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Family of Ground Beetles (Coleoptera, Carabidae) in the Arctic Fauna: Communication 1

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Abstract—Ground beetles are a group of insects most successfully occupying tundra landscapes. Their share in the fauna of Coleoptera is much higher in tundra, than in other natural zones. In Eurasia, about 90 carabid species have been recorded from tundra and about 170 from the tundra and forest-tundra combined. The potential carabid fauna of the whole Arctic in the broadest limits is estimated to comprise 240–300 species, which constitutes 0.6–0.8% of the total number of species in this family. The number of proper arctic species cannot be precisely determined as yet, but it is in any case no less than 35. The list of arctic, and tending to Eurasian Arctic, ground beetles includes 67 species. The northern limit of the family distribution almost coincides with the latitude 76° N. Ground beetles are absent from polar deserts. The number of species in local faunas within the tundra zone is closely correlated with the average July temperature. The spectrum of life forms is characterized by the absence of specialized types, small number of geobionts, and relatively high share of epigeobionts. Typical carnivorous and some polyphagous species capable of phytophagy appeared to be most successful in tundra conditions. Specific features of the latitudinal (zonal) and meridional (sectoral) distribution of carabids in the tundra zone are discussed.

The decrease in the diversity of the fauna at high latitudes varies widely between taxa. Some of them retain considerable species diversity and demonstrate clear evidence of biological progress in arctic landscapes. An example of such a group is the family Carabidae. The increase in their role in tundra communities correlates well with the rising share of carnivores in the fauna from equator to poles (Chernov, 1992). A high share of predacious insects, carabids among them, was recorded as a characteristic feature of the arctic insect fauna as early as in 1938 by Kuznetsov (1938). Undoubtedly, studying the structure of taxa forming the core of the arctic fauna and reflecting, in their distribution, the global trends of the biota is of special interest. This paper is a continuation of a series of publications by the Laboratory of Synecology, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, analyzing the taxonomic composition of different groups in the arctic insect fauna (Lantsov and Chernov, 1987; Chernov *et al.*, 1993; Chernov, 1995a; Khruleva and Korotyaev, 1999; etc.). This paper is based on the available publications, mainly concerning the Eurasian sector of the Arctic, field research of the authors, and examination of collections deposited at the Zoological Institute, Russian Academy of Sciences, and Zoological Museum, Moscow State University, and those supplied by T.R. Andreeva (Yamal Peninsula), A.B. Babenko (Taimyr and other regions), V.I. Bulavintsev (Novosibirsk Islands, Severnaya Zemlya), E.M. Veselova (Yamal Peninsula), K.Yu. Es'kov (Taimyr, Putorana Plateau), R.I. Zlotin (Chukotka Peninsula), Yu.I. Korobeinikov (Yamal), V.I. Lantsov (Taimyr), O.L. Makarova (shore of Lake Taimyr, Putorana Plateau, upper Nizhnyaya Agapa River), O.A. Khruleva (Wrangel Island, Taimyr), and A.I. Tsybul'skii (Ust'-Lenskii Nature Reserve). Some important data on the distribution of arctic carabids were supplied by D.E. Lomakin (Tyumen'), R.Yu. Dudko (Novosibirsk), and A.E. Brinev (Moscow).

The field research by Yu.I. Chernov has been performed since 1957 in different regions of the tundra zone from the Yugorskii Peninsula and Bol'shezemel'skaya Tundra to Gulf of Anabar, mainly in Taimyr: Dikson Town and to the south of it, in the basins of the Ragozinka and Efremovka Rivers; in the lower sections of the Uboinaya and Lenivaya Rivers; on the shore of Marii Pronchishchevoi Bay; in the basin of Syradasai; near Tareya Village (lower Pyasina River), Kresty (upper Pyasina), and also in the American sector of the Arctic (Alaska, Devon and Ellesmere Islands). The faunistic data obtained in these studies have been published in part (Chernov, 1964, 1966, 1973, 1978a, etc.).

P.K. Eremin performed field observations from 1988 till 1993 in the Kanin Peninsula, basins of the Oma and Pechora Rivers, Yugorskii Peninsula (Kartaikha, Amderma, Ust'-Kara), S Yamal (basin of the Shchuch'ya River, Salekhard), Taimyr (Lake Taimyr, Logata, Novorybnoe, Khatanga), and in the lower Kolyma. This material was partly included in taxonomic publications (Eremin, 1990, 1998, etc.).

The authors are based in providing the species characteristics, calculating the ratios between faunal components, and correlating these with elements of the environment on this very extensive material, which cannot be cited entirely in a journal paper. The main faunistic material, including an annotated list of arctic Carabidae, will be published in subsequent papers.

The scheme of zonal and subzonal subdivision of the Arctic, used in the paper, has been repeatedly described in previous publications (Chernov, 1978a, 1985; Chernov and Matveyeva, 1979, 1997).

