhang, 2011), includes about a hundred arctic species (Chernov and Makarova, 2008) in a broad sense (following Chernov and Matveyeva, 2002). The Arctic fauna shows a disproportionate predominance of species of carabids and diving beetles, as compared with other beetle families (Chernov, 1992; Chernov and Makarova, 2008). The family Carabidae is represented in high latitudes by approximately 200 species, about 70 of which are specialized cryophilic forms (Chernov et al., 2000, 2001).

No studies of ground beetles of the Ola Plateau have been carried out before. Therefore we found it pertinent to publish the results of our small collections made in early August 2011.

The Ola Plateau is situated 130 km from the Sea of Okhotsk coast, to the northwest of Magadan. It occupies the area of about 100 km^2 (Yurtsev and Khokhryakov, 1975) and consists of flat-topped mountains (Fig 1, *1*) mainly formed by Tertiary basalts, with a well-developed river net. The mean altitudes of the plateau are 1100–1600 m (hereafter, all the altitudes are given above sea level), with some peaks reaching 2000 m. The tundra belt in the study district (the upper reaches of the Ola River, 60°39′N, 151°16′E) begins from 900–1200 m, depending on the slope orientation. Beetles were collected on 7–12 August 2011 using soil traps (250-ml plastic glasses with the upper diameter 65 mm) filled with water by one-third. In each biotope, 10–20 traps were placed for 3–5 days and checked every 1–2 days. Altogether, 15 biotopes were examined, situated in the following areas:

(a) in the forest belt of the Ola valley, 820–980 m: a willow grove in the floodland (figure, *2*), a willow bog, and a larch forest;

(b) along the bed of a nameless stream, at the timber line, 985–1149 m: an alder grove (figure, *3*), a wet meadow, a mossy cliff, meadow patches in the stream bed, and a snowbed at different altitudes (I–III, figure, *4*, *5*);

(c) on the upper terraces of a cirque slope, 1227–1470 m: a grass meadow, a forb meadow with abundant legumes (figure, *6*), a nival community with *Cassiope tetragona*, a dryas-forb tundra (figure, *7*), and a ridge-top dryas-moss tundra (figure, *8*).

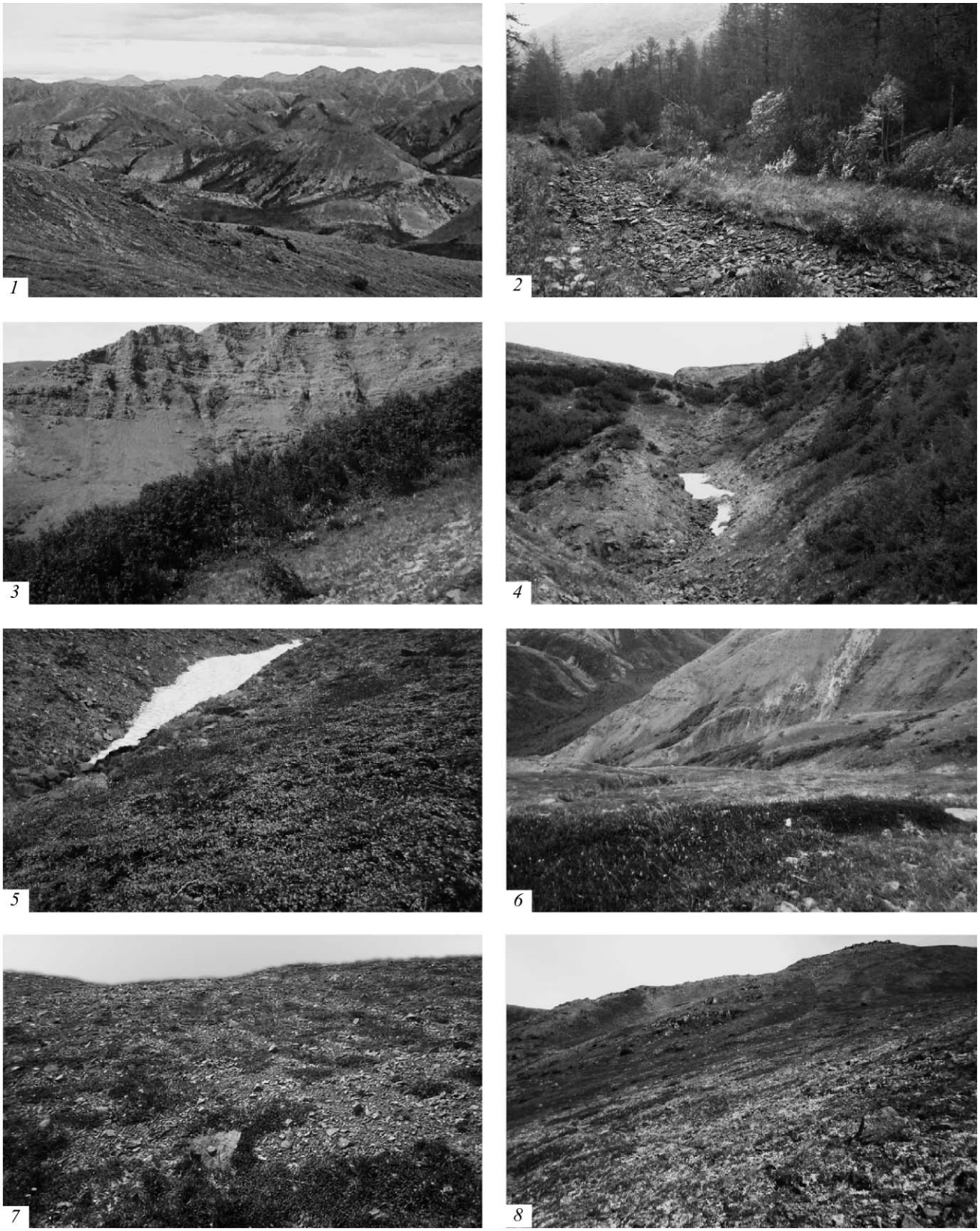
The total material comprised 130 adult ground beetles and 33 larvae captured in 835 trap-days. Their ranges were analyzed using the catalogues (Bousquet, 1991; Kryzhanovskij et al., 1995; Ball and Currie, 1997; Zinoviev and Olshvang, 2003; Silfverberg, 2004) and the updatable database of Carabidae of the former SSSR (Makarov et al., 2012), a brief variant of which is available on the website of the Zoological Institute of the Russian Academy of Sciences.

