

GROUND BEETLES (COLEOPTERA, CARABIDAE) IN FUMAROLE FIELDS OF KUNASHIR ISLAND, KURIL ARCHIPELAGO, RUSSIA

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Five species of ground beetles are permanent inhabitants of the fumarola fields on Kunashir Island: *Cicindela* (*Cicindela*) *sachalinensis* A. Morawitz, 1862; *Cylindera* (*Eugrapha*) *elisae* (Motschulsky, 1859); *Bembidion* (*Ocydromus*) *dolorosum* (Motschulsky, 1860); *B.* (*Peryphanes*) *sana-tum* Bates, 1883, and *Poecilus* (*Poecilus*) *samurai* (Lutshnik, 1916). These species respond differently to extreme conditions. In some species, the size is decreased (*C. elisae*, *B. dolorosum*), but is increased in *P. samurai*; in *B. dolorosum*, the pigmentation is decreased, while increased in others (*C. sachalinensis*, *C. elisae*, *P. samurai*). The degree of these variations depends neither on taxonomic relations nor the adaptation time. The areas of moderate thermal activity of Kunashir volcanoes could have served as refugia during the colder climatic periods. Based on data on the variability and barcoding of *B. dolorosum*, the following new synonymy is established: *Bembidion* (*Ocydromus*) *dolorosum* (Motschulsky, 1860) = *Bembidion* (*Ocydromus*) *negrei* Habu, 1958, **syn. nov.** = *Bembidion* (*Peryphus*) *kuznetsovi* Lafer, 2002, **syn. nov.**

Keywords: adaptation, Carabidae, extreme conditions, isolation, Russian Far East, volcano.

INTRODUCTION

The Kunashir Island is the southernmost and one of the largest within the Greater Kuril Chain. It is 123 km long, 7–30 km wide, and has an area of 1490 km². The island consists of three mountain blocks formed by four active volcanoes: Tyatya (1819 m) and Ruruy (1485 m) in the north, Mendeleev (889 m) in the centre, and Golovnin (541 m) in the south. These blocks are separated by the South Kuril and Sernovodsk isthmuses, composed of quaternary marine sediments and volcanic-sedimentary folded Neogene rocks.

Volcanism played and continues to play the leading role in influencing the landscapes on the island. Due to residual volcanism, the soil, water and air in the fumarole fields are enriched with sulfurous compounds; the vegetation

is strongly depressed and degraded, while the temperature of the soil and above-soil air is markedly increased. As a result, the original landscapes are destroyed, while pioneer or modified habitats are formed.

Although Kunashir Island is the most biodiverse one of the Kuril Archipelago, the study of its carabid fauna started relatively recently: the first information appeared only in the second half of the 20th century (KONAKOV 1956, HABU 1967, KUWAYAMA 1967, KRYZHANOVSKIY 1968). These publications contain data about 24 ground beetle species, 20 of which were listed by KUWAYAMA (1967).

Further research during the last quarter of the 20th century increased the taxonomic diversity of Carabidae of the island to 119 species (KRYVOLUTSKAJA 1973, KRYZHANOVSKIY *et al.* 1975, 1995, LAFER 1989, 1992). Taking into account all recorded and still unpublished data, the carabid fauna of Kunashir Island currently amounts to at least 180 species (SUNDUKOV, 2001, 2008, 2011, MAKAROV *et al.* 2013, 2019a-b, MAKAROV & SUNDUKOV 2011, 2014, 2016, SUNDUKOV & MAKAROV 2016, 2019). However, there are no publications on the carabid fauna of the fumarole fields of Kunashir. Only one paper, reports three species on the fumarole fields of the volcanoes of the South Kurils *Cicindela sachalinensis* A. Morawitz, 1862, *Cylindera elisae* (Motschulsky, 1859), and *Carabus blaptoides rugipennis* Motschulsky, 1861 (KONAKOV 1956).

Thus, the adaptive responses of Carabidae to the extreme conditions of the fumarole fields on Kunashir Island remain to be described, and this is the main objective of the present paper.

MATERIAL AND METHODS

Research area

According to the geological morphogenetic classification (FEDORCHENKO *et al.* 1989), active Kunashir volcanoes belong to three types: Tyatya is a single stratovolcano, Ruruy and Mendeleev are isolated "cluster" stratovolcanoes, while Golovnin is a caldera pumice-pyroclastic volcano destroyed mainly by erosion and denudation. The latter three volcanoes are presently at a hydrothermal-solfataric stage of activity. Thus, denuded fumarole fields occupy the slopes or calderas of volcanic edifices, with several rivers and streams flowing from there. The temperature of these streams reaches 100 °C, sulphate and sulphate-chloride waters are acidic (minimal pH ca. 2.0), while hydro-carbonate-sulphate sodium-calcium waters are subneutral (pH up to 8.5). A detailed description of the studied solfatara fields is given in Appendix 1.

Ground beetle collections

This study is based on the material taken on Kunashir Island during nine field seasons. The first and third authors, together with I. V. Melnik, A. A. Zaitsev and A. S. Prosvirov (all from Moscow), captured beetles in 2008, 2009, 2011, 2013 and 2017. The second author, together with L. A. Sundukova (Lazo, Primorsky Territory), collected insects from

mid-May to mid-October 2013–2018. Over that time, more than 200 sites were surveyed (Appendices: Fig. A1) with the following details:

Ruruy Volcano – Neskuchenskie Streams (7–12 August 2013); Dal'nie Streams (21–23 June 2017, 4–9 August 2017).

Mendeleev Volcano – Northeastern solfatara field (19 June 1990, 18 June 2011; 23–24 June 2016, 3–4 August 2016, 22 September 2016, 8 June 2017, 14–16 July 2017).

Golovnin Volcano – caldera (24 June 2008; 11 July 2009; 28 May 2011; 24–28 July 2011; 7–9 June 2013; 14–20 July 2015; 2–11 September 2015; 23–25 June 2016; 30 June–8 July 2016; 23–25 July 2016; 5–10 July 2017; 22–24 June 2018; 16–18 July 2018).

The ground beetles were mainly hand-collected, with occasional pitfall trapping and night sampling. The material was fixed with ethyl acetate or for molecular studies, in 96% alcohol.

During the entire research period, 15,748 adults belonging to 165 species of ground beetles were collected. Besides, 644 specimens of 44 carabid species from the collection of D. N. Kochetkov (Arkhar, Amur Region), as well as 99 adults of 15 carabid species from the collections of the Federal Scientific Center of East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok (FEB) and the Zoological Institute of the Russian Academy of Science, St. Petersburg (ZISP) were also studied. Most of the collected individuals are kept in the collections of the FEB and Moscow State Pedagogical University, Moscow (MPU); several specimens were transferred to the collections of the Zoological Museum of the Moscow State University, Moscow (ZMMU) and ZISP. The details are as follows (all labels are shown in Appendix 2.):

Cicindela (*Cicindela*) *sachalinensis sachalinensis* A. Morawitz, 1862 – Collected: 95 ♂♂, 138 ♀♀; measured: 94 ♂♂, 130 ♀♀; genital prepate: 12 ♂♂; 10 ♀♀.

Cylindera (*Eugrapha*) *elisae* (Motschulsky, 1859) – Collected: 83 ♂♂, 82 ♀♀; measured: 83 ♂♂, 82 ♀♀; genital prepate: 29 ♂♂; 6 ♀♀.

Bembidion (*Ocydromus*) *dolorosum* (Motschulsky, 1860) – Collected: 535 ♂♂, 514 ♀♀; measured: 299 ♂♂, 301 ♀♀; genital prepate: 42 ♂♂; 13 ♀♀.

Bembidion (*Peryphanes*) *sanatum* Bates, 1883 – Collected: 25 ♂♂, 30 ♀♀; measured: 8 ♂♂, 7 ♀♀; genital prepate: 5 ♂♂; 5 ♀♀.

Poecilus (*Poecilus*) *samurai* (Lutshnik, 1916) – Collected: 67 ♂♂, 54 ♀♀; measured: 50 ♂♂, 37 ♀♀; genital prepate: 9 ♂♂.

Specimens were examined under MBS-1 or Leica M165C stereoscope, the slides of male genitalia studied under a Zeiss Axio Scope.A1 microscope, and photographed with a Canon EOS 5D Mark III camera with a Canon MP-E 65 mm macro lens, or a Canon EOS 6D camera attached to a Zeiss Axio Scope.A1 microscope. In both cases, the extended focus technique was used, and photos were processed using the Zerene Stacker software. For preparing the slides, the aedeagi of some male specimens were consistently kept in 10% KOH (24 h.), 4% acetic acid (5 min.) and cold water (5 min.), and then mounted with Hoyer fluid or Euparal (D~1.05) media.

DNA extraction and amplification

The genetic studies were carried out at the Natural History Museum, University of Oslo. DNA was extracted from the prothorax, hind legs or testis accessory gland from specimens previously fixed in absolute alcohol, using the Qiagen DNeasy Blood & Tissue Kit® (QIAGEN, Hilden, Germany) following the manufacturer's protocol for animal tissue,

with minor modifications (ELVEN *et al.* 2010). The voucher specimens and the DNA extracts are deposited in the collection of MPU.

Samples were incubated in lysis buffer ATL and proteinase K at 55 °C for 24 h. A region of ~700 bp from the mitochondrial cytochrome oxidase subunit I (COI) was amplified with both forward primer LCO 1490 and reverse primer HCO 2198 (FOLMER *et al.* 1994). PCR was performed in a 25 µl reaction volume using 14 µl Master Mix 1 (8.76 µl dsH₂O, 0.24 µl BSA, 2.5 µl GeneAmp dNTP Mix, 1.25 µl of each primer), 8 µl Master Mix 2 (5.375 µl dsH₂O, 2.5 µl 10X Dream Taq buffer, 0.125 µl Dream Taq polymerase) and 3 µl of the respective DNA extract.

The general PCR profile consisted of an initial activation step at 95 °C for 2 min, followed by 34 amplification cycles consisting of 95 °C for 30 s (denaturation), 49 °C for 30 s (annealing) and 72 °C for 1 min (extension), and a final extension step of 72 °C for 10 min. The success of the PCR was ascertained in a 1% agarose gel in TAE buffer, and FastRuler Low Range DNA Ladder was used as the molecular weight marker.

The PCR products were purified using ExoSAP45[®] protocol (USB Corporation, Cleveland, Ohio, USA), and then all fragments were sequenced in both directions either externally by the StarSEQ (Mainz, Germany).

