

A Contribution to the Knowledge of the Arctic Forms of the Genus *Chrysomela* L. (Coleoptera, Chrysomelidae)

L. N. Medvedev and O. A. Khruleva

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia

Received February 1, 2011

Abstract—Detailed morphological (including description of the larva) and ecological characteristics of the leaf beetle *Chrysomela wrangeliana* L. Medvedev, endemic to Wrangel Island (the Chukchi Sea), are given. The annual life cycle of the species is similar to that of *Ch. collaris* L., with hibernation at the larval stage. In nature, *Ch. wrangeliana* develops on *Salix glauca*, a prostrate willow species, the larval development taking 20–25 days at the mean air temperature of about 6°C. The distribution pattern of *Ch. wrangeliana* on Wrangel Island is discussed, and a sharp increase in its abundance following a series of warm seasons is recorded. The ranges of Arctic species of the subgenus *Pachylina* L. Medvedev are separated from that of the nominotypical subspecies of *Ch. collaris* by a wide disjunction in the Subarctic regions of Siberia. The taxonomy of the subgenus *Pachylina* is reconsidered, with a new subspecies *Ch. collaris hyperborea* L. Medvedev subsp. n. being described from North Yakutia and continental tundra of the Chukchi Autonomous Area. *Chrysomela wrangeliana* L. Medvedev and *Ch. taimyrensis* L. Medvedev are regarded as distinct species, rather than subspecies of *Ch. blaisdelli*.

DOI: 10.1134/S0013873811080057

INTRODUCTION

Although Arctic species of leaf beetles were known already in the XVIII century, their comprehensive studies began only in the second half of the XX century. One of the most peculiar groups of leaf beetles in the Arctic includes representatives of the subgenus *Pachylina* L. Medvedev, 1969 with an annual life cycle. Species with such a development cycle are rare in the tundra landscapes, which are usually dominated by insects with multiyear life cycles, including the most common Arctic leaf beetle species (Chernov et al., 1993; Khruleva, 1994, 1996). The unusual life cycle of the Arctic species of the genus *Chrysomela* Linnaeus, 1758 was repeatedly discussed in the literature (Medvedev and Chernov, 1969; Chernov, 1978); however, no detailed studies of their biology, similar to those of the Alpine Scandinavian population of *Ch. collaris* Linnaeus, 1758 (Hägvar, 1975), have been carried out so far.

In this communication we describe the larva and consider the life cycle and ecological specificity of one of the northernmost representatives of the subgenus *Pachylina*: the High Arctic species *Ch. wrangeliana* L. Medvedev, 1973 occurring on Wrangel Island (71°N). Besides *Ch. wrangeliana*, the subgenus

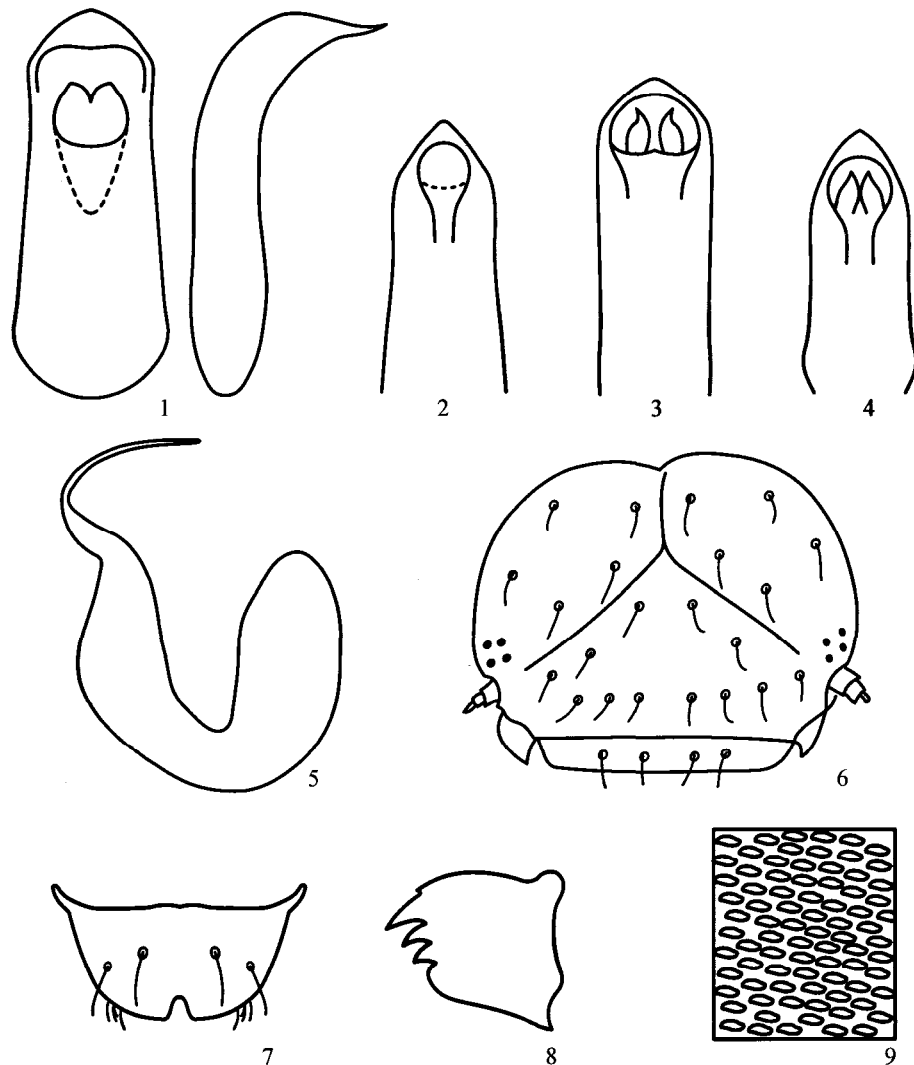
Pachylina includes a number of northern forms whose taxonomic status remains obscure. We have analyzed the specific features of ecology and distribution of these forms (including the fossil data), and propose an emended system of the subgenus based on the new morphological data on the Arctic and boreal forms.¹

Morphology and Ecology of Chrysomela wrangeliana

Chrysomela wrangeliana was described from a series of specimens collected near the Tundrovaya River on Wrangel Island (Medvedev, 1973). Examination of the vast material of adults collected by O.A. Khruleva in 1983–1994 and 2006 in many localities of Wrangel Island, and also the larva, has allowed us to emend the description and give a detailed ecological characteristic of the species.

Morphology of adult. Body coloration black, rarely with weak metallic sheen. Bases of antennae, femora, tibiae (with black knees), and sides of ultimate abdominal sternite yellow or reddish yellow, lateral pronotal ridges and dorsum under elytra grayish brown. Sides of pronotum and legs of varying color.

¹ The taxonomic part of this communication was prepared by L.N. Medvedev, the ecological part, by O.A. Khruleva.



Figs. 1–9. *Chrysomela (Pachylina)* spp.: (1–4) aedeagus in dorsal and also lateral (1) view: (1) *Ch. wrangeliana*, (2) *Ch. collaris*, (3) *Ch. taimyrensis*, (4) *Ch. blaisdelli*; (5) *Ch. wrangeliana*, spermatheca; (6–9) *Ch. wrangeliana*, details of larval morphology [(6) head, (7) labrum, (8) mandible, (9) integument microsculpture].

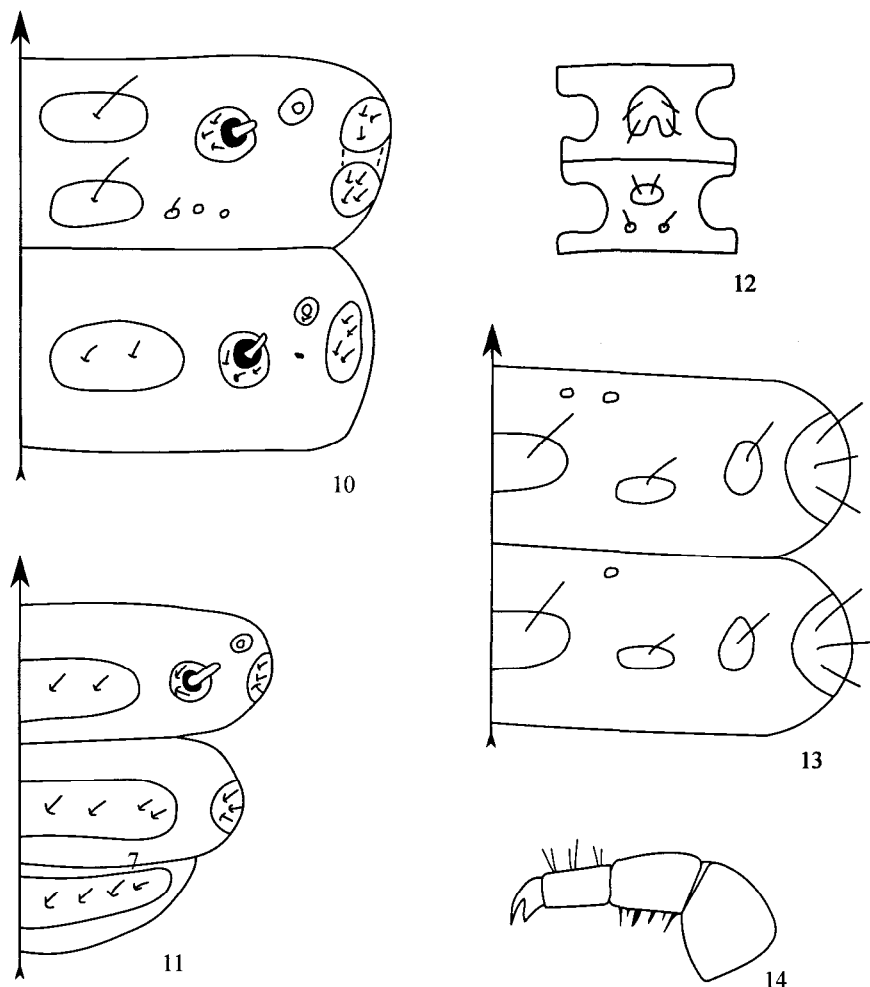
Lateral pronotal ridges appear black to unaided eye but distinctly grayish brown when viewed using a dissecting microscope.