The Composition of the Fauna and the Catch Indexes

No ground beetles were found in the traps located in the forest belt and on the mossy cliff above the stream. Sixteen species were found above the timber line (table), which is comparable with the diversity revealed during the 3–4-year study in the mountain tundras in the Kolyma upper reaches at the "Aborigen" field stations (20 species) (Berman et al., 1984) and "Kontakt" field station (12 species) (Bukhkalo, 1997). These two localities are situated about 100 km apart and 180 and 220 km from the Ola Plateau, respectively. The faunistic similarity (Jaccard's coefficient) between the highlands of the study district and those of the upper Kolyma mountain tundras was only 22–29%, whereas the similarity between the two stations was greater, 48%. The species present in the tundras of all the three district were: the widespread *Notiophilus aquaticus*, *Agonum quinquepunctatum*, and *Dicheirotrichus mannerheimii*, as well as the mainly arctic *Pterostichus agonus* and the East Siberian mountain species *Carabus kolymensis*.

The low similarity of the ground beetle species composition in the Ola Plateau highlands and the fairly close upper Kolyma localities can be attributed to a considerable difference in their soils and vegetation. The mountain tundras in the vicinity of the Aborigen station have developed on granites which disintegrate into druss, therefore they have acidic and well-drained soils. The mountains in the region of the Kontakt station mainly consist of shale rock, therefore the dominant highland landscapes also have humid acidic soils and low vegetation diversity. The Ola Plateau differs sharply from both districts of the upper Kolyma in the unique alkalinity of soil-forming materials and, correspondingly, in the soil acidity value close to neutral one. This factor, in turn, has determined the dominance or considerable participation of meadow elements in the vegetation.

Up to 7 species of ground beetles were found in individual biotopes, but 5 out of 15 localities revealed only 1 species each. The mean catch index on the ridge-top terraces of the plateau (2.4 ind./10 trap-days) was a little higher than in the stream valley with a snowfield (1.9 ind./10 trap-days), where larvae (mainly of *Nebria frigida* and *Notiophilus aquaticus*) comprised almost half the sample, possibly due to a later beginning of the active periods here. These values were rather close to those reported for the mountain tundras of the upper Kolyma area (Berman et al., 1984; Bukhkalo, 1997). The greatest catch indices and/or the number of species were recorded in the near-top dryas-moss tundra (7.1 ind./10 trap-days, 7 species) and isolated meadow patches in the stream bed (8.0 ind./10 trap-days, 3 species), where the onset



The Ola Plateau and the biotopes studied, August, 2011: (*1*) view of the plateau from the cirque top; (*2*) a willow grove in the Ola floodplain; (*3*) a shrub alder stand on the slope; (*4, 5*) a snowbed in the stream gully (levels I and II, respectively; see table); (*6*) a forb meadow with abundant legumes on the terrace; (*7*) a dryas-forb tundra on the terrace; (*8*) watershed dryas-moss tundra.