Sequence alignment

The nucleotide sequences obtained were manually edited to correct possible sequencing errors and to delete low-resolution terminal segments using the Unipro UGENE v33.0 (OKONECHNIKOV *et al.* 2012) and then aligned in MEGA-X v10.1.6 using the MUSCLE algorithm (KUMAR *et al.* 2018). Ambiguously aligned regions were excluded from the downstream analyses. The edited nucleotide sequences were deposited in GenBank under accession numbers MW240488-MW240502.

Phylogenetic analysis

To clarify the taxonomic status of the particular populations of *Cylindera* (*Eugrapha*) *elisae* (Motschulsky, 1859) from different Kunashir Island localities, additional *C. elisae* sequences from GenBank from various localities in Japan, Korea and Taiwan were used, and the sequences from GenBank corresponding to specimens of *C. (E.) bonina* (Nakane et Kurosawa, 1959) were also applied to the analysis as outgroup. A haplotype network to visualize the relationships among haplotypes for the *C. elisae* sequence dataset was calculated using PopART v.1.7 (LEIGH & BRYANT 2015). A Minimum spanning network was constructed with default settings for the aligned haplotype sequences (BANDELT *et al.* 1999).

To confirm the conspecificity of *Bemdidion* (*Ocydromus*) *dolorosum* (Motschulsky, 1860) and *B. (Ocydromus) negrei* Habu, 1958, additional sequences from GenBank corresponding to ten species of the subgenus *Ocydromus* Clairville, 1806 were also included (see Appendix 3).

The evolutionary analysis was inferred by using the Maximum Likelihood method and Kimura 2-parameter model (KIMURA 1980, TAMURA *et al.* 2012). Initial tree(s) for the heuristic search were automatically obtained by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with the superior log likelihood value. This analysis involved 113 nucleotide sequences. A total of 849 positions were in the final dataset. Evolutionary analyses were conducted in MEGA X (KUMAR *et al.* 2018).

Measurements

The measurements (in mm) were made with an ocular-micrometer mounted on a Leica M165c (Carl Zeiss) stereo microscope, as follows: CI — confidence interval; EL — greatest length of elytra; EW — greatest width of elytra; Lae — length of the aedeagus; Llm2 — length of lamina 2; Lms — length of main sclerite; PLm — length of pronotum, measured along the median line; PW — greatest width of pronotum; TL — total body length without labrum (from anterior margin of clypeus to the elytral apex along the suture). The nomenclature of the sclerites of the male internal sac in *Bembidion* follows BELOUSOV and SOKOLOV (1996), as well as NERI and VIGNA TAGLIANTI (2010).

Data analysis

Statistical analysis was performed using the PAST v4.0 software (HAMMER *et al.* 2001). The significance was determined by Tukey's and Mann-Whitney *U*-test for independent variables, with a 95% confidence interval. If statistically significant differences were found, pairwise Dunn's *a posteriori* tests were additionally executed. Frequencies of colour variants were analysed by Mann-Whitney and χ^2 tests. The influence of temperature and pH was assessed using a multivariate multiple linear regression analysis.

RESULTS AND DISCUSSION

A total of 846 specimens belonging to 29 species of ground beetles (Appendix 4) were collected in the fumarole fields, but only five species (780 specimens) were permanent inhabitants of these unusual habitats.

1. *Cicindela* (*Cicindela*) *sachalinensis sachalinensis*

Cicindela sachalinensis occurs in eastern and central China, Korea, eastern Mongolia, the Russian Far East, and Japan (WIESNER 1992, PUCHKOV & MATALIN 2003, 2017). Among the five subspecies, the nominal one is known exclusively from insular habitats of Sakhalin, Moneron, Iturup, Kunashir, Shikotan (KRYZHANOVSKIY *et al.* 1975, 1995, LAFER 1978, 1999, MAKAROV *et al.* 2020), Hokkaido and Honshu (WIESNER 1992, PUCHKOV & MATALIN 2003, 2017). This species is widely distributed over the Kunashir Island (Appendices: Fig. A13) and is mostly observed in habitats without or only with scant plant cover (KRYZHANOVSKIY *et al.* 1975, LAFER 1978, 1999, MAKAROV *et al.* 2019b, this paper). It was present in almost all fumarole fields studied (Appendices: Fig. A8) but recorded in high numbers only in Golovnin Volcano on the fumaroles of the central domes. The specimens inhabiting the fumarole fields were similar in size to specimens from other habitats, except for the significantly smaller females (Figs 9A, B). On the fumaroles, significantly more ($p < 0.01$) dark-pigmented adults were collected (Fig. 8A, Appendices: Figs A18, A19).

2. *Cylindera (Eugrapha) elisae*

Cylindera elisae is an Asiatic tiger beetle occurring from the Amur River valley through Mongolia, Korea and China (PUCHKOV & MATALIN 2003, 2017) to northern Vietnam (WIESNER *et al.* 2017), and also in Sakhalin, Kunashir, Taiwan and various Japanese islands. On Kunashir Island, this species is found only on fumarole fields of two volcanoes (Appendices: Figs A9, A12). One form, *C. e. kunashirensis* Pütz et Wiesner, 1994, inhabits the valley of Kislaya River on the Mendeleev Volcano (KRYZHANOVSKIY *et al.* 1975, LAFER 1978, PÜTZ & WIESNER 1994, SABIROV *et al.* 2014, MAKAROV *et al.* 2019b, SUNDUKOV & MAKAROV 2019), while a different form populates the Neskuchenskiye Streams on the Ruruy Volcano (MAKAROV *et al.* 2019b, SUNDUKOV & MAKAROV 2019). The specimens from these localities are well distinguishable by size, the proportions of the labrum, and elytral coloration. Thus, *C. e. kunashirensis* is smaller: in males, TL = 8.74 mm [CI = 7.8–9.2 mm] *vs.* 9.38 mm [CI = 8.55–10.05 mm] in the specimens from the Ruruy Volcano ($p < 0.01$), in females, TL = 9.81 mm [CI = 8.6–10.6 mm] *vs.* 10.19 [CI = 8.8–11.3 mm] in specimens from the Ruruy Volcano ($p < 0.05$). Besides, *C. e. kunashirensis* shows a significantly ($p < 0.001$) narrower labrum, darker elytra (Figs 1A–F), and darker elytral punctation. The barcoding technique also verified the distinction of *C. e. kunashirensis*. According to the data obtained, specimens from the Kislaya River formed a compact cluster clearly separated from most other local forms of *C. elisae* (Fig. 2), their haplotypes being separated from the basic one by 206 mutational steps. By the white pattern on the elytra (Figs 1B–F), as well as the shape of the aedeagus (Figs 1G–L), specimens from the Ruruy Volcano are more similar to those from Sakhalin and the continental Russian Far East than to *C. e. novitia*, the latter inhabiting northern Hokkaido. All these observations allow us to conclude that the Ruruy specimens belong to the nominative subspecies. Interestingly, in the Japanese sub-prefecture of Nemuro, where the eastern coast of the Shiretoko Peninsula is 24–43 km from the Kunashir Island, *C. elisae* has not yet been recorded (KIMOTO & YASUDA 1995).

3. *Bembidion (Ocydromus) dolorosum*

Bembidion dolorosum is widespread in Japan (Hokkaido, Honshu), also inhabiting southern Sakhalin (north to Dolinsk, 47°19') and Moneron Island, as well as the southern Kuriles (Urup, Iturup, Kunashir, Shikotan, and islands of the Lesser Kuril Chain) (NAKANE 1963, INOUE 1971, KRYZHANOVSKIY *et al.* 1975, WATANABE 1989, LAFER 1998, 2002a, 2006, YOSHITAKE *et al.* 2011, SUNDUKOV 2017, SUNDUKOV & MAKAROV 2013, 2016, MAKAROV *et al.* 2019b). On Kunashir Island, it occurs on the banks of almost all rocky or sandy rivers and streams

(Appendices: Fig. A14), in all fumarola fields studied (Appendices: Figs A2, A4, A6), sometimes in very high numbers. In fumarolas, we observed it feeding on small dead insects, mostly flies (Appendices: Figs A10, A11).



Fig. 1. Males of *C. elisae*: A, G = *C. elisae kunashirensis* (Kunashir Isl., Kislyi Stream); B–D, H–J = *C. elisae elisae* (B, H = Kunashir Isl., Neskuchenskie Streams; C = Sakhalin Isl., Susuya River; D = Khabarovsk Krai, Korsakovo; I = Sungari River; J = Primorsky Krai, Kedrovaya Pad' National Reserve); E, K = *C. elisae novitia* (Japan, Ishigaki); F, L = *C. elisae mikurana* (Japan, Kozushima); A–F = left elytron; G–L = aedeagus, left lateral view

In the northern part of the distribution area (Sakhalin and Kuril Islands), *B. dolorosum* is characterized by moderate variability and a clear-cut sexual dimorphism (Figs 10A, B). In males, TL = 5.19 mm [CI = 5.14–5.23 mm], in females, TL = 5.35 mm [CI = 5.30–5.39 mm]. The proportions of the head and pronotum are slightly variable. The differences between the populations from different islands are usually not significant, only the males from Yuriy Island and the females from Sakhalin Island in most cases differ significantly.