Sculpture of dorsum, in particular elytra, almost invariable; this character clearly distinguishes *Ch. wrangeliana* from *Ch. taimyrensis* L. Medvedev, 1969.

Ventral surface of elytra uniformly concave; 3 thickened areas (visible in transverse section of elytron) exactly correspond to 3 principal ribs on disc. Ventral side of elytra yellow with numerous black embossed dots corresponding to upper-side punctation; with 3 distinct yellow impunctate stripes corresponding to dorsal ribs.

Wings well developed, about 1.3 times as long as elytra, about 0.95 of body length. Venation not quite developed; veins weakly sclerotized, cubital vein reduced basally and apically. Aedeagus (Fig. 1) of almost the same shape as in other species of this subgenus (Figs. 2–4). Spermatheca C-shaped (Fig. 5). Body length 5.3–7.7 mm.

Morphology of the 3rd-instar larva. Body elongate, moderately wide, with flat ventral side and uniformly convex dorsal side. Head, all sclerites, and legs black or blackish brown, soft parts of integument pale yellow, with dense grayish brown microsculpture consisting of transverse-oval plates 0.015 mm long separated by pale narrow gaps.



Figs. 10–14. *Chrysomela (Pachylina) wrangeliana*, larva: (10) metanotum and the 1st abdominal tergite, (11) 7–9th abdominal tergites, (12) sternites of pro- and mesothorax, (13) 1st and 2nd abdominal sternites, (14) leg.

Head (Fig. 6) convex, rounded but appears transverse in dorsal view. Mandibles (Fig. 8) short, robust, with 5 teeth; 4 upper teeth sharp, lower tooth blunt, with straight cutting margin; uppermost tooth very small. Maxillae typical of the subfamily; maxillary palps 4-segmented, 3rd segment large, cylindrical, ultimate segment conical.

Labrum distinctly transverse, with broadly rounded anterior margin medially incised by about 1/4, with transverse row of 4 macrochaetae and group of microchaetae on anterior margin on either side of incision (Fig. 7). Clypeus clearly transverse, short, narrowing in the middle, with row of 4 macrochaetae. Frons flattened, in posterior half with large rounded depressions on either side, partly connected medially; frontal sutures straight, forming right angle; disc with 6 pairs of macrochaetae. Vertex uniformly convex, with 5 pairs of microchaetae.

Prothorax about 1.5 times as wide as head. Pronotal sclerite covers its entire surface; medially divided by more or less distinct light stripe, with transverse depression behind anterior margin and numerous microchaetae along all margins; sclerotization uneven, heavier at margins (better noticeable in freshly molted larvae). On each side of pronotal sclerite there is a small oval sclerite with 4 or 5 microchaetae, probably corresponding to alar sclerite, and a pair of epipleural sclerites adjacent to each other and to coxa, each with 3 or 4 setae. Pronotal stigma rounded, rather large, shifted to mesonotum. Meso- and metanotum (Fig. 9) with 2 rather large, transverse-oval inner posttergal sclerites, each with 1 seta; with an outer group of 2 or 3 small irregular-shaped sclerites, 2 of them usually with 1 seta each. They appear to correspond to strongly reduced outer pre- and posttergal sclerites. Large conical sclerite with gland opening and 2 or 3 macrochaetae topologically corresponds to alar

sclerite. Two partly merged epipleural sclerites lie on lateral margins, each with 3 or 4 microchaetae.

First abdominal tergite (Fig. 10) bearing 1 pair of large tergal sclerites, each with 2 microchaetae, conical sclerite with gland opening and 3 or 4 microchaetae (probably modified outer pretergal sclerite), small stigmal sclerite with round stigmal opening and rudimentary 1 or 2 microchaetae, and large epipleural sclerite with microchaetae.

Small secondary sclerites at anterior margin of tergite, typical of the closest species *Ch. taimyrensis*, are absent in *Ch. wrangeliana*. 2nd–6th tergites resemble 1st tergite; starting from 7th tergite, tergal sclerites merge into one unpaired sclerite (Fig. 10). All tergites with very short, often barely noticeable setae, which are longer and more conspicuous on ultimate abdominal segments. Anal opening ventral, situated on 10th abdominal segment. Integument microsculpture as in Fig. 9.

Prothorax with characteristic horseshoe-shaped sclerite formed by merged sternal and parasternal sclerites, bearing 2 pairs of setae (Fig. 12). Mesothorax with transverse sternal sclerite bearing pair of setae, and with 2 small rounded parasternal sclerites, each bearing 1 seta, but without very small presternal sclerites at anterior margin (Fig. 12). Abdominal sternites with transverse row of 5 sclerites: unpaired sternal, 2 parasternal, and 2 hypopleural; unpaired sclerite with 2 setae, others with 1 long seta each (Fig. 13). Parasternal sclerites very small on 1st sternite and rather large on others. Anterior margins of most sternites often with very small sclerites without setae, corresponding to presternal ones. Starting from 7th sternite, sternal sclerites merge into unpaired transverse plate.

Legs rather short. Femur with 4 pairs of robust macrochaetae on lower side; tibiotarsus more than twice as long as wide, with 3 pairs of fine macrochaetae on upper side and with a few microchaetae on lower side. Claw with large, almost rectangular denticle, thin and sharp apical part, and long seta near base on upper side (Fig. 14).

Larva develops with 3 instars, easily distinguishable by width of head capsule: 0.5 mm in 1st instar, 0.9 mm in 2nd instar, 1.2–1.4 mm in 3rd instar. The only known 1st-instar larva was desiccated and could not be described. Larvae of the 2nd and 3rd instars morphologically identical.

The larva is very similar to that of *Ch. taimyrensis*, differing in the absence of small secondary sclerites at the anterior margin of the 1st abdominal tergite.

Ecology. The adults emerge after hibernation during the snowmelt period (mid-June, in years with average weather conditions). No laid eggs were found in the nature, whereas in cages 3 batches of eggs were obtained (30.VI.1993: 15 and 18 eggs; 19.VI.2006: 19 eggs). In the summer of 2006, when weather conditions were close to average, the adults were recorded in mid-June (the beginning of the observation period), and the larvae, in early July. All the larvae were found on prostrate shrubs of the willow *S. glauca* L., 10–20 cm above ground; the beetles at the beginning of the season were also observed on erect shrubs of *Salix lanata* L. subsp. *richardsonii* (Hook.) 50–70 cm above ground, but no larvae were subsequently found on these shrubs. In 2006, above-zero air temperatures established at the end of the 1st decade of June, and the first larvae that had completed development and prepared to pupation were found on June 19, i.e., approximately 20 days after the appearance of the larvae in the nature, or 40 days after positive temperatures were established in the central mountainous part of the island; the mean air temperature during this period was about 6°C.

The growth rate and duration of development of immature stages of *Ch. wrangeliana* were also studied under laboratory conditions in 2006. The rearing technique was similar to that previously used for *Ch. collaris* (Bogacheva and Khruleva, 2002).² During the first days, the larvae were offered the leaves of two willow species which are the most common in the study region: the erect shrub *Salix lanata* and the

² The experiments were carried out at temperatures varying both during a day and from day to day. The temperature was recorded using electronic loggers. The material consisted of the larvae collected in the nature soon after they molted to the 3rd instar; therefore, the growth rate of most larvae was determined not for the complete duration of the 3rd instar but only from the beginning of captive rearing until the larva reached the maximum weight. The growth rate was determined using the formula $RGR = (\ln Pt - \ln Po)/T$, where Pt and Po are the initial and final weight of the larva, T is the duration of the record period in days. The larvae were kept separately in Petri dishes and weighed daily, at the same time. The development rate (for eggs, prepupa, and pupa) was determined as an inverse value of the duration of development. Since in some cases the larvae pupated without attaching themselves to the substrate, we determined the beginning of the prepupal stage as the moment when the larva stopped feeding.