Findings of ground beetle species (number of ind.) in the biotopes of the tundra belt, the upper reaches of the Ola, Magadan Province, 7–12.VIII.2011

Species	Terraces; altitude, m					Stream valley; altitude, m					
	1470	1278	1275	1270	1227	1149	1127	1023	1005	1007	985
	Dryas-moss tundra	Dryas-forb tundra	Snowfield with *Cassiope tetragona*	Grass meadow	Meadow with legumes	Snowfield III (*Rhododendron redowskiana*)	Snowfield II (*Salix reticulata*)	Snowfield I (*Oxyria digyna*)	Meadow patches in stream bed	Wet meadow on slope	Alder stand in floodplain
Nebria* (*Boreonebria*) *frigida R. Sahlb., 1844								1 (2)	(10)		1 (4)
Notiophilus aquaticus (L., 1758)	2					(6)	1(3)	(3)	1		
Carabus* (*Morphocarabus*) *odoratus magadanicus Obydov, 1999	1 (2)										
C.* (*Aulonocarabus*) *kolymensis viridicupreior Deuve et Mourzine, 1993	6	3		(1)							
C.* (*Megodontus*) *vietinghoffii vietinghoffii M. Ad., 1812	1				1						
Pterostichus* (*Petrophilus*) *eximius A. Mor., 1862	18	4									
P.* (*Lenapterus*) *agonus G. Horn, 1880			1			1					
P.* (*Cryobius*) *nigripalpis Popp., 1906	23			6	1		6				
***P.* (*Cryobius*)** sp.						7					
P.* (*Cryobius*) *ventricosus ventricosus (Esch., 1823)	1										
P.* (*Cryobius*) *middendorffi middendorffi (J. Sahlb., 1875)				6		2	10	5	1		
Agonum* (*Olisares*) *quinquepunctatum Motsch., 1844			1	1							
Amara* (*Celia*) *praetermissa (C. Sahlb., 1827)										1	
A.* (*Bradytus*) *glacialis (Mnnh., 1853)						1		1			
Dicheirotrichus* (*Oreoxenus*) *mannerheimii mannerheimii (R. Sahlb., 1844)		1									
Cymindis* (*Tarulus*) *vaporariorum (L., 1758)	14				(1)	(1)					
Number of trap-days	96	100	50	50	100	96	96	40	15	45	30

Note: In parentheses, the number of larvae are given.

of the vegetation season may be delayed. The most abundant species in the plateau tundras were the Palaearctic arcto-montane *Pterostichus nigripalpis*, the Palaearctic polyzonal *Cymindis vaporariorum*, the East Siberian boreal *Pterostichus eximius*, and the East Siberian mountain *Carabus kolymensis*.

The ground beetle population of the mountain tundras in the upper reaches of the Kyubyume River (the Suntar-Khayata Range), situated still farther from the Ola Plateau (about 600 km), was quite different despite the similar values of diversity (19 species) and mean catch index (2.7 ind./10 trap-days; calculated

from the data by Khruleva, 2005). The similarity between the mountain tundra fauna of the upper reaches of the Kyubyume and the fauna of the studied area of the Ola Plateau was only 18%, the dominant species composition was different, and one third of them in the upper Kolyma area were specific inhabitants of East Siberian mountains. However, the quantitative dominance of representatives of the genera *Carabus* L., 1758 and *Pterostichus* Bon., 1810 (Berman et al., 1984; Bukhkalo, 1997; Khruleva, 2005; new data) seems to be a common feature of all the mountain tundras in Northeast Asia. Their other common features are small diversity of the genera *Bembidion* Latr., 1802 and *Amara* Bon., 1810, which usually prevail in the southern Siberian mountains (Shilenkov, 1992; Dudko and Sambyla, 2005; Dudko, 2010; Dudko et al., 2010; Khobrakova and Dudko, 2010), and also complete absence of members of the genus *Trechus* Clairv., 1806. The prevalence of the genera *Carabus* and *Pterostichus* (both in species number and in abundance) and the absence of *Trechus* were also recorded in the Polar Urals (Kolesnikova et al., 2007).