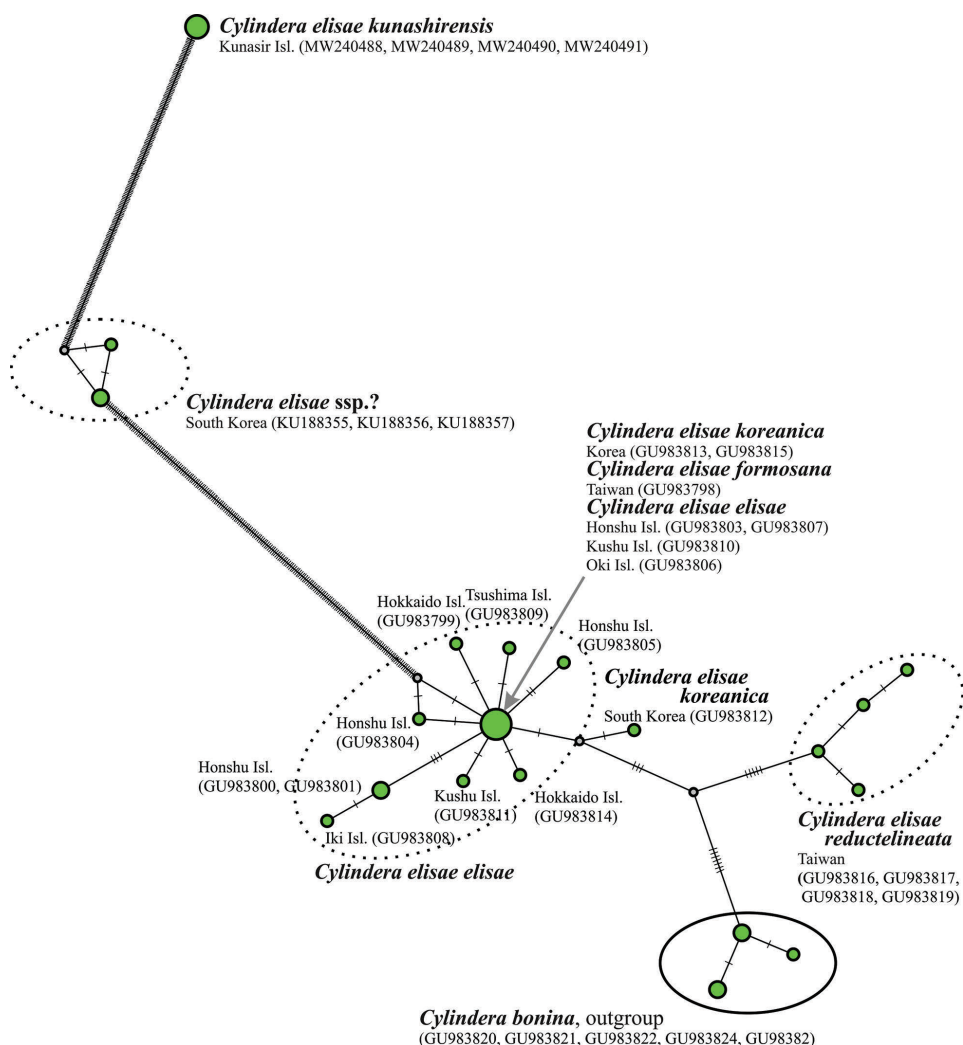


Fig. 2. Position of *Cyllindera elisae kunashirensis* in the *Cyllindera elisae* haplotype network (minimum spanning network, mutations show as hatch marks, GenBank accession numbers for each isolate indicated in brackets)

Specimens living in the fumarole fields of the Kunashir Island are significantly ($p < 0.01$) smaller than elsewhere; in males, $TL = 4.76$ mm [$CI = 4.69\text{--}4.82$ mm], in females, $TL = 4.87$ mm [$CI = 4.81\text{--}4.94$ mm], and the sexual dimorphism is less pronounced. Beetles from the fumarole fields also differ by a decreased elytral pigmentation (Fig. 3, Appendices: Figs A10, A20–A39, A40–A64), an increased pronotum and elytra (Figs 10C, D), as well as by shorter claws and the ventro-apical setae of the tarsomeres (Appendices: Figs A65–A67).

These demonstrate clinal variability, because the body size, coloration and main body proportions gradually changed under an environmental acid-

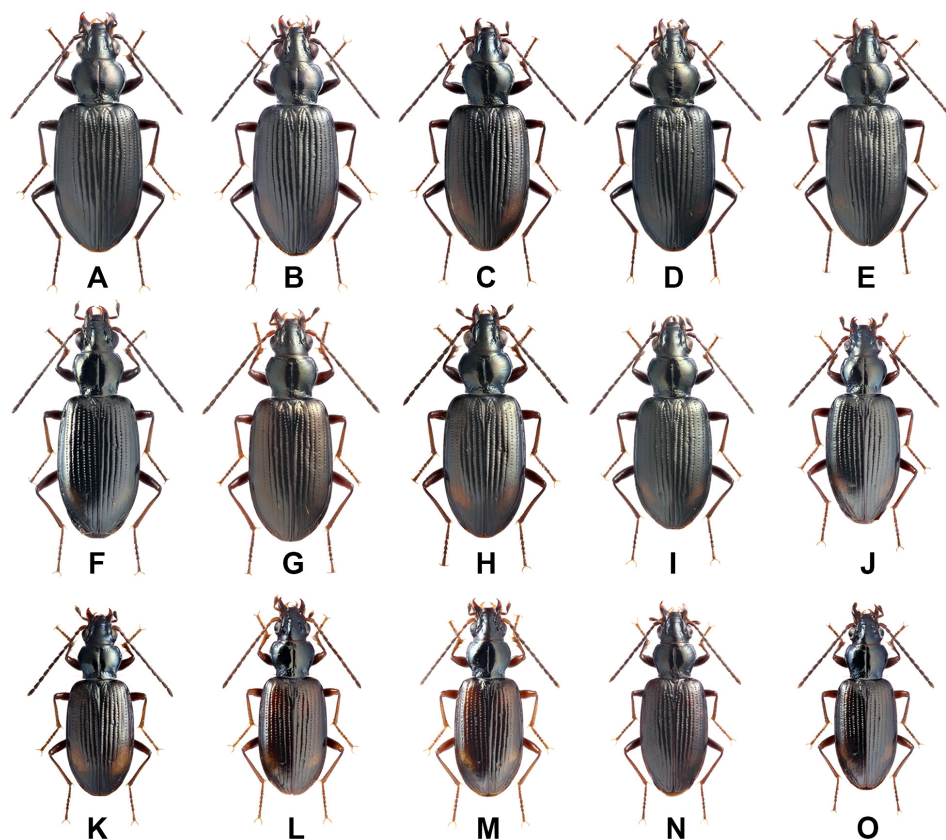


Fig. 3. Variability *B. dolorosum*, females: A = Kunashir Isl., mouth of the Ozernaya River; B = Kunashir Isl., mouth of the Mednyi Stream; C = Sakhalin Isl., near Khomutovo; D = Sakhalin Isl., Rogatka River; E = Kunashir Isl., caldera of Golovnin Volcano, near cordon Ozernyi; F = Yuriy Isl., Shirokaya Bay; G = Kunashir Isl., Mendelev Volcano, mouth of Kislyi Stream; H, K = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field "Bolshoye"; I = Shikotan Isl., Tserkovnaya Bay; J, L, O = Kunashir Isl., caldera of Golovnin Volcano, solfatara field "Cherepakhovoye"; M = Kunashir Isl., Mendelev Volcano, source of Kislyi Stream; N = Kunashir Isl., caldera of Golovnin Volcano, Kipyashcheye Lake (loc. typ. *B. kuznetsovi*)

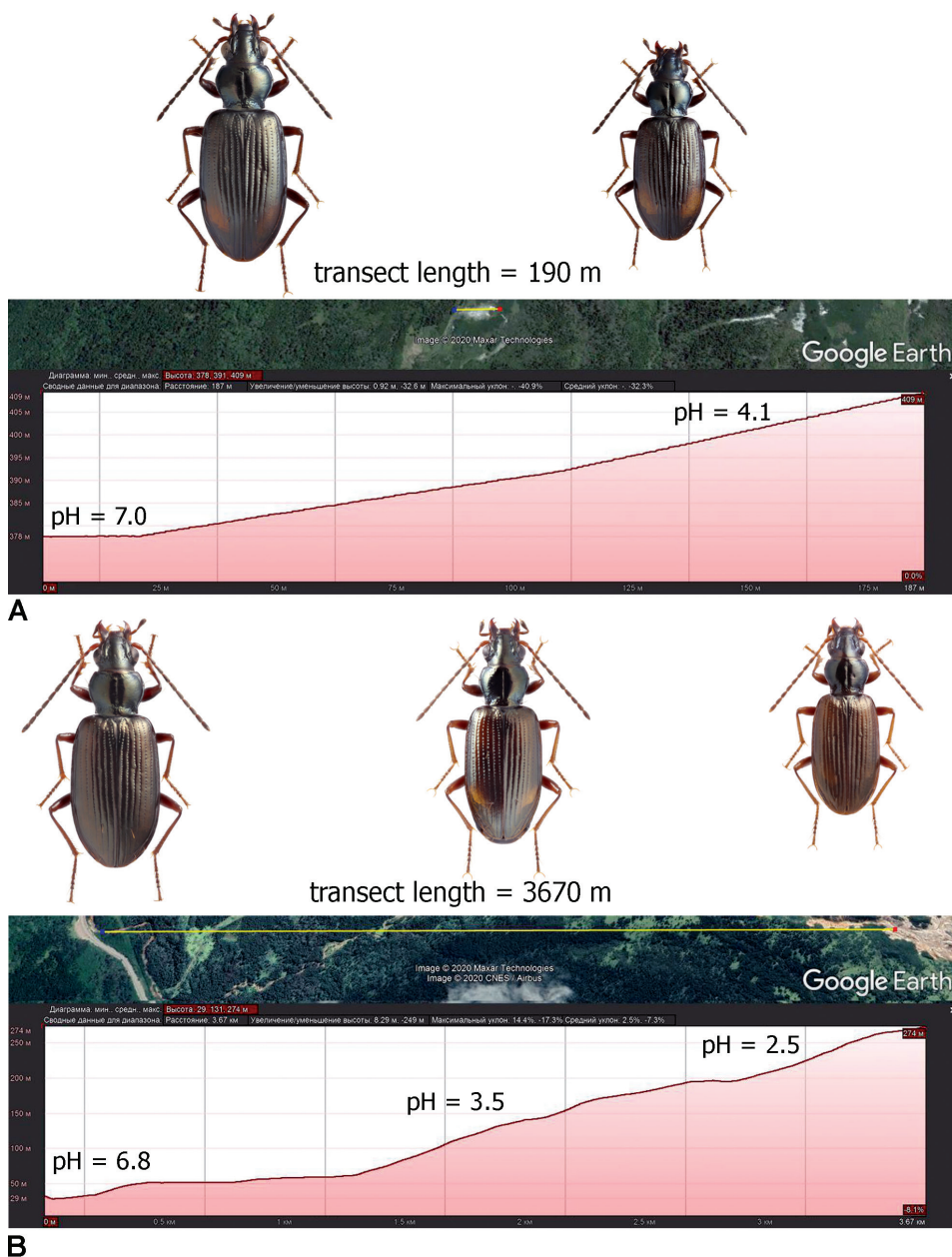


Fig. 4. Size and color variability *B. dolorosum* with an increase in the acidity of watercourses: A = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field "Bolshoye"; B = Kunashir Isl., Mendelev Volcano, Kislyi Stream

ity gradient. Along transects with a moderate gradient, these changes are relatively small (Fig. 4A), but is more pronounced under greater range (Fig. 4B). There was a significant dependence of body length and the proportions of the pronotum on both temperature and water acidity (multiple linear regression, Wilks lambda = 0.4075; $F = 84.12$; $p = 1.401 \times 10^{-56}$; see Appendix 5).