Share of Carabids in the Arctic Insect Fauna

Judging from the approximate calculations based on "Opredelitel' nasekomykh..." (1965), the obligatory and facultative predators constitute about a quarter of the total number of species of Coleoptera in the temperate zone. The share of carabids among them is about 36%. In total, the family Carabidae comprises almost 10% of species in the order. In the arctic fauna, zoophages (in a broad sense) constitute more than half of the coleopteran fauna, most of them being carabids.

Danks (1981) recorded 185 beetle species from arctic America, with about 125 predators included and 85 carabids among these. Khruleva (1987) found 53 beetle species in Wrangel Island, with 30 predators and conventional predators included and 17 carabid species among them. The ratios in local faunas are no less indicative. Near mouth of Tareya, a tributary of the Pyasina River (subzone of typical tundra), 30 beetle species occur, including about 15 carabids (Chernov, 1978a). Farther northwards, in the lower Uboinaya River (arctic tundra), 9 beetle species have been recorded, with 4 carabids among them. In the northernmost parts of the tundra zone, Coleoptera are usually represented mainly by Carabidae, together with a few species of Dytiscidae, Staphylinidae, sometimes Chrysomelidae, Curculionidae, Catopidae, etc. On the whole, carabids constitute more than a third of the beetle species in the tundra zone. Their share is even higher among the arctic species proper of this order.

In the Arctic, the Carabidae surpass other beetle families in the integrated characteristics of biological progress, such as taxonomic and ecological diversity, cenotic importance, colonization of biotopes, and lansdcape-zonal distribution (Chernov, 1978a). Of particular role is the presence of the examples of very extensive adaptive radiation of superspecies taxa in the tundra conditions (see below) within the family. Most of the beetles inhabiting zonal communities of flat interfluves are carabids (Chernov, 1966, 1978a). Only Staphylinidae can to some extent compete with Carabidae in colonization of flat interfluves in the tundra zone.

High adaptive abilities of the Carabidae in the Arctic are especially pronounced as compared with those of the largest beetle families, Chrysomelidae and Curculionidae, representing in the arctic fauna the main part of phytophagous and the most advanced groups of Coleoptera. In high-latitude landscapes, the family Carabidae is represented by a number of species about 3 times that of these two families combined. Danks (1981) recorded from arctic America 13 species of Chrysomelidae, 14 species of Curculionidae, and 85 species of Carabidae. A total of about 40 species of Chrysomelidae have been recorded from the Arctic. Only 4 of them are undoubtedly arctic, and no more than 9 can be included in the arctic complex taken in a very broad sense (Chernov *et al.*, 1993). The number of typical arctic species of carabids cannot be determined precisely as yet, but in any case it is no less than 35 (see Communication 2).

Clearly, these ratios strongly vary between different sectors of the Arctic, depending on historical, landscape, climatic, and cenotic factors. So, the chrysomelid and curculionid species diversity in NE Asia, including Wrangel Island, much exceed that in other regions of the Arctic and, in total, is comparable with the taxonomic diversity of carabids (see, e.g., Khruleva, 1987; Khruleva and Korotyaev, 1999). This is most likely correlated with the wide distribution in this sector of the so-called tundra-steppe communities characterized by increased diversity of phytophages.

It is well known that the order Coleoptera is the largest in the class Insecta, constituting about 40% of the world insect fauna. In the arctic insect fauna, its share decreases to 13%, and precedence is taken by the Diptera constituting about 50% of insect species (Chernov, 1995a, 1995b). At the same time, when the diversity and role in biocenoses of the tundra zone are compared at the level of insect families, it appears that

Table 1. Number of species recorded from northern landscapes of Eurasia and America (after Lindroth, 1966, 1968, 1992; Danks, 1981; Kryzhanovskij, 1983; Kryzhanovskij *et al.*, 1995; the authors' material)

Genus	Eurasia			America
	tundra zone and forest-tundra	tundra zone	subzone of arctic tundra	tundra zone and forest-tundra
Carabus	16	7	1	4
Cychrus	1	0	0	0
Nebria	3	2	0	4
Pelophila	1	1	1	1
Notiophilus	6	4	1	2
Blethisa	2	1	0	1
Diacheila	2	2	2	1
Elaphrus	5	3	0	2
Loricera	1	0	0	1
Dyschirius	6	2	0	1
Miscodera	1	0	0	0
Trechus (Epaphius)	1	0	0	0
Bembidion	35	18	1	20
Patrobus	2	1	0	1
Poecilus	3	2	0	1
Pterostichus	44	34	9	29
Agonum	11	4	0	3
Calathus	1	0	0	0
Amara	13	5	2	5
Curtonotus	5	4	2	5
Trichocellus	2	1	0	1
Cymindis	4	0	0	1
Total number of species	165	91	19	83

carabids rank with Tenthredinidae (Hymenoptera), Noctuidae (Lepidoptera), and Tipulidae (Diptera), which are examples of the most successful colonization of the Arctic. Undoubtedly, analysis of the taxonomic structure, adaptive traits, and ranges of such groups largely contributes to clarifying the ways of colonization of tundra by insects.

