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Family of Ground Beetles (Coleoptera, Carabidae) in the Arctic Fauna: Communication 2

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Abstract—The Arctic fauna of ground beetles includes 25–27 genera belonging to about 20 tribes, most of which are represented by 1–2 genera. Many genera and taxa of the higher rank, constituting a significant part of the Holarctic fauna, are absent from Arctic. As in other insect groups, the number of Arctic species in a given taxon shows no direct relationship with the total species number in this taxon. Small genera constitute an essential part of the Arctic ground beetle fauna. A review of the species diversity of tribes and genera constituting the Arctic carabid fauna is presented. The Mountain Siberian, tundra-steppe, and intrazonal hygrophilous complexes are characterized. The family does not contain hyperarctic forms; 2–3 euarctic, about 15 hemiarctic, and 20 hypoarctic forms can be distinguished. The general trend of increasing number of taxa from the basal part of the family's phylogenetic scheme and number of groups and species with some primitive and plesiomorphic features is noted.

In the first communication (Chernov *et al.*, 2000), we discussed the specific diversity of ground beetles and latitudinal limits of their distribution in the Arctic in relation to the landscape and climatic conditions, ecological composition of the fauna, etc. This analysis was primarily based on the available literature (mostly concerning the Eurasian Arctic sector), results of the authors' field work, and the collection material. The present communication is devoted to analysis of the taxonomic structure of ground beetle fauna in the Arctic and to some aspects of the formation of this fauna in the tundra zone.

Number of Representatives and Species Composition of Higher Taxa

The Arctic ground beetle fauna includes about 25–27 genera belonging to nearly 20 tribes. Most tribes are represented by only one or two genera: Carabini (*Carabus*), Notiophilini (*Notiophilus*), Bembidiini (*Bembidion*), Agonini (*Agonum*), Pterostichini (*Poecilus* and *Pterostichus*), Nebriini (*Nebria* and *Pelophila*), Zabrini (*Amara* and *Curtonotus*); and only the tribe Elaphrini comprises three genera (*Blethisa*, *Diacheila*, and *Elaphrus*). This structure evidently results from the reduction of the initial complex and can be regarded as a good example of a deficient fauna.

The ground beetle fauna of the Arctic lacks a number of major higher taxa, which constitute an essential part of the Holarctic complexes, in particular the subfamilies Cicindelinae, Omophroninae, Brachininae, and Paussinae. Of the subfamily Carabinae, the Arctic fauna includes no representatives of the supertribes Siagonitae, Panagaeitae, and Callistitae, and also of the large and diverse complex of tribes belonging to Lebiomorpha (except for a few species of *Cymindis*). A considerable number of genera, well represented in the boreal forest zone, such as *Harpalus*, *Loricera*, *Trechus*, and *Dyschirius*, can only tentatively be included in the Arctic fauna, because their northern distribution is restricted to the forest-tundra or southernmost tundra areas.

The number of representatives of a particular taxon found in the tundra is not proportional to its total diversity. Among the largest genera (*Nebria*, *Carabus*, *Dyschirius*, *Bembidion*, *Pterostichus*, *Amara*, and *Harpalus*), only *Pterostichus* and (to a lesser extent) *Bembidion* show no abrupt decrease of diversity at the southern tundra boundary. *Pterostichus* is characterized by high level of biological advance and a rather broad adaptive radiation in these landscape and climatic conditions. Several large carabid genera are represented in the Arctic fauna by certain subgenera only (e.g., *Aulonocarabus* and *Morphocarabus* within *Carabus*, *Europhilus* within *Agonum*, etc.). At the same time, a considerable part of the fauna, including its Arctic fraction proper, is formed by such small genera as *Pelophila*, *Notiophilus*, *Diacheila*, and *Elaphrus*. A similar proportion of taxa is observed in

the Arctic fauna of Diptera. This phenomenon indicates that the adaptation to Arctic conditions is determined primarily by specific biological preadaptations and ecological peculiarities, rather than by the overall diversity and evolutionary potentials of a taxon (Chernov, 1984, 1995a).

The tribe Pterostichini is a major group of the Arctic ground beetle fauna. The vast majority of species of this tribe, present in the tundra zone, belong to the genus *Pterostichus*, whereas another genus, *Poecilus*, is represented by only two species not characteristic of tundra. Relatively few subgenera of *Pterostichus*, namely, *Cryobius*, *Stereocerus*, *Tundraphilus*, and *Lenapterus*, have successfully adapted to the tundra landscapes.

The features of Arctic fauna are most evident in species of the subgenus *Cryobius*, which includes typical tundra forms, associated with zonal communities, in particular various kinds of the moss-sedge small-tussock and patchy tundra. This subgenus mostly comprises small or, less frequently, medium-sized beetles. The adaptive success of this group in the Arctic conditions is in agreement with the general trend of miniaturization, characteristic of the high latitudes (Matveeva and Chernov, 1976; Chernov, 1984, 1985).