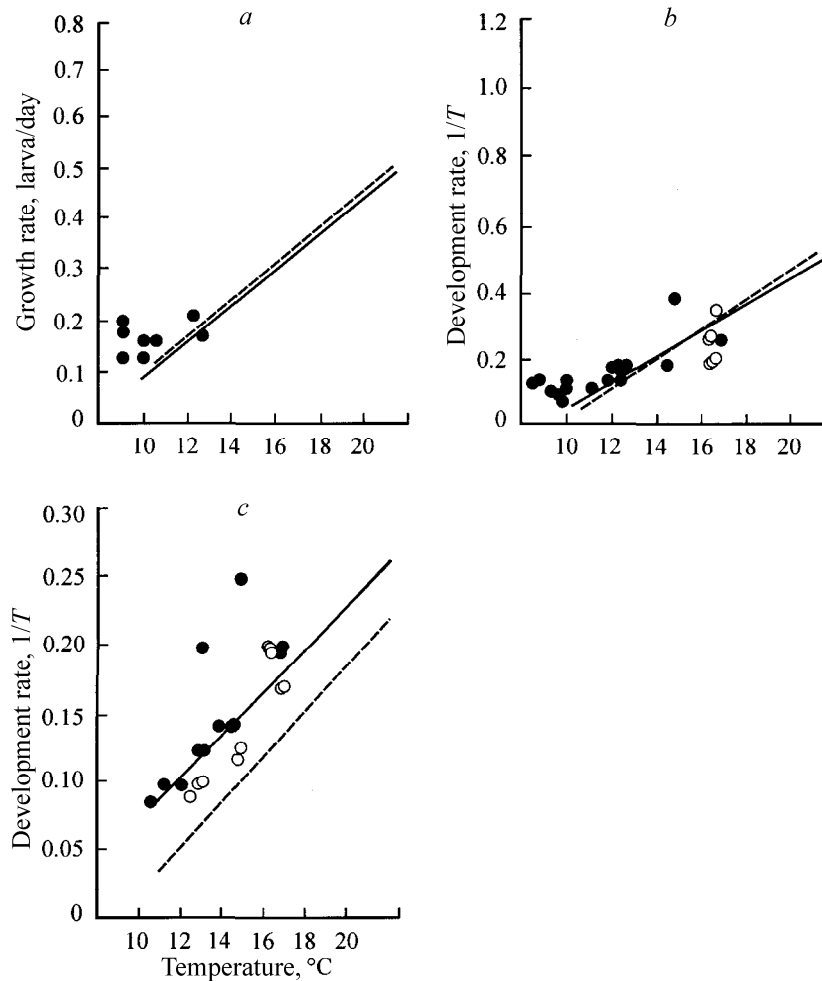


Fig. 15. Development rates of the leaf beetles *Chrysomela wrangeliana* (black circles) and *Ch. taimyrensis* (white circles): (a) 3rd-instar larva, (b) prepupa, (c) pupa. Solid line: mean development rate of *Chrysomela collaris* in the Polar Urals; dashed line: the same in Kostroma Province (after Bogacheva and Khruleva, 2002).

hemiprostrate *S. glauca*. The larvae in all the cages consumed the leaves of *Salix lanata* less actively or did not eat them at all; therefore in the subsequent days they were offered only leaves of *S. glauca*. Of the larvae kept at the mean temperature of about 10°C, less than one-fourth (5 out of 21) developed to the adult stage; the rest of them died. Of the larvae that developed at a higher temperature (12.8°C), almost 60% completed metamorphosis (16 out of 27). The data on the growth and development of immature stages of *Ch. wrangeliana* are shown in Fig. 15. Comparison of our data with the results previously obtained for *Ch. collaris* (Bogacheva and Khruleva, 2002) showed that at temperatures of 12–16°C, the development rate of different stages of the life cycle of *Ch. wrangeliana* in most cases fell within the variability range of *Ch. collaris* in different parts of its distribution area. At temperatures of about 10°C and below,

the development rate of some larvae and most prepupae of *Ch. wrangeliana* (Fig. 15) was found to be higher than the expected development rate of these stages in *Ch. collaris*. For example, the prepupal development of *Ch. wrangeliana* took about 7 days at 10°C, whereas the prepupal development of *Ch. collaris* should take about 10.5 days according to the calculations³ of Bogacheva and Khruleva (2002). The development rate of the only egg batch of *Ch. wrangeliana* was also noticeably higher: 6 days at 15.8°C, as compared to about 9 days in *Ch. collaris* at similar temperatures.

The development of this species at high temperatures can be characterized by the data obtained in

³ The data on the development of *Ch. collaris* were obtained at the minimum temperature values of about 11.5–12°C.

1993, when several adults and larvae were kept indoors at about 20°C. The development of 2 egg batches under these conditions lasted 5 days (from June 30 to July 5), whereas the development of the 1st- and 2nd-instar larvae (body mass 2 and 6 mg) collected in the nature on June 28 took about 10 days.

Distribution over the island and population dynamics. The prostrate and hemiprostrate willows occur on Wrangel Island within an area much exceeding the known distribution of the leaf beetle *Ch. wrangeliana*. During the 12 seasons of field research, this species was found only in the central mountainous part of the island, which differs considerably from the coastal areas in a warmer and more continental climate during summer (Svatkov, 1970; Alfimov, 2007). The mean temperatures of July are about 5–7°C; the vegetation of this part of the island belongs to the typical tundra subzone, whereas most of its territory is covered with Arctic tundras (Yurtsev, 1986, etc.). Since *Ch. wrangeliana* was not found not only in the plains⁴ but also on the periphery of the mountains (including the areas with large south-facing slopes), it may be assumed that its distribution is primarily limited by the mesoclimatic parameters, and that the threshold values of heat availability ensuring stable existence of *Ch. wrangeliana* populations are reached only in the center of the island. It is noteworthy that in all the areas of the central mountainous part of the island where the species was found, the beetles occupied a wide range of biotopes: from forb-moss bog assemblages to rubble hill slopes with scattered willow shrubs and forb clumps (Table 1).

One of the best studied localities was the middle course of the Mamontovaya River (71°09'N, 179°45'E). The material collected in 1983 (Berman, 1986) and our collections of 1992–1994 revealed relatively low abundance of *Ch. wrangeliana* in this area; most adults were found in dry forb-hemishrub assemblages on well-drained ridges and raised terraces. In 2006, when we re-examined the same biotopes after a 12-year interval, the abundance of the species was found to have increased by hundreds of times: the

beetles could be seen everywhere, resting on willows and crawling on the ground in great numbers. Contrary to what was observed in the 1990s, the adults were collected practically in all the biotopes examined. It is interesting that the highest Barber trap capture rates were observed in the river bottomland where there no willows were present. The beetles, which must have migrated from the adjacent biotopes, accumulated in great numbers at the water edge. They were repeatedly observed to spread their wings, apparently trying to fly up; yet no flying individuals were recorded.

Despite the ubiquitous occurrence of adults in the summer of 2006 in the middle course of the Mamontovaya River, the only biotope showing sufficient abundance of the larvae (including the Barber trap data) was a part of the first raised terrace with forb-willow-dryas vegetation. At the same time, during a noticeably colder season of 1983 the larvae were found in different biotopes, their abundance in some places exceeding that of the adults (Table 1). It may be assumed that in 2006 many adults did not participate in reproduction; this is indirectly confirmed by the fact that only one egg batch was produced by 20 pairs of adults which were collected in mid-June and kept in cages until mid-August.

Although meteorological observations in the central mountainous part of the island have been carried out for a short period only, long-term data are available from the weather station of Rogers Bay, one of the coldest points of the island (Svatkov, 1970). Analysis of the climatic parameters of the summer months shows that the summer temperatures have risen considerably during the 10 years preceding the abrupt increase in the abundance of *Ch. wrangeliana*. In particular, the long-term mean temperatures of June, July, and August at Rogers Bay are 0.4, 2.4, and 1.9°C (Svatkov, 1970), whereas the mean temperatures of these months in 1996–2005 were 1.3, 3.1, and 2.8°C, respectively. In addition, during that decade a positive temperature of September (0.6°C) was recorded for the first time, and the amount of precipitation noticeably increased in the summer months. Since the summer temperatures at Rogers Bay are several (3–5) degrees lower than in the center of the island, while the difference between mean monthly air temperatures in the center and on the coast is the most noticeable in the warm seasons (Alfimov, 2007), we may assume that the recent climatic changes were even more essential in the center of Wrangel Island than on this coast. In our opinion, this increase in temperature and a signifi-

⁴ The labels of the holotype and the paratype series read “Somnitelnaya Bay, Tundrovaya River, 9.VII.1972,” 16 males, 14 females (Medvedev, 1973). Since the two localities specified are actually about 60 km apart, this must be a labeling error. We collected material in the Somnitelnaya Bay area during 3 field seasons (1986, 1989, and 2006) but never found adults or larvae of this species, both in the coastal biotopes and in the mountains, 8–10 km from the sea.

Table 1. Biotopic distribution and relative abundance of adults and larvae of *Chrysomela wrangeliana* in different areas of the central mountainous part of Wrangel Island (Barber traps, ind./100 trap-days)

Biotopes	Middle Neizvestnaya River	Upper Neizvestnaya River	Middle Mamontovaya River		
	year of collection				
	1983	1991	2006	1992–1994	2006
Pebbly and sand-pebbly river floodlands	(+)	–	–	–	280
Humid herb-moss assemblages in depressions	1 (4)	5	1 (1)	–	1
Raised terraces with forb-willow-dryas vegetation	1 (+)	1	–	1	98 (15)
Moderately humid ridges with moss-herb-shrub vegetation	1 (12)	3	(1)	–	43
Dryas and forb assemblages on drained slopes and ridges	(1)	1	–	1	96
Tundra-steppe forb-sedge assemblages on terraces		p	–	1 (2)	98
Rubble hill slopes with forb clumps and separate willow shrubs	p	1	?		
Total number of individuals:					
adults	20	32	1	11	3495
larvae	(126)	–	(2)	(5)	(59)

Notes: Data on the larvae are given in parentheses. “+” less than 0.5 ind./100 trap-days; “–” species not found; “p” collected by other methods. *Empty cells* indicate that no such biotopes were present in the area.

cantly prolonged frost-free season may have resulted in an abrupt increase in the abundance of *Ch. wrangeliana*. Considering the relatively low fecundity of the species, the increase is likely to be related to the higher survival rates at immature stages, and also to the fact that development could be completed not only in the warmest biotopes with the earliest snowmelt dates, but in other habitats as well.