Number of Species and the Distribution Limits

More than 90 carabid species of 16 genera have been recorded from the territory of the Eurasian tundra zone (Table 1). About 170 species have been recorded from the Eurasian Arctic in broader sense, i.e., in arctic and subarctic landscapes including forest-tundra; this is evidently below the actual number. In all probability, this number should be increased to no less than 200. Data on various groups of insects testify that every species widespread in the taiga belt can occur in forest-tundra. Taking into account the small width of this transitional, ecotone landscape and its varying latitudinal position (in Eurasia the shift in zonal boundaries reaches 4°), any species of its fauna can be considered a potential inhabitant of southern variants of the tundra landscapes.

According to our interpretation of Danks's (1981) data, 65 carabid species have been recorded from the American sector of the tundra zone, and, when combined with the forest-tundra territories, about 85 species, which constitutes about 10% of the arctoboreal-forest belt fauna of America (see Danks, 1979). The broader taxonomic diversity of the Palaearctic arctic fauna is attributable to a greater landscape variety and

Table 2. Number of carabid species in local faunas of the Taimyr Peninsula (the authors' material)

Locality	Zonal position	Average July temperature, °C	Carabini	Elaphrini	Bembidiini	Pterostichini	Zabrini	Total number of species
Marii Pronchishchevoi Bay	Northern belt of arctic tundra	4.0	0	0	0	2	1	3
Uboinaya River, lower section	Middle belt of arctic tundra	4.5	0	0	0	2	1	3
Dikson Town	Southern belt of arctic tundra	5.0	0	0	1	5	1	9*
Northern shore of Lake Taimyr	Boundary between typical and arctic tundra	7.0	0	0	1	5	2	8
Ragozinka River	Boundary between typical and arctic tundra	7.5	1	1	2	4	1	11*
Tareya Village	Northern belt of typical tundra	8.5	1	2	2	8	2	16*
Lake Logata	Northern belt of typical tundra	9.5	1	1	1	7	2	13
Novorybnoe Village	Southern tundra	10.5	1	3	2	7	2	15
Nizhnyaya Agapa River, upper section	Southern tundra	11.0	1	1	2	8	2	21
Lukunskaya River	Southern tundra	11.5	1	4	7	19	6	43
Khatanga Village	Forest-tundra	12.5	4	6	8	19	10	59

* Based on data of long-standing collecting.

vast continental territory. Faunogenetic reasons must not be ruled out, either.

Based on our own and published data and also on collections, we estimate the circumpolar carabid fauna of the tundra zone (without forest-tundra) to comprise about 160 species, which constitutes about 0.4–0.6% (depending on an estimation of the total species number) of the world fauna. The total diversity of the arctic carabid fauna in the broadest sense, i.e., with all records from forest-tundra regions and those from southern parts of the tundra zone included, may be estimated at 240–300 species, which constitutes 0.6–0.8% of the world fauna of the family.

In continental regions of Eurasia, the number of carabid species sharply decreases from forest-tundra to the subzone of arctic tundra (Table 2). Local forest-tundra faunas usually comprise more than 60 species. Clearly, the regional faunas are more diverse. For example, a thorough collecting by T.R. Andreeva and E.M. Veselova in the middle course of Shchuch'ya River in the Yamal Peninsula revealed 85 species, with 103 species found over the entire S Yamal, including tundra, forest-tundra, and, partly, northern-taiga areas (Andreeva and Eremin, 1991).

In the subzone of southern tundra, each local fauna comprises about 30–50 species; for the subzone of typical tundra, most characteristic figures are 10–20 species. In the subzone of arctic tundra in Taimyr, we found only 10 carabid species, with 3–4 species in each particular locality. At the same time, the diversity and composition of regional and local faunas may strongly vary within each subzone (see below).

Carabids usually do not penetrate into the zone of polar deserts. They have not been recorded from Franz Josef Land, Severnaya Zemlya (Bulavintsev and Babenko, 1983), and flat interfluve areas of Cape Chelyuskin (Chernov *et al.*, 1979). In the American sector of the Arctic, carabids have not been found in N Ellesmere Island (Oliver, 1963; our observations), Bathurst Islands (Danks, 1980), and Ellef Ringnes Island (McAlpine, 1965) with landscapes of polar-desert type. Thus, as regards the penetration into the highest-latitude landscapes, carabids are inferior to many groups of Diptera, Lepidoptera, and Hymenoptera, and also to the two families of Coleoptera (Staphylinidae and Dytiscidae) represented by 1–3 species in the listed islands. Even few specimens of Chrysomelidae (*Chrysolina subsulcata* Mnnh.) have been found in Severnaya Zemlya (Chernov *et al.*, 1993; collected by V.I. Bulavintsev and O.L. Makarova).