Of the 44 species of this subgenus found in Russia and adjacent countries (Eremin, 1990), about 20 species have been recorded in the tundra zone. Of these, about 15 species are endemic to this zone or predominantly distributed in the tundra landscapes. Most characteristic Arctic elements within *Cryobius* are the Holarctic, nearly circumpolar species *P. brevicornis* Kirby and, to a lesser extent, *P. pinguedineus* Eschsch., inhabiting the Siberian tundra landscapes from forest-tundra to the northern zonal boundary, and from Yamal Peninsula to Wrangel Island. *P. ventricosus* Esch. is also very characteristic of Subarctic landscapes; this species is broadly distributed in Siberian tundra, and replaced farther southwards by closely related forms, including *P. middendorfi* Mnnh. in E Siberian mountains and *P. subgibbus* J. Sahlb. in Kuril Islands. A number of species of this subgenus are broadly distributed in the American Arctic (see Ball, 1963, 1966; Lindroth, 1966; Danks, 1981; Erwin, 1997). These forms include, e.g., *P. arcticola* Chaud. (*brevicornis* group), broadly distributed in American Polar regions; *P. barryorum* Ball, occurring mostly in NW Canada and Alaska; *P. hudsonicus* LeC., found mostly in Subarctic territories of southern tundra, forest-tundra, and northern taiga; *P. caribou* Ball, inhabiting Arctic and Subarctic territories west of Hudson Bay, etc.

Danks (1981) reported 19 species of this subgenus from the American Arctic. However, the species lists compiled for the Palaearctic and Nearctic cannot be compared, because the taxonomy of the subgenus is still insufficiently developed, and the relation of some American and Eurasian forms remains obscure (see Eremin, 1998).

Some very typical inhabitants of Arctic landscapes belong to the subgenus *Lenapterus*: *P. agonus* Horn, *P. costatus* Men., *P. vermiculosus* Mén., *P. abnormis* J. Sahlb., etc. This group of medium-sized beetles reveals a distinct biotopic separation accompanied by noticeable morphological differentiation. For example, *P. costatus* is a hygrophilous species preferring moist and swamped areas; *P. vermiculosus* is a typical mesophilic species preferring in the subzone of typical tundra forb and forb-shrub communities.

Representatives of the subgenus *Stereocerus*, *P. haematopus* Dej. and *P. rubripes* Motsch., can also be regarded as typical inhabitants of tundra landscapes. According to Kryzhanovskii (1983), *Stereocerus* is one of the most ancient autochthonous taxa of the tundra.

The two last subgenera are the most important in the ground beetle fauna and communities of the typical tundra subzone. However, the diversity of these subgenera is much lower in Arctic tundra: for example, the fauna of Wrangel Island includes only one representative of either subgenus: *P. agonus* and *P. rubripes*. Species of these subgenera have not been found in the northernmost variants of the Arctic tundra subzone of Taimyr Peninsula, for example, in the lower course of Uboinaya River.

In all, more than 60 species of *Pterostichus* occur in the Arctic taken in the broadest limits, and about 50 species, within the boundaries of the tundra zone proper. Arctic representatives of this genus have no distinct morphological specializations, except for the greater diversity of sculpture, which widely varies even within a species. At the same time, a number of tundra-dwelling species of *Pterostichus* possess highly specialized relative petrobionts in Siberian mountains. These are species of the subgenera *Cryobius* (*P. negligens* Sturm, *P. kaninensis* Popp., and *P. planus*

J. Sahlb.) and *Tundraphilus*. The last subgenus reveals a morphological cline from the tundra-dwelling *P. sublaevis* J. Sahlb., via *P. kamtschaticus* Motsch. and *P. pfitzenmayeri* Popp., to the highly specialized *P. orion* Tschit., which inhabits the scree areas of mountain tundra of E Siberia (Brinev and Makarov, 1999).

The tribe Bembidiini, represented by the single genus *Bembidion*, occupies the second place in the Arctic fauna with respect to species diversity. About 20 species have been found so far in the tundra zone of Eurasia, and approximately the same number of species is known from the American Arctic (Danks, 1981). The Polar regions are mostly preferred by species of the subgenera *Bracteon* (*B. lapponicum* Zett. and *B. foveum* Motsch.), *Plataphodes* (*B. difficile* Motsch. and *B. fellmani* Mnnh.), *Plataphus* (*B. hyperboraeorum* Münster), *Trichoplataphus* (*B. hasti* C.R. Sahlb.), and to a lesser extent *Ocydromus* (*B. grapei* Gyll, *B. lenae* Csiki, *B. dauricum* Motsch., and *B. yukonum* Fall). However, the pattern of latitudinal distribution of these species, inhabiting intrazonal elements, and the number of Arctic species in this group remain obscure. Their northernmost locations lie predominantly in forest-tundra areas close to the treeline. Many boreal species enter the southern tundra subzone, whereas their number strongly decreases in the subzone of typical tundra, and only few species occur in Arctic tundra. For example, Khruleva (1987) found two species in Wrangel Island, and only *B. hasti* was found by the authors in the Arctic tundra subzone of Taimyr Peninsula. Danks (1981) reported 20 species of *Bembidion* for the "Low Arctic" of America (corresponding mostly to the typical tundra territories in our classification), and none for the "High Arctic." The highest-latitude distribution is characteristic of the circumpolar species *B. hasti*.