As compared with other northern regions (Berman et al., 1984; Bukhkalo, 1997; Ball and Currie, 1997; Khruleva, 1989, 1991, 2005; Berman, 2001; new data on Northern and Western Taimyr), a constance of biotopic preferences of some species attracts attention. For example, *Nebria frigida* and *Amara glacialis* always preferred the watercourse banks, whereas the mountain species *Carabus kolymensis* preferred open drained biotopes, such as dry tundras and mountain steppes, while *Pterostichus ventricosus* preferred mesic tundra localities. On the contrary, the typically tundra *P. agonus* and the typically forest *P. eximius* may inhabit both tundra and forest habitats in mountain areas. Such species as *Notiophilus aquaticus*, *Dicheirotrichus mannerheimii*, and *Cymidis vaporariorum* seem to have no evident biotopic preferences in Northeast Asia. They may be common components of forest, tundra or steppe communities. The polymorphic *Carabus odoratus* Motsch., 1944, forming a multitude of subspecies throughout its range (Shilenkov, 1996; Obydov, 2009), was characterized by different authors as an arctic (tundra) (Lomakin and Zinoviev, 1997), tundra-taiga (Khobrakova and Dudko, 2010), mountain-forest and highland (Shilenkov and Ananina, 2001; Ananina, 2009), mountain-tundra (Kolesnikova, 2008), and alpine species (Dudko and Sambyla, 2005). However, in Northeast Asia this species is a broad xerophile and mainly inhabits open dry plots (Berman, 2001), reaching especially high abundance on the steppified coastal slopes (D.I. Berman, new data).

The Arealogical Structure: Additional Remarks Concerning the "Arctic Species" Category in Ground Beetles

The studied fauna has a specific arealogical structure. Besides widespread polyzonal species, such as the Holarctic *Notiophilus aquaticus* and the Palaearctic *Amara praetermissa* and *Cymindis vaporariorum*, and species belonging to the arcto-boreomontane and arctoboreal complex with vast ranges of different longitudinal extension, there was also a group of species with characteristic limited distribution. It included *Carabus kolymensis*, a typical inhabitant of the mountain tundras of East Siberia, the Siberian-American, mainly arctic *Pterostichus agonus*, and the East Siberian boreal *Pterostichus eximius*.

The complex of arctoboreal and arcto-boreomontane species of the Ola Plateau includes a number of forms which are usually considered "tundra" species typical of Arctic landscapes. As a rule, their ranges in the West Palaearctic are restricted to the tundra zone (Kryzhanovskij et al., 1995). Such species are the Palaearctic *Carabus odoratus*, the Palaearctic-Beringian *Pterostichus ventricosus*, and the Siberian-American *Amara glacialis*. Findings of the Siberian-Beringian *Carabus vietinghoffii* in North America were also mainly associated with tundra landscapes (Ball and Currie, 1997). These beetles are usually characteristic of the tundra proper and near-aquatic communities (Bukhkalo, 1997; Lomakin and Zinoviev, 1997; Ball and Currie, 1997), with the possible exception of the polytopic *Carabus odoratus*. However, all these species, as well as other representatives of the arctoboreal and arcto-boreomontane complex, inhabit the vast mountain regions of Siberia as far southward as the Amur area, Transbaikalia, and the Altai-Sayan mountain system. Taking into account the relatively young age of the plain tundra biome as a distinct natural zone, not more than three million years (Tolmachev, 1957; Matthews and Ovenden, 1990; Elias et al., 2006), such ranges may point to the mountain origins of these insects.

Nevertheless, there are some species of ground beetles whose ranges practically do not transcend the limits of the Arctic proper. Such species are also present in other well-studied groups of living organisms, for instance, vascular plants (Sekretareva, 2004), leaf beetles (Chernov et al., 1993), weevils (Khruleva and Korotyaev, 1999; Korotyaev, 2012), spiders (Marusik

and Eskov, 2009), etc. Among ground beetles, these are mainly representatives of the large genus *Pterostichus* which includes many obscure forms. Such are the West and Middle Siberian *P. argutoriformis* (Popp., 1906), the mainly Siberian-Beringian *P. sublaevis* (J. Sahlb., 1880) [found by D.I. Berman in the tundras of the upper reaches of the Kolyma, i.e., in the Metaarctic, according to Yurtsev (1977)], *P. tareumiut* Ball, 1962, and *P. vermiculosus* (Mén., 1851) [also found in the tundras of the upper reaches of the Kolyma], the Beringian *P. nivalis* (F. Sahlb., 1844) and *P. similis* Mnnh., 1852, the East Beringian *P. kotzebuei* Ball, 1963, and the Nearctic *P. caribou* Ball, 1962.