A Review of Species of the Subgenus Pachylina

In all, 5 tundra and mountain-tundra species have been described in the genus *Chrysomela*. All these species are derived from *Ch. collaris* Linnaeus, 1758 and belong to a separate subgenus *Pachylina*. The status of some of these forms is disputed by experts, so that the number of species distinguished within the subgenus *Pachylina* varies from 1 to 5.

Chrysomela collaris Linnaeus, 1758 is a widespread trans-Palaeartic forest species extending into the forest-tundra in some places. Its biology in the forest-tundra (the Polar Urals in the lower Ob River, Krasnyi Kamen Station) was studied in detail and compared with the biology of a population from the forest zone (Bogacheva and Khruleva, 2002). The species feeds on willow shrubs, including rather tall ones, and rarely on aspen and poplar; the most common food plant in the forest-tundra is *Salix lanata*.

Chrysomela alpina Zetterstedt, 1838 was described from the mountains of Norway and is currently known from the tundras of Norway and Sweden. The taxonomic status of this form is still being debated; it is regarded either as a distinct species (Medvedev and Chernov, 1969; Chernov et al., 1993; Medvedev, 1996; Warchałowski, 2003; Kippenberg, 2010) or as a synonym of *Ch. collaris* (Lopatin et al., 2004). In any event, *Ch. alpina* is much closer to *Ch. collaris* than other northern forms, differing mainly in the small body size and details of coloration. However, the key of Warchałowski (2003) specifies a considerable difference between *Ch. alpina* and *Ch. collaris* in the length of the 2nd and 3rd antennal segments: the 3rd antennal segment is more than twice as long as the 2nd in *Ch. collaris*, and only 1.5 times as long as the 2nd in *Ch. alpina*. This difference was not confirmed in our material. The proportions of these antennal segments in the examined series of all the species of the subgenus were very close to 1 : 1.5 (in *Ch. collaris* and *Ch. alpina*) or only slightly different from that value: 1 : 1.55 in *Ch. taimyrensis*, 1 : 1.65 in *Ch. wrangeliana*, and 1 : 1.47 in *Ch. blaisdelli*.

Chrysomela taimyrensis L. Medvedev, 1969 was described from an adult and a larva collected near Tareya on Taimyr Peninsula. The species is common in the central areas of Taimyr, especially in the north-

ern part of the typical tundra subzone (Medvedev and Chernov, 1969); recently it was also recorded in the southern tundras. *Chrysomela taimyrensis* was previously (Medvedev and Chernov, 1969) believed to be monophagous species associated exclusively with *Salix arctica*; however, in the southeast of Taimyr Peninsula (Ary-Mas area) the larvae of this species were collected on *Salix reptans* and *S. glauca*. It is essential that the species did not occur on willow shrubs that are common in the area; all the larvae were found in the near-ground layer, being especially numerous on the prostrate *S. reptans* plants. The development rates of the prepupa and pupa in this population were very close to those found in *Ch. wrangeliana* (Fig. 15). This form was also regarded a subspecies of the American *Ch. blaisdelli* Van Dyke (Medvedev and Dubeshko, 1992; Lopatin et al., 2004; Kippenberg, 2010). The status of the population found on the Chukchi Peninsula was dubious; it was attributed either to *Ch. taimyrensis* (Medvedev and Korotyaev, 1980) or to *Ch. blaisdelli* (Medvedev, 1992). Examination of a long series of adults has allowed us to describe this population as a subspecies of *Ch. collaris* (see below).

Chrysomela wrangeliana L. Medvedev, 1973 is an endemic of Wrangel Island. The main character distinguishing it from closely related species is the presence of sharp and high ribs on the elytra. It was regarded as a distinct species by some authors (Berman, 1986; Medvedev and Khruleva, 1986; Khruleva, 1987, etc.), and later, as a subspecies of *Ch. blaisdelli* Van Dyke (Medvedev, 1992; Lopatin et al., 2004; Khruleva, 2007, 2009; Kippenberg, 2010).

Chrysomela blaisdelli (Van Dyke, 1938) was described from a short series collected in Alaska and remains poorly known. Now the species is also known from Canada (Northwestern Territories, British Columbia) (Bousquet, 1991). It occurs in the mountain tundra at 700 m above sea level (Brown, 1956).

Chrysomela engelhardti (Hatch, 1939) was described from Alaska and later found in Canada (Yukon, Northwestern Territories, British Columbia) (Bousquet, 1991). The larvae were found on prostrate willows on the Hudson Bay coast at Eskimo-Point (Brown, 1956). This form was recorded within the distribution range of the preceding species, from which it differs only in the uniformly black pronotum, whereas sides of pronotum in *Ch. blaisdelli* are reddish-brown. The material collected by E.G. Matis on *Salix arctica* near Anchorage (Alaska) included individuals with one-colored and two-colored pron-

tum as well as those with transitional coloration variants, therefore the name *Ch. engelhardti* was synonymized with *Ch. blaisdelli* Van Dyke (Chernov et al., 1993). This synonymy was accepted by other authors (Lopatin et al., 2004; Kippenberg, 2010).

Examination of a long series of adults from several localities in the Chukchi Peninsula and northeast Yakutia revealed a new subspecies of *Ch. collaris* distributed in this part of the Subarctic; it is described below.

Chrysomela collaris hyperborea

L. Medvedev, subsp. n.

Description. Body black, dorsum occasionally with more or less distinct metallic sheen; labrum, 5 basal antennal segments, legs except knees and tarsi, lateral margins of 4th and 5th abdominal sternites, pygidium, and upper side of abdomen yellow. Coloration of lateral pronotal carinae varying: either yellow with black spot in the middle, often merged with black surface of disc, or yellow areas strongly darkened and reduced or even completely absent. Lower surface of elytra yellow with dense and uniform black dots, lacking yellow longitudinal stripes.

Sculpture of head and pronotum as in nominotypical subspecies. Elytra of male 1.25–1.30 times as long as wide, densely punctate, with confused rows of dots in the center of disc and very weak, often obsolete convex punctate longitudinal stripes. Elytra of female 1.35–1.40 times as long as wide, densely punctate, with 3 or 4 convex punctate longitudinal stripes; these stripes low or moderately raised but never rib-like as in *Ch. taimyrensis* and *Ch. blaisdelli* or as distinct as in *Ch. wrangeliana*. Aedeagus as in nominotypical subspecies.

Body length of male 5.0–5.5 mm, that of female 6.5–7.5 mm.

Diagnosis. Differs from nominotypical subspecies by convex longitudinal stripes and rows of punctures on elytra, distinct in females and less distinct in males. The two subspecies can be reliably distinguished only based on females.

This subspecies is also very close to *Ch. blaisdelli*, which has 2–4 convex longitudinal stripes on elytra in both sexes; these two taxa are more reliably distinguished based on males. The similarity between *Ch. collaris hyperborea* and *Ch. blaisdelli* allows one to consider also *Ch. blaisdelli* a subspecies of *Ch. collaris*.

Material. Holotype, ♂: Chukchi Peninsula, Milkera, 9.VIII.1978 (S.V. Kiselev). Paratypes: same locality, 29.07–16.VIII.1978, 93 spms.; Chukchi Peninsula, Valkumei, 13.VII.1978 (S.V. Kiselev), 1 ♀; Chukchi Peninsula, Iul'tin, floodland area, on willows, 6.VIII.1975 (B.A. Korotyaev), 5 ♂, 8 ♀; Northern Yakutia, Cherskii, 68°40'N, 1–20.VII.1999, sand terrace in the upper segment of Karetovskaya channel (A.V. Alfimov), 1 ♂.

The type material is in the collection of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg; ZIN); 5 paratypes, in the collection of L.N. Medvedev, and 10 paratypes, in the collection of A.O. Bieńkowski. In addition to the type series, material of this subspecies was found on Cape Schmidt and the Kresta Bay coast (Chukchi Peninsula) (Medvedev and Korotyaev, 1980); it is preserved in the collection of the Institute for Biological Problems of the North, the Russian Academy of Sciences (Magadan). Two males from the Koryak Upland in the collection of O.N. Kabakov (now at ZIN: Olyutor District, 15.VI and 10.VII.1962, Il'chenko) were not included in the paratype series due to the absence of females from the same locality; these males are almost identical with males of the nominotypical subspecies of *Ch. collaris*.