The tribe Carabini is represented in the tundra zone by about 5–7 species of the genus *Carabus*. Speaking in ecological terms, the Arctic group of *Carabus* species is clearly monodominant. Among the species present in Polar landscapes, *C. (Aulonocarabus) truncaticollis* Eschsch. alone, inhabiting forest-tundra, southern and typical tundra of Eurasia from Polar Urals to Chukchi Peninsula and Wrangel Island (*C. t. fleischeri* Rtt.), and Alaska (the nominotypical subspecies), can be considered an Arctic species in Eurasia. Its distribution as a whole can be classified as metaarctic (Yurtsev, 1977), because its range includes, in addition to the tundra part, also all mountain areas of Siberia, extending southwards to Lake Baikal, Olekminsk Plateau, and Amur area. In the southern part of its range, this species is restricted to mountain tundra, where it is represented by a small melanistic form, regarded as the subspecies *C. t. dorogostaiskianus* Deuve & Imura. This kind of distribution is characteristic of many Siberian *Carabus* species. For example, the closely related species *C. kolymensis* Lafer also has a similar mountain form, *C. k. kodarensis* Brinev (Brinev, 1997). It should be noted that the common practice of giving these forms a subspecies rank is not always sufficiently justified.

Since Late Cenozoic (Pleistocene), *C. truncaticollis* has been the most abundant and broadly distributed species of the genus and one of the common carabids in northern Siberia (see Kiselev, 1981). It is very abundant in some tundra areas. For example, in Syradasai and Ragozinka basins (NW Taimyr Peninsula, northern part of the typical tundra subzone), *C. truncaticollis* was reported among the most abundant beetle species captured in pitfall traps in some years, e.g., in 1983 and 1990, respectively. Dozens of specimens were captured by pitfall traps. As shown by the mass collections from Kolyuchinkaya Inlet coast (courtesy of R.I. Zlotin), this species may also be very abundant in the Northeastern Asian tundra. Yet, *C. truncaticollis* has been only occasionally recorded, if at all, in other tundra regions. For example, it was rare during several years near the Tareya Field Station. The sharp changes in its population density are possibly accounted for by the synchronous development of most larvae in the given population and the mass emergence of adults in some years. The species is absent from most territories of the Arctic tundra subzone, but present in Wrangel Island (Khruleva, 1987). Adults of *C. truncaticollis* widely vary in coloration and size. This species can evidently serve as a good model for various population-ecological studies in the Arctic.

A quite noticeable and typical component of the Polar carabid fauna is formed by species of the subgenus *Morphocarabus* (*C. henningi* Fisch., *C. odoratus* Motsch.) and closely related forms (*C. mestscherjakovi* Lutsh., *C. shilenkovi* O. Berlov). These Siberian species are broadly distributed in the Subarctic landscapes, forest-tundra, and, partly, southern tundra. For example, *C. henningi* and *C. odoratus* were found by the authors near Khatanga and Norilsk, and also reported from the forest-tundra of Yamal Peninsula (Andreeva and Eremin, 1991). The range of *C. odo-*

ratus covers almost all mountain regions of Siberia. This species is widely variable, with more than 15 subspecies presently distinguished (Shilenkov, 1996; Obydov, 1999). *C. odoratus* exhibits various morphological clines, including the populations with clear traits of petrophilic specialization (Brinev and Makarov, 1999). Two subspecies are traditionally recognized in the northern part of its area: the western *C. odoratus septentrionalis* Breun. (west of Yenisei River), and the eastern *C. o. baeri* Mén. However, these subspecies have no clear distinction, and their status is doubtful. *C. henningi* also has broad distribution, but is absent from Northeastern Asia and Kamchatka. Among its subspecies, a specific "dark" tundra-dwelling form, *C. h. oviformis* Beham & Breun., has been described from Polar Urals. Still, none of *Morphocarabus* species can be regarded as truly Arctic species, even in the broad sense.