The species common, widespread, and often numerous in the Arctic, such as *Carabus truncaticollis* Eschsch., 1833, *Carabus odoratus*, *Bembidion hastii* C.R. Sahlb., 1827, *Pterostichus brevicornis* (Kirby, 1837), *P. pinguedineus* (Eschsch., 1823), *Stereocerus haematopus* (Dej., 1831), and *Curtonotus alpinus* (Pk., 1790), were often classified as arctic forms (Danks, 1981; Lomakin and Zinoviev, 1997; Chernov et al., 2001, etc.), moreover *Curtonotus alpinus* was even called a "truly arctic species" (Böcher, 1989). All of them inhabit the mountains of South Siberia, some are also present in the Amur area; *Curtonotus alpinus* reaches even the Rocky Mountains as far to the south as Colorado (Schwert and Ashworth, 1988), i.e., they occur far beyond the limits of the Metaarctic. Moreover, similar to the "arctic" plant species (Yurtsev, 1968; Yanchenko, 2009), in the mountains such species may be present also or exclusively in the forest belt (Bukhkalo, 1997; Shilenkov and Ananina, 2001; Dudko and Sambyla, 2005; Khruleva, 2005; Khobrakova and Dudko, 2010). According to the general arealogical scheme of Chernov and Matveyeva (2002), the above species should be placed in the geographic group of "arctic species in the broad sense" (which includes arctic proper, metaarctic, arctoalpine, and arctomontane forms), whose representatives in plain territories mostly occur within the limits of the Arctic. However, to avoid confusion between the paronymous arealogical and landscape-zonal, i.e., ecological terms (including the widely used ecological terms "hypoarctic," "hemiarctic," "euarctic," and "hyperarctic" by Chernov, 1975), a number of entomologists prefer such expressions as "species of the arctic complex" (Khruleva, 2005), "typically northern species" (Rossolimo, 1994), "tundra species" (Kryzhanovskij, 1983; Berman et al., 1984), "northern tundra species" (Rybalov et al., 2000), "northern species" or "northern, mainly tundra species" (Rybalov, 2002). It seems to be expedient to define the landscape-zonal (essentially ecological) aspect of such species horology by the terms proposed by Chernov (1975), which describe the distribution pattern of species in the Arctic, taking into account the zone of optimum. Since such forms are associated with the cold climate, they may be also referred to as "microtherm species," as is common in botany. However, in case of arealogical analysis, such species should be reasonably placed in the capacious "arctomontane" category, which unites the forms inhabiting, besides the Arctic and the Metaarctic, any belts of the southern mountain systems, i.e., the arctoalpine and arctomontane species in the scheme of Chernov and Matveyeva (2002). In view of this, the term "arctic" should be reserved for the few species whose distribution is indeed limited to the Arctic proper and the adjoining mountains, i.e., the really arctic and metaarctic species in the scheme of Chernov and Matveyeva (2002). Such delimitation may be quite useful when considering the problems of faunogenesis (speciation, dispersal, etc.) and also semantically justified. In this interpretation, the arealogical groups of "arctomontane" and "arctic" species will be not subordinate but equal in their geographic rank.

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REFERENCES

1. Ananina, T.L., "Spatial Organization of the Ground Beetle Community (Coleoptera, Carabidae) along the Altitude Gradient of the Barguzin Range," Vestnik Tomsk. Gos. Univ. Biol., No. 328, 178–182 (2009).
2. Ball, G.E. and Currie, D.C., "Ground Beetle (Coleoptera: Trachypachidae and Carabidae) of the Yukon: Geographical Distribution, Ecological Aspects, and Origin of the Extant Fauna," in *Insects of the Yukon. Terrestrial Arthropods* (Biol. Survey of Canada, Ottawa, 1997), pp. 445–489.