We also examined material from the alpine areas of Tuva (courtesy of Yu.E. Mikhailov) with the label: SE Tuva, 28 km ESE of Kungurtug, the upper reaches of the Ulin-Khan River, 50°34' N, 97°58' E, 2200–2500 m, 20–23.VI.2004 (R.Yu. Dudko, I.I. Lyubchanskii), 4 ♂, 4 ♀. These beetles can be described as follows: body and legs black, dorsum with metallic sheen, lateral margins of 4th and 5th abdominal sternites, pygidium, and upper side of abdomen yellow. Coloration of lateral pronotal carinae weakly varying: yellow with very small black spot in the middle, or yellow areas strongly darkened. Lower surface of elytra gray or grayish yellow with dense and uniform black punctures, without yellow longitudinal stripes. Elytra of male densely punctate, in some areas with confused rows of punctures, with 1 or 2 very indistinct, often obsolete punctate convex longitudinal stripes. Elytra of female densely punctate, with 2–4 convex longitudinal stripes covered with dots, at least 2 of these stripes rather strongly raised. Aedeagus as in nominotypical form. Body length of male 5.7–6.3 mm, that of female 6.1–6.9 mm. The beetles differ well from nominotypical subspecies in convex longitudinal stripes on elytra, and from *Ch. collaris hyperborea*, in distinct metallic sheen of

dorsum and black legs. Although one might consider establishing a new subspecies for this form, examination of vast material from Siberian mountains in the ZIN collections revealed similar beetles with costate elytra from another locality: Buryatia, the upper reaches of the Bolshoi Amalat River, 20.VI.1967, 1 ♂; 17.VIII.1961, 28.VI.1967 and 1.VII.1968, 3 ♀ (O.N. Kabakov). In addition, the locality in the upper reaches of the Ulin-Khan River lies between the East Tuva Upland and the mountains west of Hubsugul lake in North Mongolia, where the nominotypical subspecies of *Ch. collaris* occurs at lower altitudes (about 800 m in Tuva and Mongolia). In view of this, the populations from the mountain tundra of SE Tuva and Buryatia should be regarded an alpine form of *Ch. collaris*.

The costate sculpture of the elytra, with spaces between rows of punctures becoming convex and forming longitudinal ridges, is a characteristic feature of many alpine and Arctic taxa of leaf beetles. It was shown that this character could vary considerably between populations of one species (Mikhailov, 2010). In the genus *Chrysomela*, the costate sculpture until recently has been known only in the northern forms of the subgenus *Pachylina*, where it has been used, together with pigmentation of the lateral pronotal carinae, as an important diagnostic character. However, as mentioned above, beetles with such characters were also found in two alpine areas in the south of Siberia (Fig. 19). Individuals with costate sculpture were not found among the European mountain forms, including the population of *Ch. collaris* from the alpine areas of Scandinavia, which exists under very severe conditions comparable to those in the tundra. We may therefore conclude that costate elytra very rarely occur in the typical form of *Ch. collaris*. According to Mikhailov (2010), adults with a dark pronotum were also found only in two localities: the alpine areas of SE Tuva (the population with costate elytra mentioned above) and Ukok Plateau in the Altai, 2600–3000 m above sea level (a population with smooth elytra).

A detailed morphological examination of all the species of the subgenus *Pachylina* revealed a number of new characters, mostly related to the structure of the elytra and coloration of their lower surface, and an initial stage of wing reduction in the Arctic species.

The coloration of the lower surface of the elytra proved to be an unusual character. We studied it in a series of specimens of each species except *Ch. alpina*. In *Ch. collaris* the lower surface of the



Figs. 16–18. *Chrysomela (Pachylina)* spp., lower surface of elytra (photos): (16) *Ch. taimyrensis*, male; (17) *Ch. taimyrensis*, female; (18) *Ch. wrangeliana*, male.

elytra is usually brownish yellow with dense black punctures; occasionally the background color is blackish brown, in which case the black punctures are often surrounded with yellow rings. In the only specimen of *Ch. alpina* present in our material the lower surface of the elytra is gray, with sparse and inconspicuous dark punctures. The coloration of *Ch. wrangeliana* was described above (Fig. 18); in *Ch. taimyrensis* the coloration is of the same type as in *Ch. wrangeliana* but with much sparser black punctures and less distinct longitudinal yellow stripes (Figs. 16, 17). Finally, in *Ch. blaisdelli* (and the synonymous *Ch. engelhardti*) the background color is dark brown or black, with very indistinct black punctures.

Of all the species of the subgenus *Pachylina*, flight was observed only in *Ch. collaris*. The adults of *Ch. wrangeliana* and *Ch. alpina* do not fly (Hägvar, 1975); for the rest of the species there is no data but they seem to be incapable of flight despite having well-developed or slightly shortened wings (Table 2).

*Comparison of Characteristic Features
of the Distribution and Bionomy of Chrysomela
collaris and the Arctic Forms
of the Subgenus Pachylina*

Distribution. A detailed analysis of the distribution of *Ch. collaris* and the Arctic forms of *Pachylina* (Fig. 19) produced interesting and quite unexpected results indicating that we are dealing with two eco-

logically distinct taxa, rather than with one polymorphic species. Examination of the vast material of *Ch. collaris* in the ZIN as well as our own collections and those made by other researchers⁵ allows us to conclude that the species in question is the most common in the southern half of the taiga zone. This corresponds to the northwest of European Russia (mostly Leningrad Prov.), and in Siberia, to the southern mountain areas (south of Krasnoyarsk Territory, Khakassia, Buryatia). Thus, *Ch. collaris* may be described as a trans-Palaeartic boreomontane species with a relatively high degree of ecological plasticity. At the same time, unlike *Ch. lapponica* and other dendrophagous leaf beetles developing in early summer, the range of *Ch. collaris* extends, only in a few places and narrowly, into the polar landscapes (Poppius, 1910; Medvedev and Korotyaev, 1980; Chernov et al., 1993, etc.). The northernmost localities of these beetles in the West Palaeartic usually lie in the mountains

⁵ Judging by the available data, this species commonly occurs in Leningrad and Kostroma provinces (southern taiga), whereas only a few records are known already in Moscow Province (mixed forests) and in more southern areas. B.A. Korotyaev (pers. comm.) collected these beetles in the Moscow area only once and in one of the coldest biotopes: a bog in the northwest part of Moscow Province. In Onega District of Arkhangelsk Province (northern taiga) he also collected this species only once, on a well-drained dry ridge that becomes snowfree early in the snowmelt period. These observations fit well the concept of habitat changes along the zonal gradient.

Table 2. The length of wings in relation to the length of body and elytra in species of the subgenus *Pachylina*

Species	Ratio of wing length to	
	body length	elytra length
<i>Ch. collaris</i>	1.09	1.49
<i>Ch. taimyrensis</i>	0.90	1.30
<i>Ch. wrangeliana</i>	0.92	1.33
<i>Ch. blaisdelli</i>	0.89	1.26
<i>Ch. engelhardti</i>	0.90	1.27

(Scandinavia and the Polar Urals). The northern boundary of the range of *Ch. collaris* coincides with that of the temperate climatic region (with the exception of Northern Yakutia with its ultra-continental climate) (Fig. 19).

On the contrary, the Arctic populations of *Chrysomela*, both in Siberia and in North America (Brown, 1956; Bousquet, 1991), occur within a rather narrow belt of tundra and the adjacent mountain tundra landscapes, being generally limited to regions with the arctic climate. In their landscape-zonal distribution pattern (with the optimum in the typical tundra subzone), the Arctic forms of *Pachylina* belong to the hemiarctic group (Chernov and Matveyeva, 2002). The restricted distribution of *Ch. taimyrensis* in the continental area, where it is limited to the tundra zone and is absent in the northern sparse forests, characterizes this species as a true Arctic taxon.

Thus, the ranges of the Arctic forms are separated from the range of the nominotypical subspecies of *Ch. collaris* by a vast latitudinal disjunction covering most of the Eurasian Subarctic zone. Although the lack of records cannot be a convincing proof of the absence of the species, it certainly indicates that the species is rare in this territory and, in our opinion, demonstrates considerable ecological differences between the nominotypical subspecies of *Ch. collaris* and the Arctic *Pachylina* species. Comparison of the climatic parameters of the ranges of these taxa (Table 3) suggests that their distribution is limited by heat availability. In particular, the regions of the supposed ecological optimum of *Ch. collaris* vary strongly in the degree of their continentality but have close values of the sums of temperatures of days with mean temperatures above 10°C. This temperature (10°C) is a developmental threshold of leaf beetles of the genus *Chrysomela* (Dubeshko, 1977; Dubeshko and Medvedev, 1989; Milyashevich, 2002). In the regions where

Ch. collaris is most common, the sum of temperatures is ~1600–1900 degrees, and the total duration of the period with temperatures above 10°C is about 4 months (Isachenko, 1985). The corresponding parameters at the northern distribution boundary of *Ch. collaris* are 800–1000 degrees and 2–2.5 months, whereas the Arctic forms of the subgenus *Pachylina* mostly occur in the regions where the period with temperatures above 10°C does not exist at all.