According to some evidence, these species, like *C. truncaticollis*, are characterized by sharp changes of adult abundance in high latitudes, with long-term cyclicity and population outbreaks in some years. For example, the collection of the Zoological Institute, Russian Academy of Sciences, includes a series of over 100 *Carabus odoratus* specimens from the material of the Russian Polar Expedition, labeled "Mountains, env. of Bulun, near the Lena delta, V.93." So many specimens of *Carabus* could evidently be collected only if these large beetles were unusually abundant in that year. It is interesting that the collections of A. Tsybul'skii from Ust-Lenskii Nature Reserve included no specimens of *C. odoratus*, whereas three other *Carabus* species, *C. truncaticollis*, *C. henningi*, and *C. ermaki* Lutsh., were represented by few specimens, which indicates thorough collecting.

Several boreal species of *Carabus* occur in the forest-tundra and, partly, southern tundra of Eurasia: *C. (Morphocarabus) hummeli* Fisch., *C. (Aulonocarabus) canaliculatus* Ad., *C. (Hemicarabus) nitens* L., *C. (Megodontus) vietinghoffi* Ad., *C. (Carabulus) ermaki* Lutsh., etc. The steppe species *C. (Trachycarabus) sibiricus* Fisch. has been found in S Yamal (Andreeva and Eremin, 1991); this part of its range may be regarded a relict of the preglacial tundra-steppe fauna. One more *Hemicarabus* species, *C. macleayi* Dej., has been recorded in northern W Siberia, and *C. (Diocarabus) loschnikovi* Fisch. occurs in the mountain tundra of the Polar Urals. *C. (Hadrocarabus) problematicus* Herbst, previously considered a W European species, proved to be quite common in the mountain tundra of Khibiny, and a single specimen was found in Krasnoyarsk Territory (Nazarovo Vill., collected by Tsurikov).

Several *Carabus* species have been reported from the American Arctic: *C. chamissonis* Fisch., *C. meander* Fisch., and *C. vietinghoffi* Ad. (Danks, 1981). *C. chamissonis* is one of the smallest species of *Carabus*; it has a broad boreal American distribution and occurs in forest-tundra, where it prefers open dry areas, and, probably, in southern tundra. It seems that species of *Carabus* are more poorly represented in high latitudes in America than in Eurasia.

Thus, only one species of the genus *Carabus*, namely *C. truncaticollis*, has quite successfully adapted to the tundra environment. No less than 12 boreal species of this genus occur in Subarctic landscapes, forest-tundra, and, partly, southern tundra, and can therefore be considered to belong to the Arctic fauna in the broad sense.

The Arctic fauna also includes a very interesting species *Trachypachis zetterstedti* Gyll. This species belongs to a separate subfamily (or even family Trachypachidae), resembling the Mesozoic group Eodromaeinae in a set of archaic characters (Ponomarenko in Arnoldi *et al.*, 1977). *T. zetterstedti* was common in tundra-like, tundra-steppe, forest-tundra, and taiga landscapes of Late Cenozoic (Kiselev, 1981). Now, it is distributed in the taiga zone, reaching forest-tundra; its range extends from Scandinavia to Sakhalin and Primorskii Territory (Kryzhanovskii, 1983).

The tribe Zabrini s. l. is represented in the Arctic fauna by about 10 species (not including those occasionally present in the southern forest-tundra) of the genera *Amara* and *Curtonotus*. Similarly to what was described in the Arctic Carabini, the tribe Zabrini is dominated in high-latitude landscapes by *Curtonotus alpinus* Payk. This species is probably the most noticeable and cenotically important among not only Carabidae, but all beetles in most territories of the middle part of the tundra zone (typical tundra and southern half of the Arctic tundra subzone). It played the same role in the high-latitude carabid communities during the entire Late Cenozoic period (Kiselev, 1981). This species has an arctoalpine, almost circumpolar (except for Greenland) distribution (see fig. 1 in Chernov *et al.*, 2000). Even though its abundance decreases abruptly in Arctic tundra of Taimyr Peninsula, this species is common and polytopic in Wrangel Island. It also has the highest-altitude distribution among

ground beetles in the American Arctic sector. *C. alpinus* inhabits various intrazonal forb-shrub and mesophytic forb-grass communities (being especially abundant in the latter), as well as zonal biotopes on uplands. In other words, this species has fully explored the zonal tundra space (see Chernov, 1966, 1973, 1978, 1980) and can be regarded as a form with maximum cenotic activity in the Arctic conditions, or a superdominant in our terminology (Chernov, 1985, 1995b). In addition, this species is a good example of successful exploration of tundra by a descendant from the steppe fauna.

At least two more species of *Curtonotus*, *C. bokori* Csiki and *C. hyperboreus* Dej., are present in the tundra: the former can be considered a sibling species of *C. alpinus.* These beetles are similar in habitus and reveal almost identical variation series in coloration; they differ primarily in the morphology of genitalia and other secondary sex characters of males. However, *C. bokori* has a noticeably narrower distribution, being restricted to NW America and the eastern sector of Eurasian Arctic.