3. Berman, D.I., "Chapter 5. Invertebrates," in *The Cold Steppes of Northeast Asia* (Inst. of Biol. Problems of the North, Magadan, 2001), pp. 96–161 [in Russian].
4. Berman, D.I., Budarin, A.M., and Bukhkalo, S.P., "The Fauna and Assemblages of Invertebrates in the Mountain Tundras of the Bolshoi Annachag Range," in *The Soil Layer of in the Mountain Tundra Ecosystems of the Bolshoi Annachag Mountain Range, the Upper Kolyma* (Far East Branch of USSR Acad. Sci., Vladivostok, 1984), pp. 98–133 [in Russian].
5. Böcher, J., "First Record of an Interstadial Insect from Greenland: *Amara alpina* (Paykull, 1790) (Coleoptera: Carabidae)," Boreas **18**, 1–4 (1989).
6. Bousquet, Y., *Checklist of Beetles of Canada and Alaska (Biosystematics Research Centre, Research Branch Publication 1861/E)* (Agriculture Canada, Ottawa, 1991).
7. Bukhkalo, S.P., *The Population of Terrestrial Invertebrates at the "Kontakt" Field Station*, Part 3: *Species Composition and Biotopic Distribution of Invertebrates* (Northeast Branch of Russ. Acad. Sci., Magadan, 1997) [in Russian].
8. Chernov, Yu.I., *Natural Zonality and the Animal World of Land* (Mysl, Moscow, 1975) [in Russian].
9. Chernov, Yu.I., "Are Predators or Phytophages More Numerous in the Tundra?" in *Cenotic Interactions in Tundra Ecosystems* (Nauka, Moscow, 1992), pp. 111–127 [in Russian].
10. Chernov, Yu.I., Makarov, K.V., and Eremin, P.K., "Family of Ground Beetles (Coleoptera, Carabidae) in the Arctic Fauna: Communication 1," Zool. Zh. **79** (12), 1409–1420 (2000) [Entomol. Rev. **80** (8), 1009–1021 (2000)].
11. Chernov, Yu.I., Makarov, K.V., and Eremin, P.K., "Family of Ground Beetles (Coleoptera, Carabidae) in the Arctic Fauna: Communication 2," Zool. Zh. **80** (3), 285–293 (2001) [Entomol. Rev. **81** (1), 108–117 (2001)].
12. Chernov, Yu.I. and Makarova, O.L., "Beetles (Coleoptera) in High Arctic," in *Back to the Roots or Back to the Future? Towards a New Synthesis between Taxonomic, Ecological and Biogeographical Approaches in Carabidology. Proc. XIII European Carabidologists' Meeting, Blagoevgrad, August 20–24, 2008* (Pensoft Publ., Sofia–Moscow, 2008), pp. 213–246.
13. Chernov, Yu.I. and Matveyeva, N.V., "The Landscape-Zonal Distribution of Species in the Arctic Biota," Uspekhi Sovr. Biol. **122** (1), 26–45 (2002).
14. Chernov, Yu.I., Medvedev, L.N., and Khruleva, O.A., "Leaf Beetles (Coleoptera, Chrysomelidae) in the Arctic," Zool. Zh. **72** (9), 78–92 (1993).
15. Chernov, Yu.I. and Tatarinov A.G., "Butterflies (Lepidoptera, Rhopalocera) in the Arctic Fauna," Zool. Zh. **85** (10), 1205–1229 (2006) [Entomol. Rev. **86** (7), 760–786 (2006)].
16. Danks, H.V., *Arctic Arthropods* (Tyrell Press Limited, Ottawa, 1981).
17. Dudko, R.Yu., "The Local Faunas of Ground Beetles (Coleoptera, Carabidae) of the Highlands of the Altai-Sayan Mountain System," in *Entomological Research in North Asia. Proc. of the VIII Interregional Workshop of Entomologists of Siberia and the Far East. Novosibirsk, 4–7 October 2010* (KMK Sci. Press, Moscow, 2010), pp. 75–76.
18. Dudko, R.Yu., Matalin, A.V., and Fedorenko, D.N., "The Ground Beetle Fauna (Coleoptera, Carabidae) of Southeastern Altai," Zool. Zh. **89** (11), 1312–1330 (2010) [Entomol. Rev. **90** (8), 968–988 (2010)].
19. Dudko, R.Yu. and Sambyla, Ch.N., "The Alpine Ground Beetle Fauna (Coleoptera, Carabidae) of the Eastern Tuva Upland," Evraz. Entomol. Zh. **4** (3), 209–218 (2005).
20. Elias, S.A., Kuzmina, S., and Kiselyov, S., "Late Tertiary Origins of the Arctic Beetle Fauna," Palaeogeogr. Palaeoclimatol. Palaeoecol. **241**, 373–392 (2006).
21. Gorodkov, K.B., "The Faunistic Connections between Siberia and Central Europe," in *Proc. of the 7th Int. Symp. on the Insect Fauna of Central Europe. Leningrad, 19–24 September 1977* (Zool. Inst., USSR Acad. Sci., Leningrad, 1979), pp. 30–33.
22. Gorodkov, K.B., "The Types of Ranges of Dipterans of Siberia," in *Taxonomy, Zoogeography, and Karyology of Diptera (Insecta)* (Zool. Inst., Russ. Acad. Sci., St. Petersburg, 1992), pp. 45–55 [in Russian].
23. Khobrakova, L.Ts. and Dudko, R.Yu., "The Fauna of Ground Beetles (Coleoptera, Carabidae) of the Central Sayan Plateau (East Sayan)," Evraz. Entomol. Zh. **9** (1), 33–47 (2010).
24. Khokhryakov, A.P., *The Flora of Magadan Province* (Nauka, Moscow, 1985) [in Russian].
25. Khokhryakov, A.P., *Analysis of the Flora of Kolyma Uplands* (Nauka, Moscow, 1989) [in Russian].
26. Khokhryakov, A.P. and Yurtsev, B.A., "The Flora of the Ola Basalt Plateau (the Kolyma-Okhota Watershed)," Byull. Mosk. Obshch. Ispyt. Prirody Otdel. Biol. **79** (2), 59–70 (1974).
27. Khruleva, O.A., "An Ecologic-Faunistic Review of the Insect Fauna of Wrangel Island," in *The Flora and Fauna of Protected Islands* (Moscow, 1989), pp. 112–130 [in Russian].
28. Khruleva, O.A., "The Spatial Aspects of the Invertebrate Assemblages of Wrangel Island," in *Animal Populations and Communities of Wrangel Island* (Moscow, 1991), pp. 161–179 [in Russian].
29. Khruleva, O.A., "The Distribution of the Arctic Beetle Species (Coleoptera) in the Highlands of the Suntar-Khayata Range, East Yakutia," in *The Mountain*