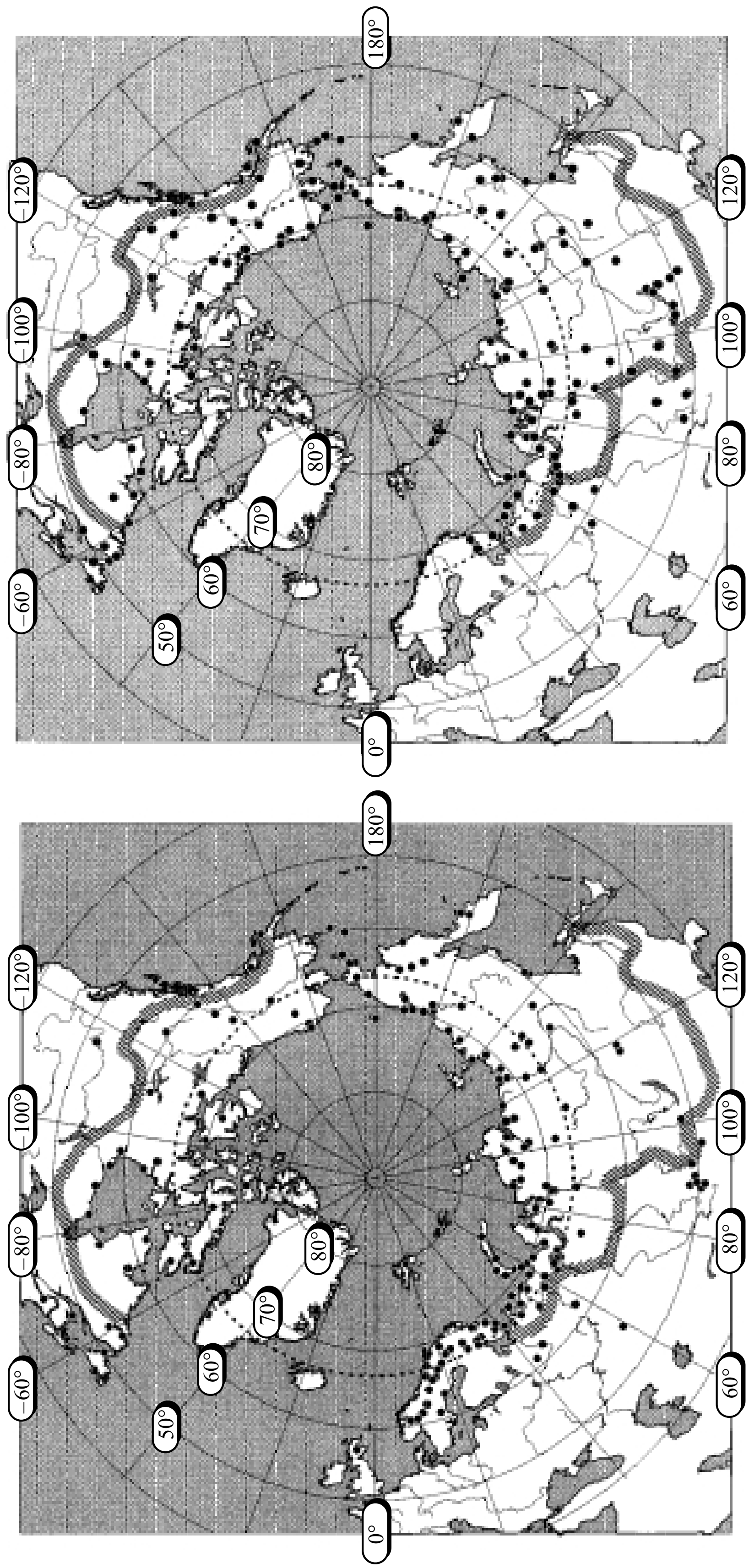

Fig. 1. Distribution of *Curtonotus alpinus* (1) and *Pterostichus brevicornis* (2) (after Lindroth, 1992; Danks, 1981; collections of different museums and the authors' material; altogether 187 localities recorded for *C. alpinus* and 168, for *P. brevicornis*). Hatched line indicates the border of maximum glaciation.

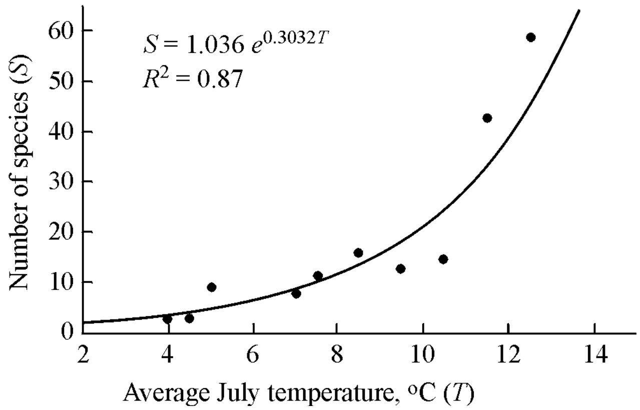

Fig. 2. Correlation between the number of carabid species in local faunas of the Taimyr Peninsula and the July temperature (according to the authors' material, see Table 2).