The genus *Amara* is represented in the Arctic by a few species of several subgenera. The most typical are two species of the subgenus *Reductocelia*: *Amara colvillensis* Lindr. and *A. arcticola* Popp. The distribution of these species resembles that of *Curtonotus alpinus* and *C. bokori*, considered above: *A. colvillensis* is broadly distributed in North America and occurs also in N Asia east of Lena River (Hieke, 1999), whereas *A. arcticola* is known from tundra of N Yakutia (lower Lena). These beetles belong to the smallest species within *Amara*: some of our specimens of *A. colvillensis* are only 4.3 mm long. The Arctic representative of the subgenus *Bradytus*, *A. glacialis*, resembles *A. colvillensis* in morphology and, probably, habits. The subgenus *Celia* is represented by the two widespread species, *A. quenseli* Schoenh. and *A. interstitialis* Dej., which occur in the entire northern territory of Eurasia and America, and partly in the mountains of Europe, Caucasus, and the Far East. Representatives of the nominotypical subgenus enter the tundra zone mostly along the intrazonal landscapes, inhabiting only warm southern slopes with meadow vegetation (e.g., *A. aeneola* Popp.).

It should be noted that typical Arctic forms of the tribe Zabrini are characterized by an unusually high morphological variability of size, coloration, and shape of pronotum and other body parts (Hieke, 1999; and our data), as compared with their congeners from more southern areas. It is important that this trend is equally distinct in remotely related species (*Curtonotus alpinus*, *Amaro glacialis*, and *A. colvillensis*).

The small tribe Elaphrini is a rather essential component of the Arctic carabid fauna. The relatively high proportion of the genera *Elaphrus* and *Bembidion* demonstrates the role of intrazonal waterside biotopes in polyzonal distribution (Chernov, 1975). At least 5 species of *Elaphrus* occur regularly in the tundra zone, reaching the northern belt of the typical tundra subzone. Among these, the commonest both in America and in Eurasia are the polyzonal *E. riparius* L. and *E. lapponicus* Gyll., preferring more northern landscapes and mountain tundra. The boreal *E. angusticollis* R. Sahlb. and *E. tuberculatus* Mäkl., are less abundant.

The remaining two genera of this tribe are represented in the Arctic fauna by two species each: *Diacheila polita* Fald., *D. arctica* Gyll., *Blethisa catenaria* Brown, and *B. multipunctata* L. All these species are broadly distributed in northern Polar regions, occur in various Subarctic landscapes, and can be included in the Arctic complex in the broad sense. These taxa exhibit the same chorological trend which was observed in the tribe Zabrini. Each genus is represented by one widespread species (although having an ecological optimum in the northern part of its range), and one species with local distribution. In particular, *B. multipunctata* is common in the tundra, reaches as far southwards as Ciscaucasia, and occurs in forest biotopes in North America. *B. catenaria* is distributed in NW America and NE Eurasia and occurs only in open landscapes (Morgan *et al.*, 1986). Most characteristic in this respect is *Diacheila polita*, a monotypic species with the broadest distribution in the tundra among Elaphrini; by contrast, *D. arctica* has a disrupted range and forms several subspecies (Lindroth, 1954).

The tribes Agonini, Nebriini, and Notiophilini are represented in the tundra zone by 4–5 species each. Some species, like *Notiophilus hyperboreus* Kryzh. and *Agonum exaratum* Mnnh., belong to the Arctic complex in the broad sense; but most species are boreal, broadly distributed in the tundra zone: *Pelophila borealis* Payk., *Nebria rufescens* Stroem, *N. nivalis* Payk., *Notiophilus aquaticus* L., and *Agonum consimile* Gyll.

Representatives of other tribes usually do not extend northwards beyond the southern tundra boundary,

and more often are restricted to forest-tundra. For example, the fauna of S Yamal includes the following common species: *Loricera pilicornis* F. (Loricerini), *Dyschiriodes nigricornis* Motsch. and *D. politus* Dej. (Dyschiriini), *Calathus melanocephalus* L. and *C. micropterus* Duft. (Sphodrini), *Harpalus fuliginosus* Duft., *H. affinis* L., *H. nigritarsis* C.R. Sahlb., *Dicheirotrichus* (*Oreoxenus*) *mannerheimi* R. Sahlb. (Harpalini), *Cymindis vaporariorum* L. and *C. macularis* Dej. (Lebiini).

In Pliocene–Pleistocene, representatives of *Harpalus* (*H. obtusus* Gebl. and *H. vittatus* Gebl. species groups) were broadly distributed over the Northeastern Asian territories, presently occupied by tundra (Kiselev, 1981). Now, however, these forms only occasionally extend beyond the Polar circle and, partly, into the tundra zone.