Systems and Their Components. Proceedings of Intern. Conference, Nalchik, 4–9 September 2005 (Nalchik, 2005), pp. 148–152.

30. Khruleva, O.A. and Korotyaev, B.A., "Weevils (Coleoptera: Apionidae, Curculionidae) of Wrangel Island," Entomol. Obozr. **78** (3), 648–670 (1999) [Entomol. Rev. **79** (9), 1119–1137 (1999)].
31. Kolesnikova, A.A., "Herpetobiont Beetles (Carabidae, Staphylinidae) of the North Urals," in *Biodiversity and Ecological Problems of the Mountain Altai and Adjoining Regions: the Present, Past, and Future. Proceedings of Intern. Conference, Gorno-Altaisk, 22–26 September 2008* (2008) [web conference].
32. Kolesnikova, A.A., Melekhina, E.N., and Taskaeva, A.A., "4.5. Soil Invertebrates," in *Biodiversity of the Ecosystems of the Polar Urals* (Inst. of Biology, Komi Sci. Center of Russ. Acad. Sci., Syktyvkar, 2007), pp. 182–202 [in Russian].
33. Konstantinova, N.A., "Analysis of the Ranges of Liverworts in the North of the Holarctic," Arctoa **9**, 29–94 (2000).
34. Korotyaev, B.A., *Doctoral Dissertation in Biology* (Zool. Inst., St. Petersburg, 2012).
35. Kryzhanovskij, O.L., *Beetles of the Suborder Adephaga, the Families Rhysodidae and Trachypachidae; the Family Carabidae (Introduction and Review of the Fauna of the USSR) (The Fauna of the USSR, Vol. 1, Issue 2)* (Nauka, Leningrad, 1983) [in Russian].
36. Kryzhanovskij, O.L., Belousov, I.A., Kabak, I.I., et al., *A Checklist of the Ground Beetles of Russia and Adjacent Lands* (Insecta, Coleoptera, Carabidae) (Pensoft Publ., Sofia–Moscow, 1995).
37. Kuznetsov, N.Ya., "The Eurasian Arctic Fauna and Its Origin (Mainly Based on the Data on Lepidoptera)," Trudy Zool. Inst. Akad. Nauk SSSR **5**, 1–85 (1938).
38. Lomakin, D.E. and Zinoviev, E.V., "The Fauna of Ground Beetles (Coleoptera, Carabidae) of Yamal Peninsula," in *Materials on the History and Recent State of the Fauna of the North of West Siberia* (Rifei, Chelyabinsk, 1997), pp. 3–15 [in Russian].
39. Makarov, K.V., Kryzhanovskij, O.L., Belousov, I.A., et al., *Taxonomical List of Ground Beetles (Carabidae) of Russia* (2012), http://www.zin.ru/Animalia/Coleoptera/eng/car_rus.htm. Updated 21.09.2012.
40. Marusik, Yu.M. and Eskov, K.Yu., "Spiders (Arachnida; Aranei) of the Tundra Zone of Russia," in *Species and Communities under Extreme Conditions* (KMK Sci. Press and Pensoft, Moscow–Sofia, 2009), pp. 92–123 [in Russian].
41. Matthews, J.V. and Ovenden, L.E., "Late Tertiary Plant Macrofossils from Localities in Arctic/Sub-Arctic North America: a Review of the Data," Arctic **43**, 364–392 (1990).
42. Obydov, D., "Faune des Carabus de Sibérie & d'Extrême-Orient russe—I," Coll. Syst. **20**, 1–148 (2009).
43. Rossolimo, T.E., "Comparative Analysis of the Cold Endurance Parameters of Some Beetles (Coleoptera) of Hypoarctic Regions," Zool. Zh. **73** (7–8), 101–113 (1994).
44. Rybalov, L.B., "The Zonal-Landscape Changes in the Soil Invertebrate Populations in the Yenisei Region of Middle Siberia and the Role of Temperature Adaptations in the Meridional (Zonal) Distribution of Invertebrates," Russ. Entomol. J. **11** (1), 77–86 (2002).