The northern limit of the family distribution in Eurasia and America approximately coincides with the latitude 76° N. Nevertheless, the type of latitudinal and zonal limits of the ranges of some species and also the distribution of the species diversity are quite different in the American and Eurasian sectors. In the Canadian sector, only few species cross the latitude of 70°, and *Curtonotus alpinus* Payk. penetrates farthest northwards (Fig. 1). For instance, it is the only representative of the family in Devon Island situated at the latitude 75°N and belonging to the subzone of arctic tundra (Ryan, 1977; our observations). Only this carabid species has been recorded from the entire American High Arctic, including polar deserts and the subzone of arctic tundra in our concept (Danks, 1981). In the Middle and Eastern Siberian sectors, almost the entire arctic fauna, i.e., several dozens of species have been found north of the latitude 70–72° N. Even at 74.5° N, on the northern shore of Lake Taimyr (boundary between subzones of the typical and arctic tundra), O.L. Makarova found 8 carabid species. This difference can hardly be accounted for by the fact that the Canadian Arctic is mostly insular; since 17 carabid species have been found in Wrangel Island (latitude ca. 71° N). It also cannot be understood in the context of other general biogeographical principles. For example, the number of spider and butterfly (Rhopalocera) species in localities with equal average July temperatures is much greater in the Canadian-Beringian sector, compared with the Middle Siberian one (Chernov, 1989; Chernov and Penev, 1993). Species ranges also demonstrate essential distinctions in latitudinal-zonal distribution between different sectors of the Arctic. For example, *Pterostichus* (*Cryobius*) *brevicornis* Kirby is widespread over the entire tundra zone of Eurasia up to the latitude 75–76° N, whereas in America it does not cross 70° N (Fig. 1). Apparently, the reason for these phenomena should be looked for in the regional-sectoral features of the landscape and climatic conditions and in faunogenetic subtleties rather than in particular biological characters of species.

Significant distinctions in the landscape-zonal and latitudinal distribution of carabids can be also traced in different sectors of the Eurasian continent. For example, in the northern part of the Yugorskii Peninsula and in Vaigach Island (i.e., northern part of the typical tundra subzone), the boreal carabids *Nebria rufescens* Stroem, *Patrobus septentrionis* Dej., and *Pelophila borealis* Payk. are common everywhere, but rarely, if at all, occur in similar landscapes of Taimyr. When explaining this fact, one should take into account that the southern border of the tundra zone runs through the latitude of ca. 71–72° N in Taimyr, and 67° N in the Yugorskii Peninsula. Clearly, regions similar in lanscape-zonal features, but lying at such remote latitudes may differ strongly in the climate. The degree of continentality and also winter temperatures, which are sharply decreasing from the west to the east in N Eurasia, may have a profound effect. The latitudinal-zonal distribution of species in different sectors of the Arctic has not been studied adequately so far. Some aspects of this problem have been discussed previously. The regional-sectoral distinctions in latitudinal distribution of species diversity in various groups, including carabids, were attributed to the temperature conditions (using as indicator the mean temperature of the warmest month) (Chernov, 1978a, 1989; Chernov and Penev, 1993). The correlation between the diversity of local faunas of carabids (and many other groups of the Arctic biota) and the summer temperatures is very strong (Fig. 2). In Taimyr, carabids do not cross the July isotherm 2°C corresponding to the boundary of polar deserts. In the temperature range from 3 to 9°C, i.e., within the arctic and the northern belt of typical tundra, the diversity of local faunas increases from 1 to 15 species. In the temperature range from 9 to 12°C (covering the forest-tundra), the number of species increases exponentially approximately to about 60.

The regional-sectoral features of the species diversity in carabids may also be associated with summer temperatures. For example, 17 species have been recorded from Wrangel Island (latitude 71.5° N), which is twice the number of species found by us in the whole territory of the subzone of arctic tundra in Taimyr, lying at much higher latitudes (the southern border of the subzone runs through latitudes of ca. 74–75.5° N). In Wrangel Island, the temperature range characteristic of this subzone (average July temperature 2–6°C) is registered mainly on the sea shore, being higher in the heart of the island (about 10°C) and, correspondingly, local plant communities having more "southern" character being observed (Stishov *et al.*, 1986). The wide species diversity of the fauna of the Chukotka Peninsula, quite poorly studied hitherto, can also be correlated with high summer temperatures, especially in the heart of the peninsula, since tundra is present there at very low latitudes, even to the south of the polar circle.