Interestingly, the structure of the aedeagus also varied. In males living under increased temperature and acidity, the aedeagus became relatively enlarged, *vs.* the endophallus sclerites (*main sclerite* = *sclerite principale* and *lamina 2* = *lama paracopulatrice*) relatively shortened (Figs 5, 6; Appendices: Figs A68–A88, A89–A94).

The COI sequences of the specimens inhabiting the fumarola fields and other habitats were identical or differed only by 1–2 mutation steps. All specimens formed a compact cluster on the *Ocydromus* phylogenetic tree (Appen-

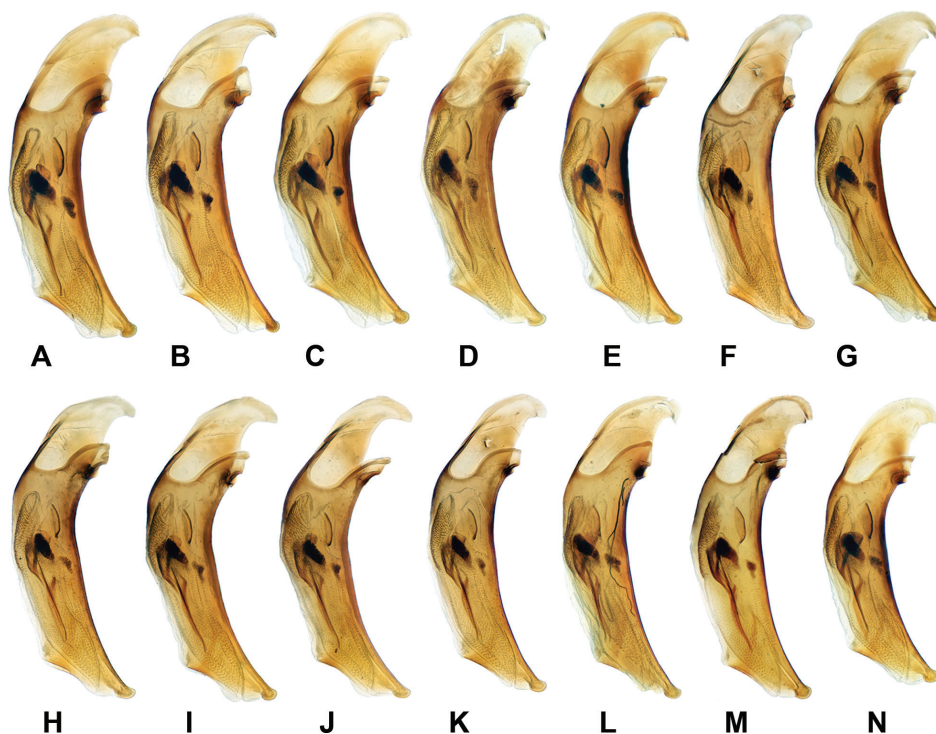


Fig. 5. Variability of the shape and size of the aedeagus *B. dolorosum*: A, E = Shikotan Isl., Tserkovnaya Bay; B = Kunashir Isl., Zmeinyy (Stolbovskoy) Stream; C = Kunashir Isl., mouth of the Ozernaya River; D = Kunashir Isl., Mendelev Volcano, mouth of Kislyi Stream; F, H, K = Kunashir Isl., Mendelev Volcano, source of Kislyi Stream; G = Kunashir Isl., caldera of Golovnin Volcano, Kipyashcheye Lake (loc. typ. *B. kuznetsovi*); I, J = Yuriy Isl., Shirokaya Bay; L, N = Kunashir Isl., caldera of Golovnin Volcano, solfatara field "Cherepakhovoye"; M = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field "Bolshoye"

dices: Fig. A95). D. Maddison (pers. comm.) has sequenced six genes (COI, 28S, wingless, CAD, topoisomerase, and Muscle-Specific Protein 300 (MSP)) for one specimen of the *B. dolorosum* form (from the Shiretoko Peninsula, Hokkaido Isl.) and one specimen we provided of the fumarole from the caldera of Golovnin Volcano, Kunashir Isl. These two specimens had identical sequences in COI, 28S, and differed by a single base (among 487 bases) in wingless, one base (among 767 total bases) in CAD, four bases (among 876 bases) in topoisomerase, and two bases (among 765 bases) in MSP.

Note. LAFER (2002b) described *Bembidion* (*Peryphus*) *kuznetsovi* from the bank of Lake Kipyashcheye and compared his new species to *Bembidion* (*Pery-*

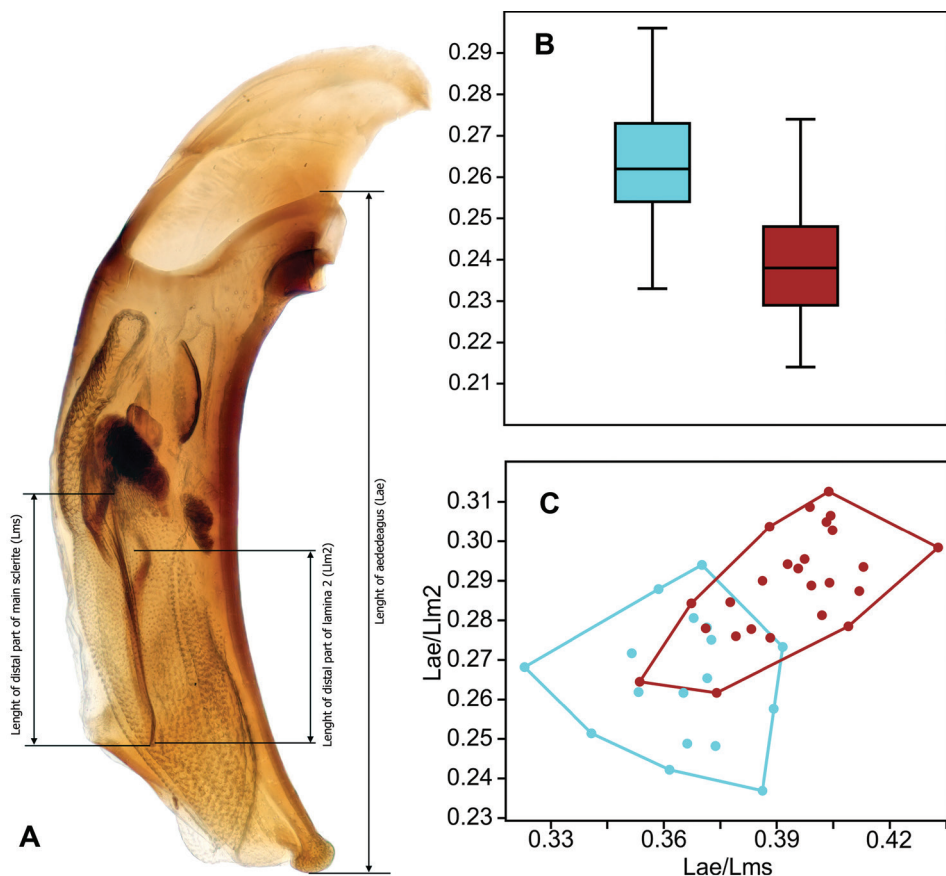


Fig. 6. Variability of the proportions of the aedeagus and its sclerites in *B. dolorosum*: A = measurement scheme; B = relative length of the aedeagus; C = relative length of main sclerite and lamina 2. Cyan = individuals inhabiting solfataric fields, brown = living under ordinary conditions

phus poppii pohlai Kirschenhofer, 1984 and *Bembidion* (*Terminophanes*) *consummatum* Bates, 1873, but not to *B. dolorosum*. Later, MORITA (2010) studied some species of *Bembidion* inhabiting fumarola fields on Hokkaido and northern Honshu and established the synonymy *B. kuznetsovi* with *Bembidion* (*Ocydromus*) *negrei* Habu, 1958. According to the data obtained, we establish here the following new synonymies: *Bembidion* (*Ocydromus*) *dolorosum* (Motschulsky, 1860) = *Bembidion* (*Ocydromus*) *negrei* Habu, 1958 **syn. nov.** = *Bembidion* (*Peryphus*) *kuznetsovi* Lafer, 2002 **syn. nov.** It is noteworthy that the diagnostic features of *Bembidion* (*Ocydromus*) *ozakii* Morita, 2010, described by MORITA (2010) from Japan, entirely correspond to the individual variation range of *B. dolorosum*. Thus, *B. ozakii* is probably only another synonym of *B. dolorosum* as well.

4. *Bembidion* (*Peryphanes*) *sanatum*

This species is widely distributed in different habitats over a wide altitudinal range on the Japanese islands of Hokkaido and Honshu (BATES 1883, JEDLIČKA 1965, WATANABE 1989, KIMOTO & YASUDA 1995, YASUI & SHIYAKE 2008, YOSHITAKE *et al.* 2011, MORI 2016, YOSHIMATSU *et al.* 2018), but in the Kunashir Island, it was found only on the slopes of the Mendelev Volcano (Appendices: Fig. A15), in the valley of Kislaya River (KRYZHANOVSKIY *et al.* 1975, SUNDUKOV & MAKAROV 2016, MAKAROV *et al.* 2019b, our data). The beetles inhabit the bank of an acidic mineralized stream flowing down from fumarola fields (Appendices: Fig. A4). It noteworthy that these fumarola fields and streams are also the sole habitat for the endemic Kunashir tiger beetle, *Cylindera elisae kunashirensis*.