The vast fossil material indicates that the Arctic species of *Chrysomela* did not recently (in the Holocene) colonize their modern ranges but existed in similar landscapes for a long time. Unlike *Ch. lapponica* and the nominotypical subspecies of *Ch. collaris*, which very rarely occur in the Pleistocene fossil records, forms of the genus *Chrysomela* with costate elytra were broadly distributed in northeastern Asia (Fig. 19); in different publications they were referred to as *Ch. taimyrensis* (see Kiselev, 1981; Kiselev and Nazarov, 2009) and *Ch. blaisdelli* (see Kuzmina and Bolshiyarov, 2002; Sher et al., 2005, 2006; Kuzmina and Sher, 2006; Sher and Kuzmina, 2007; Elias and Kuzmina, 2008). According to Kiselev (1981), the earliest fossil records of such forms occur in the Eupleistocene (the Oler superhorizon, the Chukochya River, Kolyma Lowland); most other findings occur in the Late Neopleistocene. During that period the beetles occurred in nearly all the localities of northeastern Asia for which fossil data are available, but were never abundant. Most specimens were found in deposits containing tundra-dwelling species, often with a noticeable fraction of the cryophyte-steppe complex (especially *Morychus viridis* Kuzmina et Korotyaev, 1987 of the family Byrrhidae). In the Holocene such forms were found during the boreal optimum, though in fewer profiles than in the Pleistocene. In the northwest of North America similar fossils were found in the Late Neopleistocene and Holocene deposits as part of the tundra-like beetle faunas (Elias and Kuzmina, 2008; S.A. Kuzmina, pers. comm.). Thus, judging by the fossil data, this taxon (or a group of close taxa) existed for a long time in the cold climate.

As can be seen in Fig. 19, the Arctic forms of *Chrysomela* occurred in the Pleistocene not only on Taimyr Peninsula and northeastern Asia, but also in various localities of Northern Yakutia as far as the Lena River mouth. Their disappearance from this territory probably resulted from abrupt environment changes (transgression of the sea, shifting of the boundaries of the taiga and tundra zones) that occurred in plain terri-

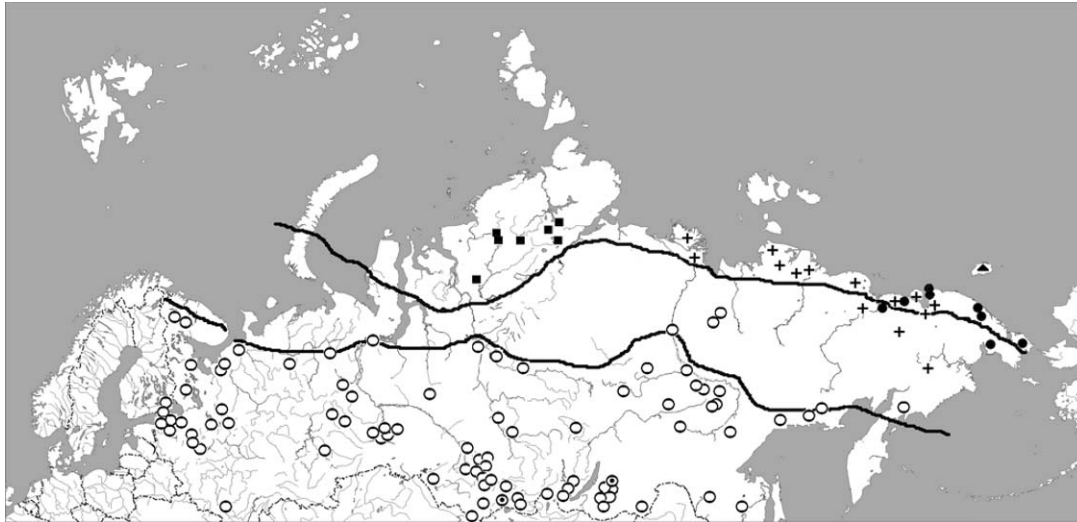


Fig. 19. Distribution of *Chrysomela collaris* and the Arctic Asian forms of the subgenus *Pachylina* in the territory of Russia: Lines: boundaries of the arctic, subarctic, and temperate climatic belts. White circles: localities of *Ch. collaris* (populations with costate elytra are designated with dotted circles); squares: those of *Ch. taimyrensis*; black circles: those of *Ch. collaris hyperborea*; triangles: those of *Ch. wrangeliana*. “+” are findings of fossil beetles from this subgenus with costate elytra in northeastern Asia (after Kiselev, 1981; Kuzmina and Bolshiyarov, 2002; Sher et al., 2005, 2006; Kuzmina and Sher, 2006; Sher and Kuzmina, 2007; Kiselev and Nazarov, 2009).

tories during the Holocene (Kiselev, 1995). In the mountain regions of the Far North such forms must have been preserved due to the variety of microstations.⁶

Ecology. As mentioned above, *Ch. collaris* is sporadically distributed in the Subarctic landscapes. Comparison of the ecology of *Ch. collaris* in the center and at the boundary of its distribution range (alpine areas of Norway, the forest-tundra of the Polar Urals) has shown that although the duration of development of the species is nearly the same in all the areas, development starts earlier and the beetles occupy lower vegetation layers in the regions with a more severe climate (Bogacheva and Khruleva, 2002). In the Polar Urals the temperature threshold of growth of *Ch. collaris* larvae is 6°C (Bogacheva, 2001). According to Hägvar’s (1975) data, under the conditions of short and cold summer in the mountain tundras of Norway the species can complete development due to a combination of several factors: an early emergence of adults after hibernation, their ability to remain active at low temperatures (about 0°C), and development of the larvae on prostrate willow species. Development can be completed only in the biotopes characterized by

early snowmelt dates. According to Hägvar, development in the surface layer was one of the key components of adaptation of this species to life in open landscapes with strong winds and a considerable heat deficiency; when placed on shrubs 40 cm above ground, the larvae either left or died with signs of dehydration.

The Arctic forms of *Chrysomela* also live on prostrate willows (Brown, 1956; Medvedev and Chernov, 1969). According to our data, *Ch. taimyrensis* and *Ch. wrangeliana* occur only on prostrate willows even in the presence of erect willow plants nearby. The life cycle of the Arctic forms of the subgenus *Pachylina* also has not changed much as compared to that of *Ch. collaris*. Most of the tundra insect species have the “passive” type of adaptive strategy based on multiyear development and the possibility of repeated hibernation at the larval stage (MacLean, 1975; Chernov, 1978, etc.); on the contrary, the Arctic representatives of *Chrysomela* retain the “active” strategy, typical of southern immigrants and characterized by rapid development of immature stages. Our data suggest that at low temperatures (about 10°C) *Ch. wrangeliana* may have even higher development rates than *Ch. collaris*. Acceleration of development at low temperatures was also observed in some other groups extending into the Subarctic, for example, in amphibians (Shvarts, 1980).

It is essential that the same complex of adaptations to the severe conditions of short and cold summer is

⁶ According to the Kiselev (1995) data, the cryoxerotic elements in the fossil beetle complexes of northeastern Asia were best preserved in the Chukchi Peninsula during the Holocene; it is in this region that many relict species of the tundra-steppe beetle complex can still be found (Berman, 2001; Khruleva, 2009, etc.).

Table 3. The principal climatic parameters in the regions inhabited by species of the subgenus *Pachylina*

Localities	<i>t</i>	<i>At</i>	<i>Et</i> ₁₀	<i>FF</i>	<i>Sn</i>	<i>r</i>
Localities of the Asian Arctic forms of the genus <i>Chrysomela</i>						
Khatanga (~ 80 km S of the locality of <i>Ch. taimyrensis</i> population)	12.2	46.3	528	73	254	355
Pevek	7.6	35.4	–	48	233	322
Vankarem	5	30.8	–	48	243	(267)
Provideniya	7.7	23.3	–	79	218	(494)
Localities near the northern distribution boundary of <i>Ch. collaris</i>						
Apatity	13.8	27.2	912	85	206	587
Salekhard	13.4	37.2	828	86	225	539
Turukhansk	15.8	42.9	1010	89	231	666
Verkhoyansk	15.2	63.8	1084	67	223	184
Localities within the zone of climatic optimum of <i>Ch. collaris</i>						
St. Petersburg	17.8	25.7	1866	156	133	673
Tyumen	17.2	35.0	1804	112	161	524
Irkutsk	17.6	38.5	1618	98	160	489
Krasnoyarsk	19.6	38.1	1913	120	153	372

Notes: *t* is the mean temperature of the warmest month; *At* is the annual range of mean air temperatures; *Et*₁₀ is the sum of temperatures for the period with daily mean temperatures above 10°C; *FF* is the duration of the frost-free period; *Sn* is the number of days with snow cover; *r* is the annual mean precipitation, mm. The figures in parentheses refer to incomplete data. The parameters are cited after Isachenko (1985).

observed both in the alpine populations of *Ch. collaris* (which have colonized such landscapes relatively recently, after the Holocene deglaciation) and in the morphologically distinct high-latitude forms of the subgenus. This fact suggests that *Ch. collaris* may have possessed some preadaptations to the cold climate. Despite the long period of existence of the northern populations in the cryoarid climate (probably during most of the Pleistocene), they have developed no new adaptations to the pessimal temperatures (such as multiyear development in species of the genus *Chrysolina*).

Although the Arctic *Chrysomela* provide an example of prolonged existence of relatively large phytophagous beetles with an annual life cycle in the northern part of the tundra zone, some features of their ecology demonstrate vulnerability of such a strategy in the Arctic. High mortality of immature stages indicates that the development of *Ch. wrangeliana* at about 10°C proceeds beyond the limits of the climatic optimum. The actual temperatures of larval development in the nature seem to be close to this threshold value,

even if we consider the additional heat obtained due to the basking behavior;⁷ at the mean monthly temperatures of 6–7°C, the actual temperature of development can hardly exceed 10–11°C. In our opinion, the low abundance of *Ch. wrangeliana* in 1980–1990, followed by an abrupt increase during a relatively short (ten years) period with longer frost-free seasons and higher summer temperatures also indicates that the island population exists under extreme conditions.