45. Rybalov, L., Rossolimo, T., and Block, W., "Temperature Adaptations of Terrestrial Arthropods of the Yenisey Region of Siberia (Asian Ecological Transect)," in *USDA Forest Service Proceedings RMRS-P-14* (Rocky Mountain Research Station, Fort Collins, 2000), pp. 57–61.
46. Schwert, D.P. and Ashworth, A.C., "Late Quaternary History of the Northern Beetle Fauna of North America: a Synthesis of Fossil and Distributional Evidence," Mem. Entomol. Soc. Canada **144**, 55–92 (1988).
47. Sekretareva, N.A., *Vascular Plants of the Russian Arctic and Adjoining Territories* (KMK Sci. Press, Moscow, 2004) [in Russian].
48. Shilenkov, V.G., "3. The High Altitude Fauna of South Siberian Mountains and Its Origin (Coleoptera, Carabidae)," in *The Biogeography of Ground Beetles of Mountains and Islands* (Intercept Ltd., Andover, 1992), pp. 53–65.
49. Shilenkov, V.G., *Ground Beetles of the Genus Carabus L. (Coleoptera, Carabidae) in South Siberia* (Irkutsk State Univ., Irkutsk, 1996) [in Russian].
50. Shilenkov, V.G. and Ananina, T.L., "Materials on the Ground Beetle Fauna (Coleoptera, Carabidae) of Barguzin Reserve," in *Biodiversity of the Baikal Region. Issue 5* (Irkutsk State Univ., Irkutsk, 2001), pp. 26–41 [in Russian].
51. Shtegman, B.K., *Principles of Ornithogeographic Subdivision of the Palaearctic (Fauna of the USSR. Birds, Vol. 1, Issue 2)* (USSR Acad. Sci., Moscow, 1938) [in Russian].
52. Silfverberg, H., "Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae," Sahlbergia **9**, 1–111 (2004).
53. Tolmachev, A.I., "The Problem of the Origin of the Arctic Flora and the History of Its Development," in *Abstracts of Papers, the Plenary Congress of the All-Union Botanical Society, 9–15 May 1957. Issue III: Section of Flora and Vegetation, Part 1* (Leningrad, 1957), pp. 47–55.
54. Yanchenko, Z.A., "The Vascular Flora of the Northwestern Putorana Plateau (the Environs of Lake Lama)," Botan. Zh. **94** (7), 83–110 (2004).

55. Yurtsev, B.A., *The Flora of Suntar-Khayata. The Problems of the History of Some Alpine Landscapes in Northeastern Siberia* (Nauka, Leningrad, 1968) [in Russian].
56. Yurtsev, B.A., "On the Relations between the Arctic and the Alpine Subarctic Floras," in *Problems of Ecology, Geobotany, Plant Geography, and Flora Studies* (Nauka, Leningrad, 1977), pp. 125–138 [in Russian].
57. Yurtsev, B.A. and Khokhryakov, A.P., "Analysis of the Flora of the Ola Plateau as Related to the History of the Plant Cover of the Kolyma Uplands," Byull. Mosk. Obshch. Ispyt. Prirody Otdel. Biol. **80** (2), 120–133 (1975).
58. Zhang, Z.-Q., "Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness," Zootaxa, No. 3148, 1–237 (2011).
59. Zinoviev, E.B. and Olshvang, V.N., "The Beetles of the North of the West Siberian Plain and the Subpolar and Polar Urals," in *Biological Resources of the Polar Urals: Collected Papers, Issue 3, Part 2* (Salekhard, 2003), pp. 37–60 [in Russian].