Notes. In the original description, BATES (1883) considered *B. sanatum* as closer to the European *B. lunatum* (Duftschmid, 1812). Later authors placed this species to the subgenus *Peryphus* Dejean, 1821 (NETOLITZKY 1943, JEDLIČKA 1965, KIRSCHENHOFER 1984), while others to *Bembidion* incertae sedis (MARGGI *et al.* 2017). Based on the structure of the male aedeagus and female spermatheca, *B. sanatum* belongs to *Peryphanes* (SUNDUKOV & MAKAROV 2016). Most species of this subgenus are restricted to the western Palaearctic. In eastern Asia, only five species are known to occur (JEDLIČKA 1933, HABU & UÉNO 1955, HABU 1973, NAKANE 1979, KIRSCHENHOFER 1984), which are recorded from Japan (*B. dostali* Kirschenhofer, 1984; *B. hayachinense* Nakane, 1979; *B. hikosanum* Habu et Uéno, 1955), China (*B. parepum* Jedlička, 1933) or Taiwan (*B. lulinense* Habu, 1973). Originally, all those species were described in different subgenera, and only recently were they all classified as *Peryphanes* (TOLEDANO 2009, 2011, MARGGI *et al.* 2017). Based on the conformation of the spermatheca (a large number of whorls of a sclerotized vas deferens, the proportions and shape of the chambers), as well as structure of the aedeagus (large lateral scler-

rites, large basal sclerites protruding far from the base, the absence of a ventral tubercle), *B. sanatum* is very similar to the western Palaearctic *Bembidion* (*Peryphanes*) *stephensii* Crotch, 1866 (Fig. 7).

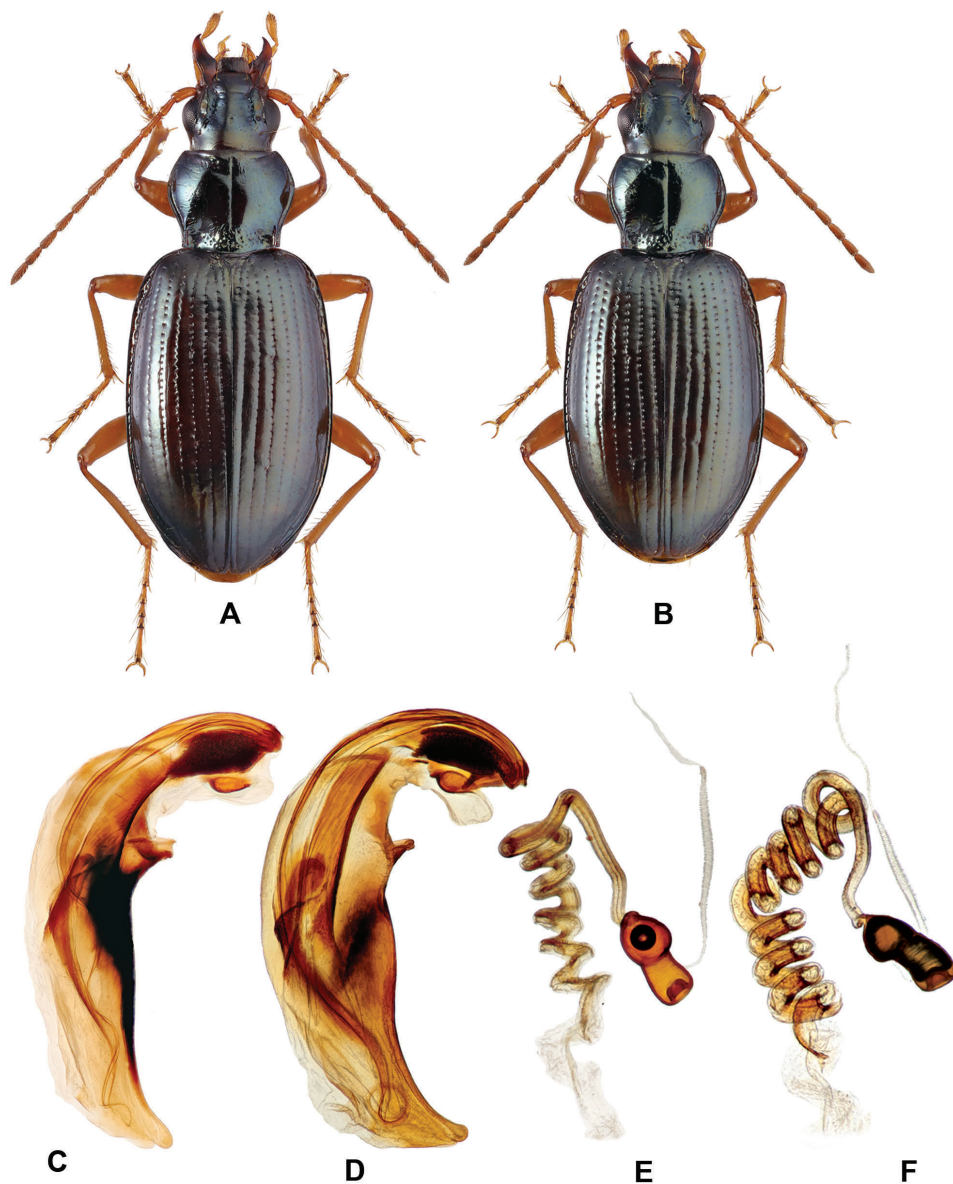


Fig. 7. *Bembidion sanatum* and *B. stephensii*: A–C, E = *B. sanatum*; D, F = *B. stephensii*; A, B = dorsal habitus, male and female; C, D = aedeagus; E, F = spermatheca

5. *Poecilus (Poecilus) samurai*

On Kunashir Island, this species lives in open habitats such as forest edges and clearings, as well as meadows, including sites with dense and tall grass (LAFER 1989, MAKAROV *et al.* 2019b, this paper). As a rule, it does not co-occur together with the closely related *Poecilus (Poecilus) fortipes* (Chaudoir, 1850) (Appendices: Figs A16, A17). In fumarole habitats, *P. samurai* was observed only on the Dokuchaev Mountain Ridge (“Bolshoye” fumarola field, Appendi-

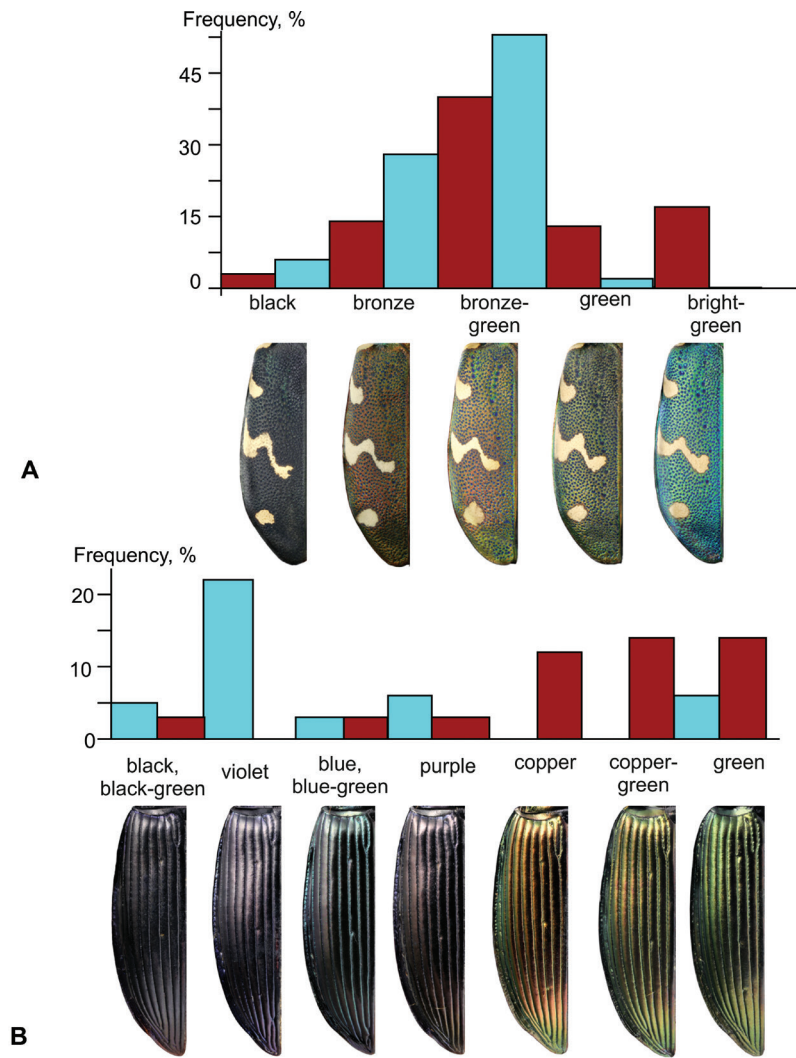


Fig. 8. Variability coloring *Cicindela sachalinensis* (A) and *Poecilus samurai* (B) on Kunashir Island. Cyan = specimens from fumarole fields; brown = specimens from common habitats

ces: Fig. A3). These specimens significantly ($p < 0.01$) differed from others both by their larger size (Fig. 9D) and the higher level of cuticular melanization (Fig. 8B, Appendices: Figs A96–A97 vs. A98–A99). However, the structure of the internal sack of the aedeagus was not different (Appendices: Figs A100–103).