Thus, the Arctic carabid complex proper includes two characteristic groups: (a) few species of large and ecologically diversified genera with boreomontane or similar type of distribution (*Nebria*, *Carabus*, *Bembidion*, *Pterostichus*, *Agonum*, *Amara*, and *Curtonotus*), and (b) species of small genera and tribes (Pelophilini, Notiophilini, and Elaphrini), mostly associated with waterside biotopes.

Faunogenetic Complexes

Owing to the small number of Arctic species and a considerable level of knowledge of ground beetles, their distribution can be analyzed by considering the possible ways of faunogenesis. Such an analysis is based not only on the present-day distribution of Arctic species and their landscape preferences, but also on their distribution in the recent geological history (Kiselev, 1981). In addition, data on the landscape distributional pattern of related taxa, zonal occurrence and endemism in Arctic species proper and related forms are taken into account. Comparative analysis of these parameters reveals three major faunogenetic complexes in the Arctic fauna of Carabidae.

The mountain Siberian complex. These forms are genealogically related to the mountain carabid complex, primarily Angarian, or E Siberian. These forms typically have closely related species or even subspecies in E Siberian mountains. For such taxa, the related forms can often be arranged in a series relating the typical tundra-dwelling beetles and mountain species: e.g., *Carabus* (*Aulonocarabus*) *truncaticollis—C. kolymensis—C. gaschkewitschi* Mor.—*C. gossarei imanensis* Lafer—*C. gossarei gossarei* Haury; *Pterostichus* (*Cryobius*) *negligens—P. kaninensis—P. planus; Pterostichus* (*Tundraphilus*) *sublaevis—P. kamtschaticus—P. orion—P. pfitzenmayeri.* These series exhibit the parallel increase of biotopic specialization: modification of sculpture, flattening and elongation of body, and elongation of appendages. In some taxa (e.g., subgenus *Lenapterus*), the transformation series can be observed only for selected characters: sculpture, body shape, etc. The tundra-dwelling forms in this faunogenetic group generally show no trend toward miniaturization. Some species of this complex are associated with plain upland tundra.

At the same time, these species usually have a complicated infraspecies structure, with the mountain form often being separated as a subspecies. The endemism in some members of the mountain Siberian complex is accounted for by disjunctions in mountain systems, whereas the Arctic forms include almost no endemics. Still, even the species broadly distributed in the tundra zone (e.g., *Pterostichus brevicornis*) have regional forms, sometimes recognized as subspecies. The geographic forms may originate, e.g., by separation of parthenogenetic populations (Ball, 1966). Geographic clines are uncommon in species of this complex; when present, they more often have a longitudinal direction.

In our opinion, this complex includes most species of *Carabus*, some subgenera of *Pterostichus*: *Cryobius*, *Lenapterus*, *Tundraphilus*, and *Stereocerus*, a number of *Agonum* species, and also *Amara aeneola*.

The Arctic distribution of these species can be regarded as the result of migrations from mountain regions of Siberia, which were not covered by the glaciers. Correspondingly, only few members of this complex have migrated into the European Arctic sector during the postglacial epoch, and almost no such forms occur in the Canadian Arctic Archipelago. The faunogenetic boundary of this complex is determined by the area of the maximum Holocene (Valdai) glaciation.

The tundra-steppe complex includes the species whose closest relatives probably inhabited the Pleistocene tundra-steppe zone (Kiselev, 1995). The recent taxa, closely related to these species, are associated mostly with arid landscapes, most often with various kinds of steppe; mountain species occur only in Middle and Central Asia.

The distribution of these species typically has disjunctions of the arctoalpine type. No series of transi-

tional forms, reflecting adaptation to the tundra conditions, are observed. Morphological adaptations are mostly related to miniaturization. Such forms are, e.g., northern species of *Amara* (*Bradytus*), *Poecilus* (representatives of the subgenus *Derus*: *P. nordenskjoeldi* J. Sahlb. in the Palaearctic and *P. nearcticus* Lindr. in North America). These species are often associated with warm slopes occupied by meadow communities.

Species of this complex are quite uniform morphologically and generally do not form subspecies. However, their overall geographic variability is sometimes quite significant, being manifested both in latitudinal clines and in the existence of local forms. The Arctic species of this group include no endemics, but closely related forms may occur in different sectors of the Arctics. This is true for, e.g., the previously considered pairs of species: *Curtonotus alpinus—C. bokori*, *Amara glacialis—A. arcticola*, etc.

This complex includes *Miscodera*, *Poecilus*, *Amara* (s. str., *Bradytus*), *Curtonotus*, *Cymindis*, and possibly some representatives of *Carabus* (*C. chamissonis*, relict populations of *C. sibiricus).*

The faunogenetic boundaries for these species are difficult to describe, because the distribution of many of them have changed repeatedly in the course of glaciations.