The local recent distribution of the Arctic forms of *Chrysomela* also demonstrates their limited abilities of colonizing tundra landscapes. As compared to noticeably broader ranges of these beetles in the past, their recent distribution is mostly restricted to areas with mountain landscapes providing high biotopic and

⁷ In the nature, the “basking behavior” allows the larvae to increase their temperature by about 4–5°C and to complete development faster than it could be expected at the corresponding air temperatures (Bogacheva, 1995). Similar data were obtained for *Ch. collaris*, both in the southern taiga and in the forest-tundra (Bogacheva and Khruleva, 2002).

microclimatic diversity. The northern distribution boundaries of the Arctic *Chrysomela* are obviously shaped by heat deficiency, whereas the factor preventing them from expanding southwards remains obscure. Considering a close association of these species with prostrate willows, it may be assumed that their expansion beyond the tundra zone is hindered by the strongly reduced role of such willows in the more southern vegetation.

Thus, close relations between the Arctic forms of the subgenus *Pachylina* and the typical *Ch. collaris* can be confirmed not only by morphological characters but also by specific traits of the life cycle. The initial ecological plasticity of this species, manifested in its ability to form stable populations in alpine areas, might have served as a prerequisite for further evolution of this taxon in the extreme northeast of Asia during the cold epoch. The fossil material reveals a long (at least since the early Pleistocene) history of the Arctic forms in this region within the tundra and tundra-steppe biotas. However, the recent distribution of *Ch. collaris* and its Arctic relatives clearly indicates that their ecological requirements are very different: they occur in different natural zones and are separated by a vast latitudinal disjunction.

Our data show that the Arctic forms of the subgenus *Pachylina* are difficult to distinguish from the typical *Ch. collaris* based on the traditional morphological approach. Different authors disagree as to the taxonomic status of these forms. In the opinion of O.A. Khruleva, the pattern of their zonal distribution suggests that we are dealing with morphologically close but ecologically distinct taxa: one boreomontane species (*Ch. collaris*) and a Siberian–American complex of Arctic forms which may in fact constitute a single species with several subspecies, as L.N. Medvedev earlier assumed (Medvedev, 1992; Medvedev and Dubeshko, 1992). However, since the populations from the Chukchi Peninsula were not specially studied from the ecological viewpoint, we propose a somewhat different interpretation of taxa within the subgenus, based on taxonomic characters; it is done in the key below.

Chrysomela alpina differs from *Ch. collaris* only in the body size and minor details of coloration of the dorsum and legs; this form may therefore be regarded a subspecies. The status of a distinct species is retained for *Ch. wrangeliana* as well as for *Ch. taimyrensis*, which may be regarded either a “young” species or a well-differentiated subspecies. These taxa are

most clearly separated from *Ch. collaris*, they noticeably differ from one another and possess isolated ranges. *Chrysomela wrangeliana* differs most clearly from other Arctic forms of the subgenus *Pachylina*, which may be explained by a prolonged development of this species under the conditions of cryoarid climate, more severe than that of the Chukchi Peninsula and resembling the recent climate of the island (Vartanyan, 2004; Alfimov, 2007), rather than by the very fact of isolation from the continent (which was established only in the Holocene). The specific distinctness of *Ch. taimyrensis* is supported by the constant pronotal coloration and the degree of costate relief on the elytra in all the material examined, including beetles from different areas of the Taimyr Peninsula.

On the contrary, examination of a long series of beetles from the Chukchi Peninsula and the extreme north of Yakutia revealed considerable variability of the pronotal coloration and the development of the carinae on the elytra, so that these populations may be regarded a subspecies of *Ch. collaris*. Finally, the synonymy of the two American species is perfectly justified since they differ only in the highly variable coloration of the pronotum, showing a complete series of transitions between the extreme variants, whereas their distribution ranges overlap completely. They are very similar to the above subspecies from the Chukchi Peninsula and may therefore be regarded as one more subspecies of *Ch. collaris*.

A Key to Taxa of the Subgenus Pachylina

The females can be easily distinguished from the males by tapered apical angles of the elytra.

- 1(4). Elytra with completely confused punctation, with no traces of rows of punctures or longitudinal convex stripes. Lower surface of elytra yellow, gray, or black with confused black punctures. Sides of pronotum yellow with black puncture in the middle. Sides of 4th and 5th abdominal sternites yellow.
- 2(3). Dorsum with distinct metallic sheen (blue, violet, or bronze). Elytra with dense and rather coarse punctation. Legs yellow with black knees and tarsi, or strongly darkened, up to completely black. Body large, 5.6–7.6 mm. Forest zone of the Palaearctic
..... *Ch. collaris collaris* Linnaeus, 1758.
- 3(2). Dorsum black with metallic sheen. Elytra with finer punctation. Legs yellow with black knees

- and tarsi. Body smaller, 4.2–5.5 mm. Mountain tundras of Scandinavia
 *Ch. collaris alpina* (Zetterstedt, 1840).
- 4(1). Elytra at least in females with longitudinal convex stripes or carinae corresponding to odd numbered intervals between rows, and confused rows of punctures between them.
- 5(10). Lower surface of elytra yellow, gray, or black, with confused black punctures but without yellow longitudinal stripes. Yellow lateral pronotal carinae often darkened. Sides of 4th and 5th abdominal sternites yellow. (Different subspecies of *Ch. collaris*).
- 6(7). Dorsum with distinct metallic sheen. Legs black. Elytra of male with 1 or 2 very weak, often obsolete convex longitudinal stripes; elytra of female with 2–4 such stripes, at least 2 of them rather convex. Body length 5.7–6.9 mm. Mountain tundra in SE Tuva the mountain-
 tundra form of *Ch. collaris* Linnaeus, 1758.
- 7(6). Dorsum black or with weak metallic sheen. Legs yellow with black knees and tarsi.
- 8(9). Elytra of male with very weak, often obsolete convex longitudinal stripes, those of females with 3 or 4 weakly or rather strongly convex longitudinal stripes covered with punctures. Lower surface of elytra gray or grayish yellow with dense and uniform black punctation. Body length 5.0–7.5 mm. Chukchi Peninsula
 *Ch. collaris hyperborea* L. Medvedev, subsp. n.
- 9(8). Elytra with 2–4 convex impunctate longitudinal stripes, sometimes inconspicuous, separated by wide intervals with confused punctation. Lower surface of elytra black or dark brown, with indistinct black punctures. Aedeagus as in Fig. 4. Body length 4.9–7.2 mm. Tundras of Alaska and Canada
 *Ch. collaris blaisdelli* (Van Dyke, 1938).
- 10(5). Lower surface of elytra yellow with numerous black convex punctures and 3 yellow longitudinal stripes. Dorsum black or with weak metallic sheen, yellow lateral pronotal carinae usually strongly darkened or even concolorous with disc.
- 11(12). Elytra with 3 distinct and high carinae and dense punctation in between, arranged in more or less confused rows. Sides of 5th abdominal sternite yellow. Aedeagus as in Fig. 1, spermatheca as in Fig. 5. Body length 5.3–6.7 mm
 *Ch. wrangeliana* L. Medvedev, 1973.
- 12(11). Elytra with 3 convex longitudinal stripes and moderately dense punctation in between, arranged in more or less regular rows. Sides of 4th and 5th abdominal sternites yellow. Aedeagus as in Fig. 3. Body length 5.4–7.2 mm
 *Ch. taimyrensis* L. Medvedev, 1969.

ACKNOWLEDGMENTS

We are very grateful to S.A. Kuzmina (Moscow) for consultation on the distribution of beetles in the Pleistocene deposits, to A.O. Bieńkowski (Moscow) and Yu.E. Mikhailov (Yekaterinburg) for the provided collection material, and to A.G. Moseiko (St. Petersburg) for the provided opportunity to examine the collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg). Special thanks are due to B.A. Korotyaev for his invaluable help during the examination of the collections, information on the distribution of beetles, and comments on the manuscript.

The work was financially supported by the Russian Foundation for Basic Research (grant no. 11-04-00941), the Presidential Program in Support of the Leading Academic Schools, and the RAS Presidium programs "Origin and Evolution of the Biosphere" and "Inventory, Functions, and Preservation of Biodiversity."

REFERENCES

1. Alfimov, A.V., "The Temperature Status of the Inner Regions of Wrangel Island," in *Nature of Wrangel Island. Recent Studies* (Asterion, St. Petersburg, 2007), pp. 237–253 [in Russian].
2. Berman, D.I., "Fauna and Assemblages of Invertebrates in the Tundra-Steppe Communities of Wrangel Island," in *Biogeography of the Beringian Subarctic Sector* (Vladivostok, 1986), pp. 148–160 [in Russian].
3. Berman, D.I., "Invertebrates," in *Cold Steppes of Northeastern Asia*, Ed. by D.I. Berman (Magadan, 2001), pp. 96–161 [in Russian].
4. Bogacheva, I.A., "Specific Traits in Adaptive Strategies of Leaf-Feeding Insects in the Subarctic," *Zool. Zh.* **74** (8), 83–93 (1995).
5. Bogacheva, I.A., "Chrysomelid Beetles in the Subarctic: Temperature Thresholds, Daily Rhythm of Activity and Time Budget," in *IV European Workshop of Invertebrate Ecophysiology, 9–15 September 2001, St. Petersburg* (St. Petersburg State Univ., 2001), p. 73.