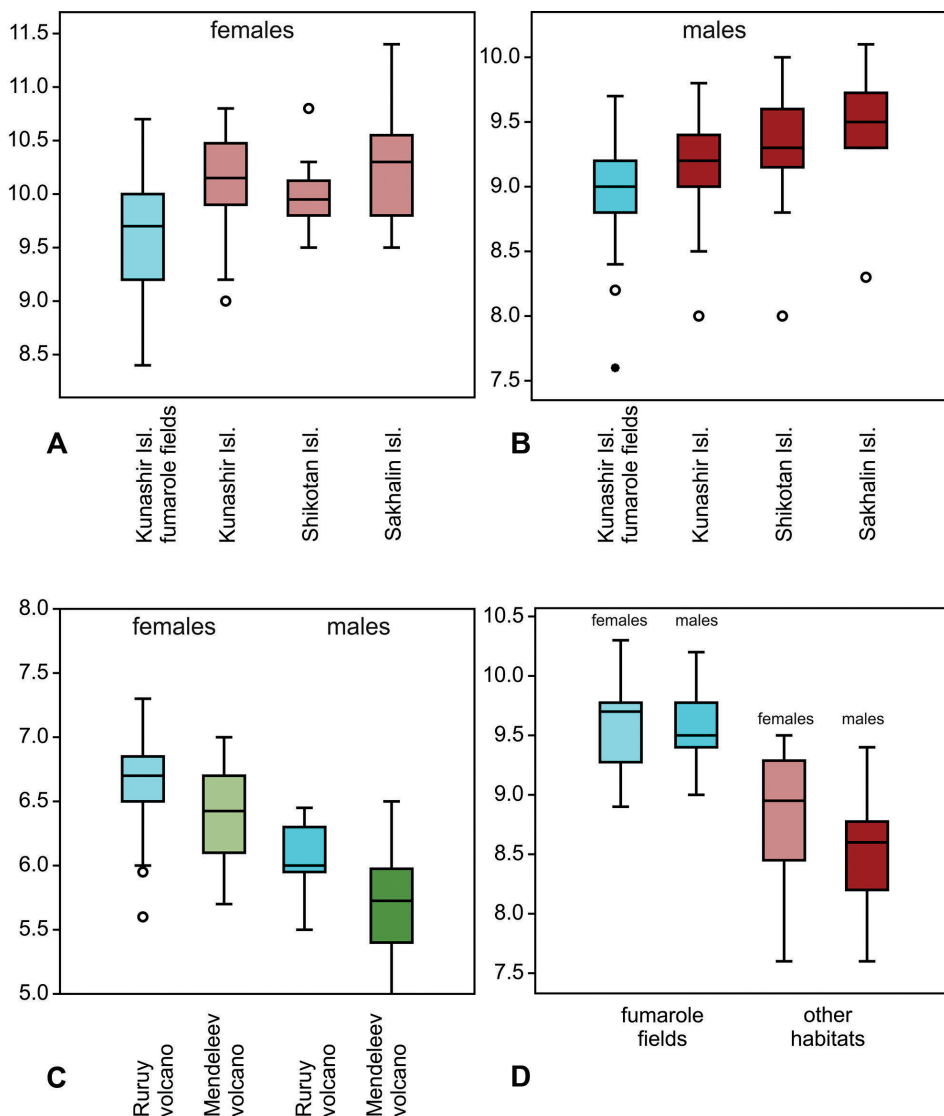


Fig. 9. Variability of sizes (EL) ground beetles inhabiting the fumarole fields: A–B = *Cicindela sachalinensis* (A = females, B = males), C = *Cylindera elisae*; D = *Poecilus samurai*

CONCLUSIONS

In most cases, the study of the influence of volcanic activity is limited to direct, often catastrophic effects on animals, including Coleoptera (see review by ELIZALDE 2014). Fumarola fields are one of the manifestations of volcanism under constant change. The micro-relief of the fumarola fields is formed or destroyed by thermal springs, mud pools and steam-gas emissions, also because hydrothermally altered rocks are subjected to denudation. According to lichen

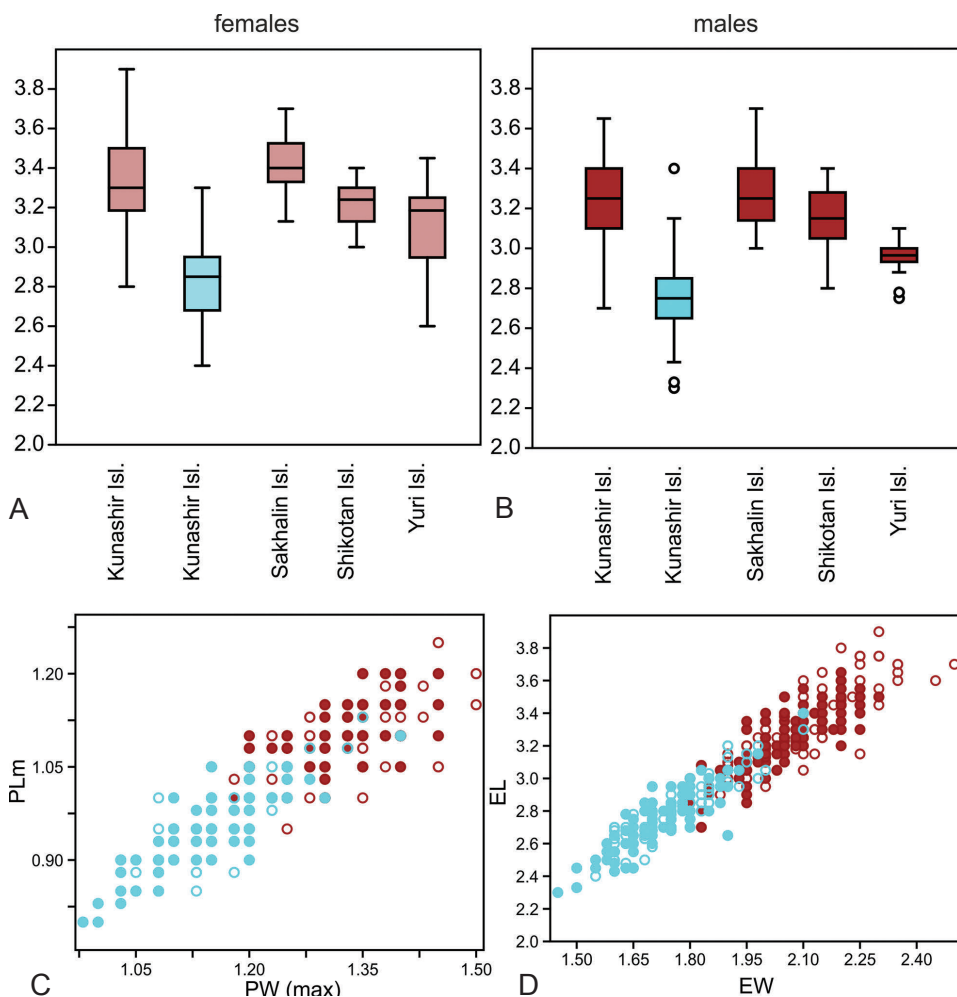


Fig. 10. Variation in size and proportion of *Bembidion dolorosum*: A, B = length of elytra, C = proportion of pronotum, D = proportion of elytra. Cyan = specimens from fumarole fields; brown = specimens from common habitats

bioindication data (EZHIN 2019), fumarola fields have an influence 'halo' of ca. 600 m on Kunashir Island, but at distances of >2 km such an effect is absent. The presence of such environmental gradients creates the prerequisites for gradual development of the adaptations in different species during their occupation of fumarola fields. Thus, the species inhabiting the fumarolas could be considered as model objects for the study of microevolutionary processes.

On Kunashir Island, only a few species of ground beetles have been able to colonize such fumarole fields. It is hardly surprising that the inhabitants of open spaces or the rocky banks of streams have become successful colonists. However, only *C. sachalinensis* and *B. dolorosum* were recorded from all volcanoes studied (Appendices: Figs A13, A14), while the remaining few species were narrowly localized. *Cylindera elisae* was found only on the Mendeleev and Ruruy volcanoes (Appendices: Fig. A12), *B. sanatum* only on the Mendeleev Volcano (Appendices: Fig. A15), while *P. samurai*, widespread across the island (Appendices: Fig. A16), only on the fumaroles of the Dokuchaev Mountain Ridge. Obviously, this unevenness and patchiness could have hardly been caused by environmental conditions, which were generally similar in all fumarole fields studied, and requires additional explanation.

The reaction of carabids to the special conditions of fumarole fields was species-specific. On the one hand, fumarola-inhabiting specimens of *C. sachalinensis* slightly differed from those in other habitats (Figs 8A, 9A, B); likewise, *B. sanatum* from the Kunashir, hardly differed from specimens from Honshu. On the other hand, specimens of *P. samurai* populating the fumarole fields differed noticeably in size and melanization (Figs 8B, 9D; Appendices: Figs A96–A97 vs. A98–A99), while *C. elisae kunashirensis*, in addition to the smaller size (Fig. 9C) and melanization (Fig. 1A), showed a relatively narrow labrum and was noticeably separated genetically (Fig. 2). The most interesting pattern of variability in all studied fumarole fields is demonstrated by *B. dolorosum*: as both temperature and acidity increase, specimens of this species become relatively small, elongated, and partially depigmented.

These differences could be associated both with certain features of different species and with the time of their adaptations to the conditions of fumarola fields. According to the data obtained, morphological changes do not depend on the taxonomic similarity of a species. Thus, *B. dolorosum* was extremely variable, while *B. sanatum* showed almost no particular change on the fumarola fields. Similar differences can also be seen between *C. sachalinensis* and *C. elisae*.

It is more difficult to assess the influence of time in the adaptation process. We can reasonably assume that widespread, flying species found in high numbers near the borders of fumarole fields (*C. sachalinensis*, *B. dolorosum*) have constantly inhabited these particular habitats. Specimens taken within or beyond fumarola fields were not distinguishable by their barcodes. Yet,

they showed differences in morphological adaptations. *Cicindela sachalinensis* changed only slightly, while *B. dolorosum*, under increasing temperatures and acidity, was capable of developing forms that could erroneously be determined as different species.

The denuded landscapes of the fumarole fields and the headwaters of the streams on the Mendeleev Volcano, the single place where both Kunashir endemic carabids, *C. elisae kunashirensis* and *B. sanatum*, have been found, are formed at the site of explosion craters about 2,100–1,500 yBP (ABDURAKHMANOV *et al.* 2004). It is evident that such landscapes could have existed on the cone of Mendeleev Volcano earlier. The oldest volcanic layers not covered by marine sediments date back to about 39,000 yBP (LEBEDEV *et al.* 1980). We believe that the conditions of thermal (including fumarole) fields could have ensured the survival of some species under the colder conditions during the Pleistocene and Holocene, as in *Bembidion ruruy* Makarov et Sundukov, 2014 and several rove beetles (SHAVRIN & MAKAROV 2019). Therefore, we believe that *C. elisae kunashirensis* might have colonized the Kunashir Island much earlier, and the time of its isolation could probably be associated with the Last Glacial Maximum, ca. 20,000 yBP (CLARK *et al.* 2009).

Earlier DNA studies support our hypothesis. Based on the sequences of the 28S rDNA and COI genes (SOTA *et al.* 2011), *C. elisae* from various localities in Korea, Japan and Taiwan shows minimal divergence, especially in the COI sequences. At all localities studied, only one haplotype is widely distributed, the one that seems to have given rise to the remaining 17 haplotypes. Thereby most of those numerous haplotypes are separated from the basal one by no more than one to three mutational steps. Only the Taiwanese *C. e. reductelineata* is distinct from the basal haplotype by 18–26 mutational steps (SOTA *et al.* 2011: fig. 5A). The divergence time of this subspecies is ca. 0.6 Mya, this being comparable with the divergence time of ca. 0.9 Mya for the more strongly related *Cylindera bonina* (Nakane et Kurosawa, 1959) which is endemic to the Bonin Islands (SOTA *et al.* 2011: Fig. 4). According to these data, most of the insular and mainland subspecies of *C. elisae* (at least *C. e. koreanica*, *C. e. novitia*, *C. e. mikurana* and *C. e. formosana*) could be considered varieties. The presence of two subspecies of *C. elisae* on the Kunashir Island is not unique, because two subspecies of this species co-occur also in Taiwan. According to SOTA *et al.* (2011), *C. e. reductelineata* could have populated Taiwan much earlier than *C. e. formosana* did. Based on the results of DNA analyses performed by us and considering the results by SOTA *et al.* (2011), we can assume that *C. e. kunashirensis* could have colonized the Kunashir Island much earlier than the nominative subspecies. In our opinion, the evolution under the particular conditions of fumarole fields and the long-term isolation might have caused a significant genetic divergence of this subspecies.