The intrazonal hygrophilous complex includes many ground beetle groups with broad Arctic distribution. In general, the high degree of hygrophily can be regarded as preadaptation to life in the tundra zone. In addition, these species have high migration potentials, related to the existence in transient biotopes. Members of this complex appear to have repeatedly colonized the tundra zone in accordance with the climatic changes. This probably prevented isolation and morphological differentiation between their populations.

These biological features have determined the rather broad distribution of many species and the absence of zonal endemics in this group (the only exception being *Notiophilus hyperboreus*).

The complex includes species of *Pelophila*, *Nebria*, *Notiophilus*, all Arctic representatives of Elaphrini, Bembidiini, Patrobini, and some species of *Agonum* (*Europhilus*). One can distinguish a group of species associated with lotic waters, typically pebbly river banks. This group includes mostly the subgenera *Bracteon*, *Plataphus*, *Plataphodes*, and *Trichoplataphus* of the genus *Bembidion*.

It is noteworthy that many of the species groups, classified into the mountain Siberian or tundra-steppe complexes, include at least one form with a broad northern Nearctic distribution. Examples of such distributional pattern can be found in the subgenera *Aulonocarabus*, *Tundraphilus*, *Derus*, *Reductocelia*, and in the genus *Curtonotus*. In all these cases, the Nearctic form is a species or subspecies, whose nearest related taxon belongs to the Palaearctic complex. The high-latitude North American representatives of the intrazonal hygrophilous complex are more often phylogenetically related to the Nearctic fauna.

Arctic Species and the Landscape and Zonal Groups

The list of Arctic forms in the broadest sense comprises over 60 species of Carabidae (see table 3 in Chernov *et al.*, 2000), which is about 1/4 of the potential ground beetle fauna of the Arctic. The species included in this list have diverse variants of landscape and zonal distribution: Arctic, arctoalpine, arctoboreal, arcto-boreomontane, etc. Ranges of some of them lie mostly outside the tundra zone. Even though the data are still insufficient to decide which species represent the most typical Arctic forms, their number can be preliminarily estimated at a minimum of 35. Based on the distribution of animals and plants in high latitudes, considering their abundance, biotopic spectra, and occurrence in zonal communities, four complexes have been distinguished (Chernov, 1978, 1985): hyperarctic (typical inhabitants of polar deserts), euarctic (having an optimum in the Arctic tundra subzone and northern part of typical tundra), hemiarctic (optimum in the typical tundra subzone), and hypoarctic (typical inhabitants of southern tundra and forest-tundra).

One can definitely state that no hyperarctic forms are present in the family Carabidae. It still cannot be decided whether any typical eurastic species are ground beetles. Judging from the material collected in Taimyr Peninsula, this kind of zonal distribution may be assumed for two species, *Pterostichus* (*Cryobius*) *brevicornis* and *P. (C.) pinguedineus*. Both manifest a broadly polytopic distribution in the Arctic tundra subzone (e.g., near Dikson, in the lower course of Uboinaya River, and on Marii Pronchishchevoi Inlet coast), as well as in northern part of the typical tundra subzone (south of Dikson, in the basins of the Efremovka, Ragozinka, Syradasai Rivers, the lower course of Pyasina River, etc.). These beetles are highly abundant in a variety of biotopes, from upland plain tundra to meadow communities. *P. pinguedineus* appears to

be more closely associated with upland dry polygonal patchy tundra, although the maximum population density of this species has been recorded, similarly to *P. brevicornis*, in meadow-like forb-grass and forb-shrub communities. These two species distinctly dominate the ground beetle complex in the Arctic tundra subzone of Middle Siberian sector, especially in its northern part: for example, they constituted 111 of the 114 ground beetle specimens collected in the lower course of Uboinaya River. They inhabit nearly the entire territory of the tundra zone, but their abundance and occurrence decrease in its southern part.

No less than 15 carabid species belong to the hemiarctic complex, although the exact number is still difficult to determine. The most demonstrative example of this group is *Curtonotus alpinus*, which inhabits the entire zone but clearly loses its ecological significance in the Arctic as well as in the southern tundra. This species is highly polytopic and abundant in the typical tundra subzone, being present both in upland plain tundra and in various intrazonal landscapes. In some biotopes, such as slopes with rich herb vegetation, *C. alpinus* sometimes surpasses all other carabids in abundance. This species can be quite common in the Arctic tundra subzone as well, mostly in its southern part. For example, it is one of the most abundant and polytopic ground beetles in Wrangel Island. In the Canadian Arctic, this species extends farther to the north than all other ground beetles (fig. 1 in Chernov *et al.*, 2000). It is possible that this species as a whole, or at least its Northeastern-Asian and American populations, should better be considered a transitional form between the hemiarctic and euarctic complexes. In our opinion, another Arctic species of this genus, *Curtonotus bokori*, also should be regarded as a hemiarctic form. *Amara colvillensis*, showing the strongest preference to Arctic habitats among representatives of the genus *Amara*, also can be classified into this complex.