Correlations of the faunal diversity with temperature are strongly modified by regional features of the landscape structure and faunogenesis. For example, an obviously incomplete collecting by A.I. Tsybul'skii revealed 24 species in the territory of Ust'-Lenskii Nature Reserve with intermittent areas of different zonal landscape variants, from arctic tundra to forest-tundra. In the Canadian Arctic, the minimum carabid diversity (1–2 species) corresponds to average July temperatures of about 4.5°C, e.g., in Devon Island. Nevertheless, carabids are absent from Ellesmere, at least from the northern part of this mountainous island, although in its heart, in the non-mountainous areas, the mean July temperatures range up to 8°C (Edlund *et al.*, 1989), and very diverse and productive plant communities are developed, providing forage for a quite numerous herd of musk-oxen. Clearly, there are no reasons to invoke the insular factor (effect of isolation) in this case, since distances between islands are very short in the Canadian Arctic Archipelago.

Many arctic species, especially those belonging to the Angarian complex, are distributed to Gydan or Yamal on the west, being absent from European tundra. On the other hand, penetration of boreal species is more pronounced in the relatively mild climatic conditions of the European sector, but this only partly compensates for the decreasing diversity of the arctic fauna proper. For example, in Vaigach Island with typical and, on the very north, arctic type of tundra (with mean July temperature of about 6°C), we found 15 species, i.e., number less than that in Wrangel Island situated 1.5° farther to the north, in the subzone of arctic tundra. In Kolguyev Island (mean July temperature 7.5°C; typical types of tundra with elements of southern tundra), only 6 species were collected. It is tempting to consider these figures an evidence of a certain trend in the diversity of the arctic fauna when moving away from the "Eoarctic," hypothetical center of formation of the arctic fauna, most probably located near the recent tundra territories of NE Asia. At the same time, it should be kept in mind that the outlined tendencies of the latitude-dependent changes in the recent species diversity are not the same in different parts of the tundra zone. For example, in the subzone of arctic tundra, the number of species is the greatest in the north-eastern sector of Eurasia and sharply decreases eastwards (within the American Arctic) and westwards (to Atlantic Ocean). In typical tundra of Eurasia, the species diversity seems to be at a minimum in the Middle Siberian sector where tundra landscapes are developed at the highest latitudes, hampering penetration of polyzonal and boreal species. In other words, the fauna here is poorer, but is to the greatest extent devoid of non-arctic elements.

The case of ground beetles reveals the general rule of relation between latitudinal-zonal faunal flows: boreal and polyzonal species penetrate into high-latitude landscapes much more actively than arctic species move to the south (Chernov, 1984, 1985). Examples can be given of penetration far into the tundra zone of many boreal and polyzonal species, e.g., *Notiophilus aquaticus* L., *Nebria nivalis* Payk., *Elaphrus riparius* L., *Patrobus septentrionis*, etc., whereas arctic species usually do not occur outside tundra landscapes. Even in high mountains located in the close vicinity of the tundra border, typical arctic species do not dominate over boreal ones. For example, of 9 carabid species collected by O.L. Makarova in the high-altitude variant of tundra communities in the Putorana Plateau, only *Pterostichus brevicornis* is a true arctic species, two species being hypoarctic, and others, boreal.

The distribution of ground beetles can exemplify the general paradoxical rule: polyzonal and boreal species are sometimes more widespread in the tundra zone than many arctic ones. For example, *Notiophilus aquaticus* inhabits the tundra zone as far as arctic tundra and is more common everywhere than the very sporadical and tending to the southern tundra belt *N. hyperboreus* Kryzh.

Ecological Groups

The ecological composition of the arctic carabid complex is not markedly distinctive. Highly specialized types are absent from the biological spectrum, geobionts are few in number, and the

Table 3. Complex of Arctic and tending to Arctic Eurasian carabids[1]