Estimating the divergence time of *B. sanatum* is more difficult because the species, both morphologically and genetically, is very close to the European *B. stephensii*, due to possible convergence (NETOLITZKY 1943: 37). Such patterns/disjunctions (amphi-Palaeartic or Euro-Manchurian) are also found among plants (NAKAMURA 2008, DENK & GRIMM 2009 *etc.*), vertebrates and various insect orders, such as Lepidoptera (DUBATOLOV & KOSTERIN 2000), Odonatoptera (KOSTERIN 2002), Diptera (OOSTERBROEK *et al.* 2001), and Coleoptera (SEMENOV-TIAN-SHANSKY 1911). Usually, the time of the origin of such disjunctions is attributed to the Pliocene or Miocene (MIKKOLA 1987, NAKAMURA 2008). However, it is likely that the later, repeated periods of warming allowed repeated recolonisation of former distribution areas, and that an estimate of 110,000–100,000 yBP is more realistic (BELOVA 1985, DUBATOLOV & KOSTERIN 2000, KOSTERIN 2002). Thus, we can assume that the ancestors of *B. sanatum* could have entered this region no later than 100,000 yBP, and the isolation of the *B. sanatum* was associated with the Last Glacial Maximum under the conditioning influence of fumarola fields.

Although the isolation of the endemic forms of *C. elisae* and *B. sanatum* on the Mendeleev Volcano might have occurred at about the same time, the level of genetic divergence differs by an order of magnitude. The variance in the COI sequence of *C. elisae elisae* and *C. elisae kunashirensis* amounts to 206 mutation steps, while the same parameter for *B. sanatum* and *B. stephensii* is only 66.

We conclude that the degree of the divergence of ground beetles, both morphological and genetic, during the adaptation to the specific conditions of fumarole fields varies very considerably and does not depend on taxonomic similarity or the time of colonization of fumarolas. This forces us to be careful in generalizations such as “the level of morphological (genetic) differences is enough to distinguish a species or subspecies”.

Taking the ground beetles living in the specific and extreme conditions of fumarola fields as examples, we can see that the combination of flexible and conservative traits is one of the important reasons for the exceptionally high biological diversity of this family

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Appendix 1. Detailed characteristics of the studied fumarola fields.

Ruruy Volcano

Despite the high density and variety of volcanic edifices in the northern part of the Kunashir Island, two areas of thermal-solfatar activity: “Neskuchenskie springs” and “Dal’nie springs” are known only on the western seashore.

The “Neskuchenskie Springs” is stretched along the seacoast for ca. 1.2 km and covers an area of about 1.5 km². The fumarola fields a total area ca. 3000 m² (ZHARKOV 2014). The “First Upper” solfatar field is located at an altitude of 70 m a.s.l. and covers an area of about 1700 m². The solfatar activity is observed in its apical part, where the gas temperature reaches 100 °C. The “Second Upper” solfatar field with an area of about 800 m², is located slightly to the north. Its fumarola outcrops also have a temperature of 100.0–100.9 °C, and the waters of the streams flowing from there are subneutral (pH = 6.9–7.3). The “Third Upper” solfatar field is located at an altitude of 210 m a.s.l. Its sulphate calcium-sodium waters are acidic (pH = 2.2), with the temperatures of up to 91.7 °C. Besides, there are two “extinct” fumarola sites and numerous acidic hydrothermal and solitary fumarola outcrops.

The “Dal’nie Springs” site was discovered only in 2017 (SUNDUKOV & KOZLOVSKI 2017) and volcanologists have never studied it. The site with hydrothermal-solfataric activity was located in a bowl-shaped depression at an altitude of 390–560 m a.s.l. and covered an area of about 1 km². It includes two solfatar fields, “Dlinnoe” and “Bolshoye”. The “Bolshoye” field is 3500 m² located at 390–400 m a.s.l. The “Dlinnoe” field is 100 m to the southwest and has an area of about 1500 m². In both these fields, only a weak solfataric activity is presently observed. The gases escaping from the fumarolas have a temperature of 18.0–22.3 °C, the temperature of the streams flowing through the fields ranges from 20.4 °C to 22.5 °C, their water being weakly acidic (pH = 4.0–4.2).

Mendeleev Volcano

The outputs of the solfatar gases are concentrated on the Mendeleev Volcano in four fields: southeastern, eastern, northeastern, and northwestern. In the valleys of the rivers and streams originating from these fields, there are groups of thermal springs with varying temperatures and chemical composition (Tables 1 & 2).

The southeastern field is 400–575 m a.s.l. and has an area of about 75,000 m², with numerous outlets of small gas jets, as well as thermal and cold mineral springs in its upper part. Thermophilic algae grow in places where the thermal waters come out, and there is a strong odour of hydrogen sulfide. The water is acidic (pH = 2.5), siliceous, sulphate-chloride, with a complex cationic composition and a mineralization level of about 1 g/l (MARKHININ & STRATULA 1977).

The eastern field is stretched out in a narrow strip along the upper reaches of Lech-ny Stream at 650–450 m a.s.l. It includes a small thermal lake ($T = 60\text{--}85\text{ }^{\circ}\text{C}$, $\text{pH} = 3.3$) and numerous springs, mud griffins and funnels with the temperatures of $53\text{--}101\text{ }^{\circ}\text{C}$ and $\text{pH} = 2.7\text{--}3.6$. The thermal waters are sulphate calcium-magnesium with increased content of Al^{3+} , Fe^{2+} , H^{+} and a mineralization level of about 1 g/l. According to the composition of gases, they are carbonic: CO_2 – 43.6%, N_2 – 39.1%, CH_4 – 14.2%, with no H_2S detected (MARKHININ & STRATULA 1977).

The northeastern field is the most active area. In 1880, a weak phreatic eruption occurred there (MILNE 1896), and in 1901, 1946, 1977 and 1987 emissions of the steam-gas jets up to a height of 150–200 m and tangible earthquakes were observed. This fumarola field is at 250–350 m a.s.l. and an area ca. 2 km². There are three eroded funnels of phreatic explosions, which are the centres of discharging acid sulphate-chloride fluids (LEBEDEV *et al.* 1977). There are numerous fumarolas with the temperatures of up to $99.6\text{ }^{\circ}\text{C}$, and in the valley of Kislaya River, flowing from this field, there are dozens of springs with the temperatures of $90.0\text{--}98.5\text{ }^{\circ}\text{C}$ and $\text{pH} = 2.4\text{--}2.5$. The waters of these springs are acidic, carbonic (CO_2 – about 89%, H_2S – up to 4.7%, O_2 – 0.5%) sulphate sodium-calcium-magnesium hydrothermal fluids (MARKHININ & STRATULA 1977).

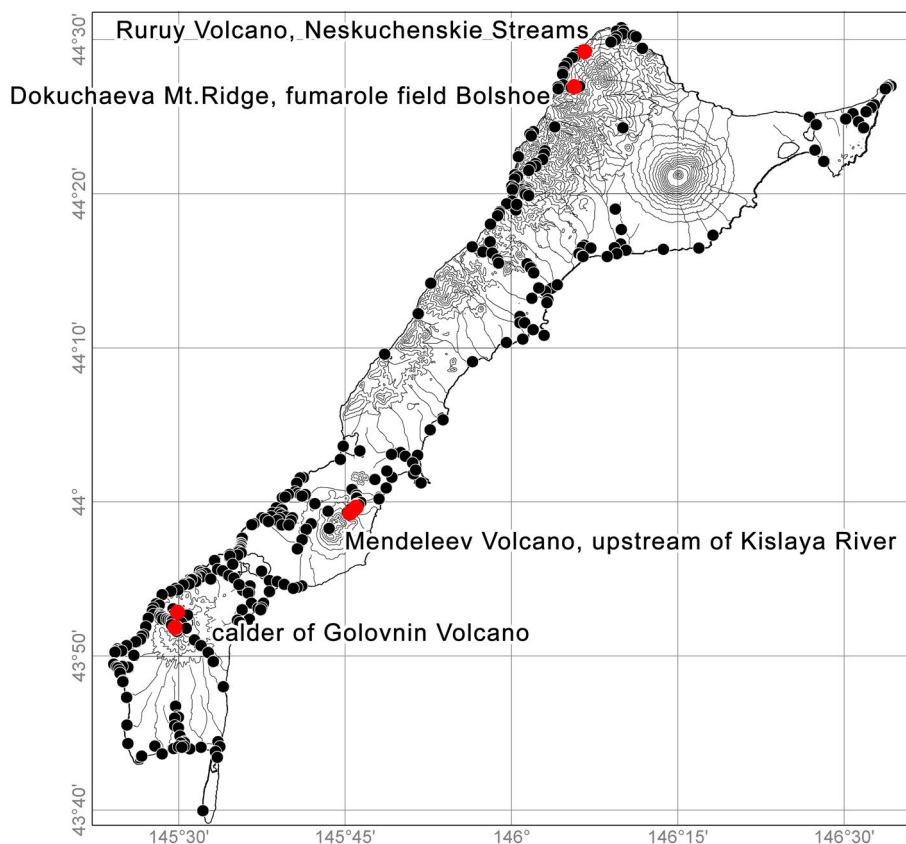


Fig. A1. Locations of the collection sites (black points) and the studied solfatar fields (red points) on the Kunashir Island

The northwest field is at a 400 m a.s.l. and is about 50,000 m² in area. Its solfataric activity is relatively high: in 1978 and 1984, the temperature increased to 111–113 °C, accompanied by the appearance of molten sulfur (ZHARKOV 2014). This field also supports a “boiling” spring with a temperature of > 90 °C. Its water is highly acidic (pH = 2.5–3.0), sulphate-chloridic, with a total mineralization level of up to 4.4 g/l. Carbon dioxide and hydrogen sulphide (CO₂ – 88.1%, H₂S – 9.8%, N₂ – 2.1%, the CH₄ content being negligible) prevail in the gas composition (MARKHININ & STRATULA 1977).