Several species of the subgenus *Lenapterus* (genus *Pterostichus*) should be considered typical hemiarctic forms. The most characteristic of them is the mesophilic *P. vermiculosus.* This species is one of the most common and highly polytopic in the typical tundra subzone. Its distribution is more strongly shifted to the south than that of *C. alpinus:* in particular, *P. vermiculosus* almost never occurs in the Arctic tundra subzone, and in Taimyr Peninsula is absent even at the northern boundary of typical tundra, e.g., in the Ragozinka basin (south of Dikson). One more hemiarctic species of the subgenus is *P. costatus* Mén., which prefers hydromorphic and swamped sedge-moss areas. The hemiarctic group includes also several species of the subgenus *Cryobius*, first of all *P.* (*C.*) *ventricosus*.

The hypoarctic group of ground beetles is evidently larger than the two preceding groups combined, but is even more difficult to outline. In many cases, the hypoarctic species cannot be easily distinguished in the continuum of forms, referred to as arctoboreal, arctoboreomontane, boreomontane, etc. by different authors. In our opinion, a typical hypoarctic form is *Carabus truncaticollis*. Yet, some populations of this species can probably be classified as transitional between the hypo- and hemiarctic complexes. This beetle has the most polytopic distribution in the southern tundra and forest-tundra (Andreeva and Eremin, 1991), but is also abundant in some areas of the typical tundra subzone (see above). It occurs also in Wrangel Island, being restricted to the warmest southern slopes (Khruleva, 1987). The hypoarctic group includes also *Diacheila arctica*, *D. polita*, *Bembidion lapponicum*, *Poecilus nordenskjoeldi*, *Pterostichus* (*Stereocerus*) *haematopus*, *P.* (*S.*) *rubripes*, *P.* (*Cryobius*) *macrothorax* Popp., *P.* (*C.*) *nigripalpis* Popp., *P.* (*Lenapterus*) *agonus*, *P.* (*Petrophilus*) *tundrae* Tschtsch., *Agonum* (*Europhilus*) *exaratum*, etc. All these species are broadly distributed and common in the southern tundra, forest–tundra, and northern taiga, where they most often inhabit various non-upland, generally moist biotopes.

In all, according to our preliminary estimations, the family Carabidae includes 2–3 euarctic, no less than 15 hemiarctic, and 20 hypoarctic species. The total number of Arctic species in the broadest sense (i.e., distributed only in the tundra zone and preferring Arctic and Subarctic landscapes: the categories of euarctic, hemiarctic, hypoarctic, arctoalpine, and arctoboreomontane forms) probably reaches 60 in the Palaearctic and no less than 70 in the entire circumpolar fauna.

General Features of the Taxonomic Structure of the Fauna

Carabidae is the only beetle family retaining in high latitudes its rather diverse taxonomic structure reflecting some characteristic features of the Arctic fauna. For example, despite the low species diversity, the Arctic ground beetle fauna follows the general trend of decreasing, in high latitudes, share of advanced taxa with most distinct apomorphic characters (Chernov, 1984, 1988, 1995a). Even though such

a comparison is to a large extent conventional, the carabid taxa of the basal half of the family's phylogenetic tree are rather well represented in the Arctic fauna. This trend is especially evident in the considerable percentage of species belonging to two small tribes: Notiophilini and Elaphrini, which, with all reservations, display some primitive features (Kryzhanovskii, 1983). Another good example is *Pelophila borealis*. This boreal species extends far into the tundra zone, being quite common in the entire continental tundra area of European Arctic and occurring also in Kolguev and Vaigach Islands. This species has been shown to possess a set of archaic characters (Kavanaugh, 1996). By contrast, the groups occupying the top position in the carabid phylogeny are characterized by the poorest representation in the Arctic.

The example of carabid beetles clearly demonstrates that successful exploration of high-latitude landscapes by a taxon is not always determined by its overall specific diversity, reflecting its ecological adaptive potentials. The greatest diversity in the Arctic is shown by large genera: *Pterostichus* and, to a lesser extent, *Bembidion*. At the same time, many very large tribes and genera of the boreal fauna are poorly represented in the tundra and include no typical Arctic species. Such genera are, e.g., *Agonum*, *Harpalus*, and *Amara*. At the same time, some smaller genera (*Elaphrus*, *Notiophilus*, *Pelophila*, and *Diacheila*) have quite successfully explored the tundra environment, which cannot always be accounted for merely by ecological reasons.

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