Species	Distribution range	Faunogenetic complex	Life form
Pelophila borealis Payk., 1790	H	IH	sZS
Nebria (*Boreonebria*) *rufescens* Stroem, 1768	P	IH	sZS
N. (*B.*) *nivalis* Payk., 1798	H	MS	sZS
Notiophilus aquaticus L., 1758	H	IH	sZS
N. borealis Har., 1869	H	IH	sZS
N. sibiricus Motsch., 1844	EP	IH	sZS
N. hyperboreus Kryzh., 1995	S	IH	sZS
Carabus (*Morphocarabus*) *henningi* Fisch., 1817	EP	MS	lZE
C. (*M.*) *odoratus* Motsch., 1844	EP	MS	lZE
C. (*M.*) *mestscherjakovi* Lutshn., 1918	S	MS	lZE
C. (*Aulonocarabus*) *truncaticollis* Esch., 1833	EP	MS	lZE
Diacheila arctica Gyll., 1810	P	IH	ZS
D. polita Fald., 1835	H	IH	sZS
Blethisa catenaria Brown, 1944	H	IH	sZE
B. multipunctata L., 1758	P	IH	sZE
Elaphrus (*Arctelaphrus*) *lapponicus* Gyll., 1810	H	IH	sZE
E. (s. str.) *parviceps* Van Dyke, 1925	H	IH	sZE
E. (s. str.) *riparius* L., 1758	P	IH	sZE
E. (s. str.) *tuberculatus* Mäkl., 1877	H	IH	sZE
E. (*Elaphroterus*) *angusticollis* R. Sahlb., 1844	H	IH	sZE
Miscodera arctica Payk., 1798	H	TS	ZG
Bembidion (*Bracteon*) *lapponicum* Zett., 1828	H	IH	sZE
B. (*Plataphus*) *hyperboraeorum* Munst., 1923	H	IH	sZS
B. (*Plataphodes*) *arcticum* Lindr., 1963	H	IH	ZS
B. (*P.*) *crenulatum* R. Sahlb., 1844	P	IH	sZS
B. (*P.*) *difficile* Motsch., 1844	P	IH	sZS
B. (*P.*) *fellmanni* Mnnh., 1823	P	IH	sZS
B. (*Hirmoplataphus*) *hirmocoelum* Chaud., 1850	P	IH	sZS
B. (*Trichoplataphus*) *hasti* C. Sahlb., 1827	H	IH	sZS
B. (*Ocydromus*) *grapei* Gyll., 1827	H	IH	sZS
B. (*O.*) *yuconum* Fall, 1926	H	IH	sZS
B. (*O.*) *dauricum* Motsch., 1844	H	IH	sZS
B. (*O.*) *lenae* Csiki, 1928	H	IH	sZS
Patrobus septentrionis Dej., 1828	H[2]	IH	ZS
Poecilus (*Derus*) *nordenskjoeldi* J. Sahlb., 1880	EP	TS	sZS
Pterostichus (*Tundraphilus*) *sublaevis* J. Sahlb., 1880	H	MS	bZS
P. (*Cryobius*)[2] *ventricosus* Esch., 1823	H	MS	bZS
P. (*C.*) *middendorffi* J. Sahlb., 1875	EP	MS	bZS
P. (*C.*) *brevicornis* Kirby, 1837[3]	H	MS	bZS

Table 3. (Contd.)

Species	Distribution range	Faunogenetic complex	Life form
P. (*C.*) *pinguedineus* Esch., 1823	H	MS	bZS
P. (*C.*) *theeli* Mäkl., 1877	EP	MS	bZS
P. (*C.*) *longipes* Popp., 1906	S	MS	bZS
P. (*C.*) *nigripalpis* Popp., 1906	P	MS	bZS
P. (*C.*) *macrothorax* Popp., 1906	EP	MS	bZS
P. (*C.*) *scitus* Mäkl., 1877	EP	MS	bZS
P. (*C.*) *parviceps* Popp., 1906	EP	MS	bZS
P. (*C.*) *argutoriformes* Popp., 1906	EP	MS	bZS
P. (*Lenapterus*) *agonus* Horn, 1880	H	MS	bZS
P. (*L.*) *costatus* Mén., 1851	H	MS	bZS
P. (*L.*) *vermiculosus* Mén., 1851	H	MS	bZS
P. (*L.*) *abnormis* J. Sahlb., 1880	S	MS	bZS
P. (*Petrophilus*) *tundrae* Tschit., 1894	EP	MS	bZS
P. (*Stereocerus*) *rubripes* Motsch., 1860	H	MS	bZS
P. (*S.*) *haematopus* Dej., 1831	H	MS	bZS
Agonum (s. str.) *dolens* C. Sahlb., 1827	P	IH	sZS
A. (s. str.) *ericeti* Panz., 1809	P ?ep	IH	sZS
A. (*Europhilus*) *consimile* Gyll., 1810	H	IH	sZS
A. (*E.*) *exaratum* Mnnh., 1853	H	IH	sZS
A. (E.) gratiosum Mnnh., 1853	H (A)	IH	sZS
Amara (s. str.) *aeneola* Popp., 1906	EP	MS	sMS
A. (*Celia*) *interstitialis* Dej., 1829	H	MS	sMS
A. (*Reductocelia*) *arcticola* Popp., 1906[4]	S	?TS	zMS
A. (*R.*) *colvillensis* Lindroth, 1968	H	?TS	zMS
A. (*Bradytus*) *glacialis* Mnnh., 1853	H	TS	zMS
Curtonotus alpinus Payk., 1790	H	TS	zMS
C. bokori Csiki, 1929	?H	TS	zMS

Distribution range: H, Holarctic; P, Palaearctic; EP, Eastern Palaearctic; S, Siberian. Faunogenetic complex: MS, montane Siberian; TS, tundra steppe; IH, intrazonal hygrophilous. Life forms: sZE, small zoophagous epigeobionts; lZE, large zoophagous epigeobionts; sZS, slit-dwelling zoophagous stratobionts; bZS, burying zoophagous stratobionts; ZG, zoophagous geobionts; sMS, slit-dwelling mixophytophagous stratobionts; zMS, zabroid mixophytophagous stratobionts.

[1] Systematics and distribution are cited according to: Jacobson, 1905–1916; Lindroth, 1966, 1968, 1992; Kryzhanovskij, 1983; Kryzhanovskij *et al.*, 1995; Erwin, 1997; the authors' data and collection material.