6. Bogacheva, I.A. and Khruleva, O.A., "Leaf Beetle *Chrysomela collaris*: Adaptations to the Existence in Mountains and in the Arctic Region," *Zool. Zh.* **81** (6), 678–685 (2002) [*Entomol. Rev.* **82** (9), 1238–1245 (2002)].
7. Bousquet, Y., *Checklist of Beetles of Canada and Alaska* (Biosystematics Research Centre, Ottawa, 1991).
8. Brown, W.J., "The New World Species of *Chrysomela* L. (Coleoptera, Chrysomelidae)," *Canad. Entomol.* **88** (Suppl. 3), 1–54 (1956).
9. Chernov, Yu.I., "Specific Adaptive Traits of Insect Life Cycles in the Tundra Zone," *Zh. Obshch. Biol.* **39** (3), 394–402 (1978).
10. Chernov, Yu.I. and Matveyeva, N.V., "Landscape-Zonal Distribution of Species in the Arctic Biota," *Uspekhi Sovrem. Biol.* **122** (1), 26–45 (2002).
11. Chernov, Yu.I., Medvedev, L.N., and Khruleva, O.A., "Leaf Beetles (Coleoptera, Chrysomelidae) in the Arctic," *Zool. Zh.* **72** (9), 78–92 (1993).
12. Dubeshko, L.N., "Leaf Beetles (Coleoptera, Chrysomelidae) as Willow Pests in Central Siberia," in *Fauna and Ecology of Insects in East Siberia and the Far East* (Irkutsk, 1977), pp. 102–121 [in Russian].
13. Dubeshko, L.N. and Medvedev, L.N., *Ecology of Leaf Beetles in Siberia and the Far East* (Irkutsk, 1989) [in Russian].
14. Elias, S. and Kuzmina, S., "Response of Chrysomelidae to Quaternary Environmental Changes," in *Research on Chrysomelidae, Part 1*, Ed. by P. Jolivet (Brill Academic, 2008), pp. 174–194.
15. Hägvar, S., "Studies on the Ecology of *Melasoma collaris* L. (Col., Chrysomelidae) in Alpine Habitats of Finse, South Norway," *Norw. J. Entomol.* **22** (1), 31–47 (1975).
16. Isachenko, A.G., *Landscapes of the USSR* (Leningrad State Univ., Leningrad, 1985) [in Russian].
17. Khruleva, O.A., "Invertebrates," in *Fauna of the Wrangel Island Reserve. Annotated Species Lists* (Moscow, 1987), pp. 6–36 [in Russian].
18. Khruleva, O.A., "The Life Cycle of *Chrysolina subsulcata* (Coleoptera, Chrysomelidae) on Wrangel Island," *Zool. Zh.* **73** (3), 29–38 (1994).
19. Khruleva, O.A., "Biology of Arctic Leaf Beetle *Chrysolina cavigera* on Wrangel Island," in *Chrysomelidae Biology, Vol. 3* (SPB Academic Publ., Amsterdam, 1996), pp. 259–270.
20. Khruleva, O.A., "Specificity of the Fauna of Terrestrial Arthropods of Wrangel Island as a Reflection of Specific Traits of Its Environment," in *Nature of Wrangel Island. Recent Studies* (Asterion, St. Petersburg, 2007), pp. 136–181 [in Russian].
21. Khruleva, O.A., "Arthropod Assemblages of Wrangel Island in the Context of the Recent and Pleistocenic Tundra-Steppe Insect Faunas of Northeastern Asia," in *Species and Communities under Extreme Conditions. Collected Works Dedicated to the 75th Anniversary of Academician Yu.I. Chernov* (KMK Press—PENSOFT Pbl., Moscow–Sofia, 2009), pp. 124–167 [in Russian].
22. Kippenberg, H., "Subfamily Chrysomelinae," in *Catalog of Palaearctic Coleoptera. Vol. 6. Chrysomeloidea*, Ed. by I. Löbl and A. Smetana (Apollo Books, Stenstrup, 2010).
23. Kiselev, S.V., *Late Cenozoic Beetles of Northeast Siberia* (Nauka, Moscow, 1981) [in Russian].
24. Kiselev, S.V., *The Environment of North Eurasia in the Pleistocene and Holocene, as Inferred from Studies of Coleoptera*. Doctoral Dissertation in Geology (Moscow, 1995).
25. Kiselev, S.V. and Nazarov, V.I., "Late Cenozoic Insects of Northern Eurasia," *Paleontol. J.* **43** (Suppl. 7), 1–128 (2009).
26. Kuzmina, S. and Bolshiyarov, D., "Forest Insect Spectra in Late Holocene Deposits of the Lena Delta Terrace, North of the Actual Tree Line," *Polarforschung* **70**, 101–105 (2002).
27. Kuzmina, S. and Sher, A., "Some Features of the Holocene Insect Faunas of Northeastern Siberia," *Quaternary Science Reviews* **25** (15–16), 1790–1820 (2006).
28. Lopatin, I.K., Aleksandrovich, O.R., and Konstantinov, A.S., *Check List of Leaf-Beetles (Coleoptera, Chrysomelidae) of the Eastern Europe and Northern Asia* (Mantis, Olsztyn, 2004).
29. MacLean, S.F., "Ecological Adaptation of Tundra Invertebrates," in *Physiological Adaptation to the Environment*, Ed. by F. John Vernberg (Intex Educational Publ., New York, 1975), pp. 269–300.
30. Medvedev, L.N., "New Leaf Beetles (Coleoptera, Chrysomelidae) from the Palaearctic," *Entomol. Obozr.* **52** (4), 876–886 (1973).
31. Medvedev, L.N., "Family Chrysomelidae, Leaf Beetles," in *Keys to Insects of the Soviet Far East. Vol. 3, Part 2* (Nauka, St. Petersburg, 1992), pp. 533–602 [in Russian].
32. Medvedev, L.N., "Leaf Beetles in the Arctic," in *Chrysomelidae Biology, Vol. 3* (SPB Academic Publ., Amsterdam, 1996), pp. 57–62.
33. Medvedev, L.N. and Chernov, Yu.I., "A New Leaf Beetle of the Genus *Chrysomela* (Coleoptera, Chrysomelidae), an Important Component of Taimyr Biocenoses," *Zool. Zh.* **48** (4), 532–537 (1969).
34. Medvedev, L.N. and Dubeshko, L.N., *A Key to Leaf Beetles of Siberia* (Irkutsk, 1992) [in Russian].
35. Medvedev, L.N. and Khruleva, O.A., "Leaf Beetles (Coleoptera, Chrysomelidae) of Wrangel Island," in *Fauna of Wrangel Island* (Vladivostok, 1986), pp. 135–146 [in Russian].
36. Medvedev, L.N. and Korotyayev, B.A., "Essays on the Fauna of Leaf Beetles (Coleoptera, Chrysomelidae) of the Arctic Asia and Kamchatka," in *Studies of the Insect Fauna of the Northeastern Region of the USSR* (Vladivostok, 1980), pp. 77–96 [in Russian].

37. Mikhailov, Yu.E., *Specific Traits of the Montane Faunas of Phyllophages, by the Example of Leaf Beetles (Coleoptera, Chrysomelidae) of the Urals and the Mountains of South Siberia*. Doctoral Dissertation in Biology (Moscow, 2010).
38. Milyashevich, O.Yu., *Leaf Beetles of the Genus Chrysomela L. in the Palaearctic Fauna: Morphology, Taxonomy, Ecology, and Practical Significance*. Candidate's Dissertation in Biology (Priluki, 2002).
39. Poppius, B., "Die Coleopteren des arktischen Gebietes," *Fauna Arctica* **2**, 1–291 (1910).
40. Sher, A.V., Kuzmina, S.A., Kuznetsova, T.V., and Sul'erzhitsky, L.D., "New Insights into the Weichselian Environment and Climate of the East Siberian Arctic, Derived from Fossil Insects, Plants, and Mammals," *Quaternary Science Review* **24**, 533–569 (2005).
41. Sher, A.V., Kuzmina, S.A., Kiselev, S.V., et al., QUENSIB—The Database on Quaternary Insects of North-Eastern Siberia. Preliminary version 3 (04.06), 2006.
42. Sher, A.V. and Kuzmina, S., "Beetle Records," in *Late Pleistocene of Northern Asia. Encyclopedia of Quaternary Science, Vol. 1*, Ed. by S. Elias (Elsevier, 2007), pp. 246–267.
43. Shvarts, S.S., *General Ecological Trends of Evolution* (Nauka, Moscow, 1980) [in Russian].
44. Svatkov, N.M., "Wrangel Island," in *The Soviet Arctic* (Nauka, Moscow, 1970), pp. 453–481 [in Russian].
45. Vartanyan, S.L., *Palaeogeography of the Late Neopleistocene and Holocene of the Wrangel Island Area*. Candidate's Dissertation in Geography (St. Petersburg, 2004).
46. Warchałowski, A., *Chrysomelidae. The Leaf-Beetles of Europe and the Mediterranean Area* (Natura Optima Dux Foundation, Warszawa, 2003).
47. Yurtsev, B.A., "Megaberingia and Cryoxeric Phases in the History of Its Vegetation," in *V.L. Komarov's Memorial Lectures, Issue 3* (Vladivostok, 1986), pp. 3–53 [in Russian].