[2] Including Greenland.

[3] Berlov (1998) regarded *brevicornis* species group as a subgenus *Cryobiopterus*. We consider this inexpedient and retain the traditional concept of the subgenus *Cryobius*.

[4] Status and distribution of *Amara arcticola* and *A. colvillensis* are given according to Hieke (1999).

share of epigeobionts is relatively high (Table 3). Therewith, medium-sized species prevail in all groups of life forms, the smallest and largest species being absent.

As to the taxonomic diversity and species richness, the prevalence of typically carnivorous carabids is more clearly pronounced in the tundra zone than in the southern faunas. They furnish most impressive examples of successful adaptation to the arctic environment, inhabiting zonal flat interfluve conditions and northernmost tundra variants. A very poor representation of species morphologically specialized to feeding on a restricted range of prey is characteristic. The sole exception is *Notiophilus* with imagines and larvae feeding mainly on collembolans (Schaller, 1950; Bauer, 1979, 1980, 1982). However, with the high numbers of Collembola in the Arctic taken into account, the abundance of *Notiophilus* species here is relatively low.

In relatively poor tundra communities, the spectrum of available prey must largely determine the structure and diversity of the carabid fauna. Probably it is the lack of food resources that is responsible for the distribution limits of some carabid groups (e.g., such large predators as Carabini) in the Arctic.

The diversity of mainly phytophagous groups sharply decreases as compared with that of the fauna of the temperate belt. The disappearance of Harpalini at the boundary of the tundra zone is especially indicative. At the same time, one group of mainly phytophagous carabids (tribe Zabrini) has adapted to arctic conditions quite successfully. Moreover, one species of this group, *Curtonotus alpinus* (most important dominant of various kinds of communities), shows successful adaptation to a broad spectrum of tundra conditions, including all the subzones. This astoundingly resembles the situation in the avifauna, where, on the background of generally increasing share of carnivores, a few species of polyphages capable of phytophagy show especially striking examples of ecological prosperity at high latitudes (Chernov, 1992).

Such an important indicator as cold resistance varies widely in arctic ground beetles. The typical tundra species *Pterostichus brevicornis* tolerates winter temperatures as low as –35°C, and even short-term freezing to –87°C (Miller, 1969). On the other hand, a temperature of –10°C appears to be lethal for *Pelophila borealis*, the widespread and common in tundra species (Conradi-Larsen and Sömme, 1973).

The developmental biology of arctic carabids is poorly known (Kaufmann, 1971; Larsson and Gigja, 1959; Lindroth, 1966, 1968, 1992; Thiele, 1977; Korobeinikov, 1980, 1981, 1982, 1984; Ryabitsev, 1997; etc.). Generally, an increase in the number of species hibernating as larvae is characteristic of the North. So, in the territory of western Europe the share of such species ranges between 7 and 38%, reaching 50% in Greenland and 56% in Iceland (Larsson and Gigja, 1959; Heydemann, 1962; Thiele, 1977). As regards the seasonal dynamics, traditional groups of species with vernal and autumnal reproductive activity can be distinguished (Korobeinikov, 1981, 1984; Ryabitsev, 1997). However, peaks of activity are largely overlapping because of the short vegetation season, which corresponds to the tendency of zonal shift of developmental cycles, common to carabids (Sharova, 1990). In addition, some species can develop as either “vernal” or “autumnal,” depending on weather conditions and biotope. In fact, the seasonal dynamics of most arctic carabids should be characterized as a polyvariant one (Makarov, 1994) with prevalence of one or another seasonal strategy.

Possibly, the ability to extend the developmental cycle to several seasons, with larvae hibernating repeatedly and imagines living several years, is the only feature characteristic of the arctic carabid biology (Lindroth, 1966, 1968, 1992; Korobeinikov, 1982, 1984; Ryabintsev, 1997). The prolongation of development has been recorded for all carabid groups inhabiting the Arctic, being an exception rather than the rule only for Notiophilini and Bembidiini. This phenomenon has also been recorded for some xerophilous carabids. This feature of the carabid development is in agreement with the character of life cycles and adaptive strategies in other groups of arctic insects (Chernov, 1978b, 1984).

The limits of distribution and variation of the total species diversity of carabids in the Arctic territory mainly result from the combination of three groups of factors: climatic conditions, landscape structure, and the history of the fauna formation. Hitherto, the role of ecological, morphological, and physiological features of carabid species and higher taxa in adaptation to arctic conditions has not been clarified adequately. The tendencies of trophic specialization, adaptive features in life cycles, and ways of formation of the adaptive strategy in arctic species deserve special consideration. The problem of phylogenetic prerequisites and the importance of the degree of evolutionary advancement are of particular interest and will be discussed in the next communication. It is obvious that carabids, one of the dominant groups in the arctic insect fauna, can serve as an excellent model object for studying the adaptive mechanisms in high-latitude conditions.

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