Golovnin Volcano

A large eruption that formed the modern caldera about 4.7 km in diameter, according to various estimates, occurred about 52,000–30,000 yBP (MELEKESTSEV *et al.* 1988, BULGAKOV 1994). At present, the caldera contains five terrestrial and one underwater fumarola fields and two lakes, with thermal waters. Its chemical composition is given in Tables 1 and 2.

The Central Eastern solfatar field is located at the foot of the southern slope of the Central Eastern dome. All gas outlets and thermal springs are situated along the shores or under the water of Lake Kipyashcheye. Both solfataras (T = 90–100 °C), as well as the boiling cauldrons of various sizes, consistencies and colors (T = 60–95 °C), are located there. Their waters range from subneutral hydrocarbonate-sulphate sodium-calcium (pH = 6.0–8.5) to acidic sodium sulphate (pH = 2.0–2.5) (ZHARKOV 2014).

Lake Kipyashcheye is a phreatic explosion funnel filled with water, with an area of 66,000 m² and a depth of 16 m (KOZLOV & ZHARKOV 2010). Its acidic (pH = 2.5), chloride-sulphate sodium waters are heated up to 90 °C in the places where gas-hydrothermal vents emerge. In the central part of the lake, the chemical composition of the water is predominantly sodium chloride, pH = 3.7, and the surface temperature is about 30 °C (MARKHININ & STRATULA 1977).

Lake Goryacheye occupies the northern part of the caldera with a 3.1 km² area, 62.3 m maximum depth, and a surface water temperature of 17–18 °C. The water is acidic (pH = 2.5–3.0) and contains sulphate-chloride sodium-calcium (ZOTOV *et al.* 1988). There are four fumarola fields at the lake shores.

The Central Western solfatar field is at the southern shore of the lake. Its formation seems to have been associated with a phreatic eruption on the northern slope of the Central West extrusive dome. The solfataras and thermal boilers are the hottest ones on the volcano – from 90 °C to 102.5 °C (ZHARKOV 2014). In terms of gas composition, they are similar to the solfataras of the Central Eastern field, but carbon dioxide and hydrogen sulphide are contained in equal proportions (48% each), and the condensate of the gases has a sulphate calcium chemical composition and pH = 2.8 (MARKHININ & STRATULA 1977). The lower part of this field shows a temperature of 98 °C and has highly acidic (pH = 2.0), sulphate-chloride calcium-sodium waters.

At the northern bank of Lake Goryacheye, three small solfatar fields are located: Cherepakhovoye, Nabokovskoye, and Bezymyannoye. The solfataras and hydrosulfataras of the Cherepakhovoye field are quite intense. The temperature of the solfataras reaches 98 °C, while the temperature of the springs is 80 °C; the solfataras are carbonic (CO₂ – 94%) with acidic spring (pH = 2.3), while sulphate calcium-sodium with medium mineralized, waters (MARKHININ & STRATULA 1977). The Nabokovskoye field has four low-rate extinct sources with a temperature of 38–52 °C and pH = 6.0 (ZHARKOV 2014). Within the Bezymyannoye field, the solfataras are concentrated to two areas: at and a few dozen meters off the bank of

Lake Goryacheye. This field is characterised by the development of mud pots with temperatures up to 89 °C and pH = 3.4. In the channel of the stream and the upland areas, there are



Figs A2–A7. Habitats of ground beetles in the solfatar fields of Kunashir Isl.: A2 = Ruruy Volcano, Neskuchenskie Streams (*C. elisae elisae*, *B. dolorosum*); A3 = Dokuchaeva Mt. Ridge, solfatar field “Bolshoye” (*C. sachalinensis*, *P. samurai*); A4 = Mendelev Volcano, upstream of Kislyi Stream (*C. sachalinensis*, *B. dolorosum*, *B. sanatum*); A5 = Mendelev Volcano, Northeastern solfatar field (*C. elisae kunashirensis*); A6 = caldera of Golovnin Volcano, solfatar field “Cherepakhovoye” (*B. dolorosum*); A7 = caldera of Golovnin Volcano, Central West solfatar field (*C. sachalinensis*)

Table 1. Summary data on the chemical composition of the waters of the thermal springs on Kunashir Island (from ZHARKOV 2014).

Volcanoes	T, °C	pH	Na ⁺	K ⁺	Ca ⁺	Mg ²⁺	Fe ²⁺	Fe ³⁺	Al ³⁺	Cl ⁻	SO ₄ ²⁻	HCO ₃ ⁻	SiO ₂
Ruruy Volcano	42.6–99.6	2.2–7.5	29.3–124.0	0.4–24.2	33.1–173.0	8.5–35.9	0.025–10.5	0.025–5.6	20.2–45.0	8.2–56.4	223.0–794.0	183.0–372.0	91.0–181.0
Mendeleev Volcano	55.6–96.7	1.9–3.3	6.0–588.0	0.9–70.0	1.0–165.0	5.8–77.2	0.05–85.6	0.2–27.9	6.8–46.8	6.0–1652.0	125.0–1071.0	0.0	28.5–252.0
Golovnin Volcano	60.0–95.0	2.0–8.5	17.3–164.0	2.46–16.3	34.1–72.0	8.6–24.2	0.05–13.5	2.68–36.6	3.6–45.0	43.0–517.0	202.0–2496.0	<5.0	36.5–90.5

Table 2. The composition of the gases freely released from the waters of the thermal springs on Kunashir Island (from ZHARKOV 2014).

Volcanoes	CO ₂ %	CO, %	O ₂ %	N ₂ %	CH ₄ %	C ₂ H ₆ %	C ₃ H ₈ %	C ₃ H ₄ %	C ₃ H ₈ %	C ₄ H ₁₀ %	S-gases, %
Ruruy Volcano	0.04–0.27	0.0	2.27–5.88	93.93–97.46	0.005–0.145	0.00002–0.00151	0.0–0.00017	0.0	0.0	0.0–0.00002	0.0
Mendeleev Volcano	16.88–66.75	0.0–0.00007	4.12–17.56	23.28–61.31	0.116–6.654	0.00085–0.09397	0.00007–0.00857	0.0	0.0	0.0–0.00009	0.0–4.15
Golovnin Volcano	33.46–37.60	0.00005–0.00007	4.49–10.28	30.51–36.46	0.071–0.098	0.00086–0.00215	0.00006–0.00030	0.0	0.0	0.0–0.00001	19.70–27.40

numerous outlets of gases with a temperature of 100–101 °C (ZHARKOV 2014).

Aggressive gases and high-temperature solutions continually affected the lithogenic base of all fumarola fields for an extended period. These processes have completely changed the composition of loose sediments and bedrocks, being accompanied by exogenous processes and the transformation of landforms (RAZJIGAEVA 2005). These resulted in denuded volcanic landscapes with destroyed or sparse vegetation (Figs A2–A7) and a buried soil cover (GANZEY 2004).

Pioneer plants very slowly colonize active fumarola fields. In this case, the high concentrations of toxic gases, rather than pH or soil temperature, is the main limiting factor (MANKO & SIDELNIKOV 1989).

Appendix 2. Studied material

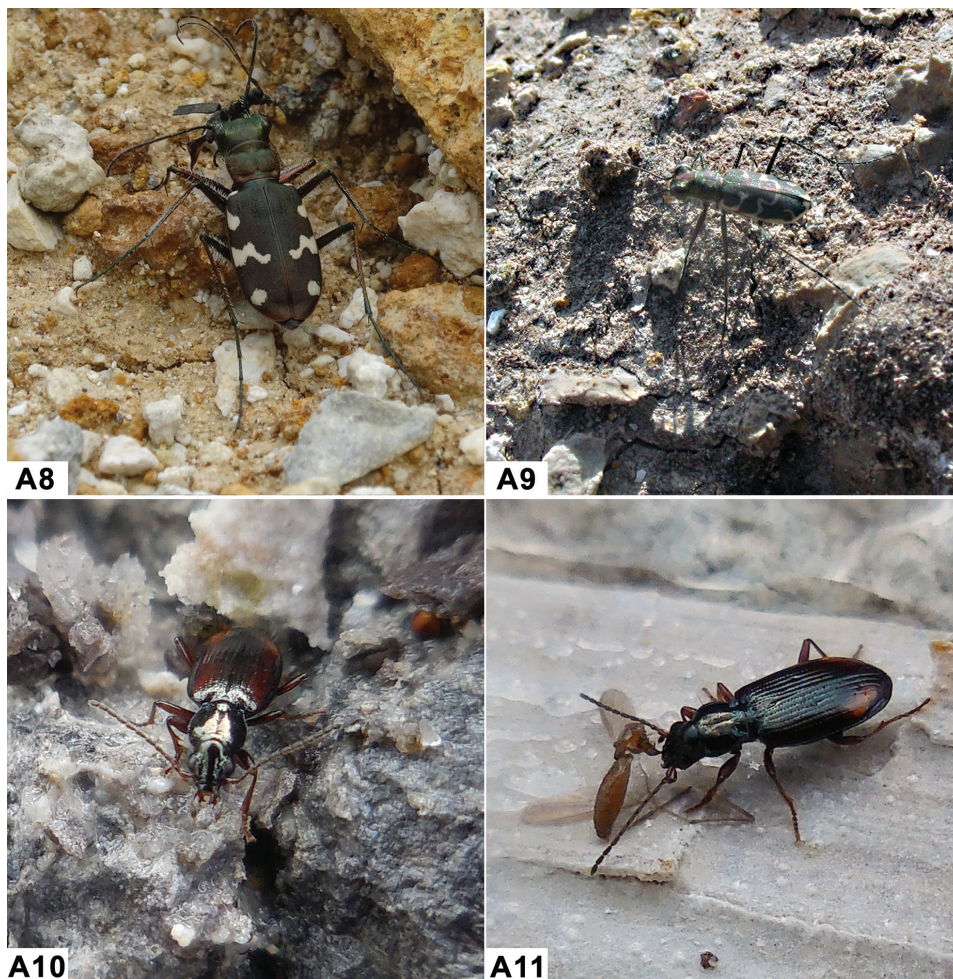
Cicindela (Cicindela) sachalinensis sachalinensis A. Morawitz, 1862:

Sachalin Isl.: Ins. Sachalin, 180-I TYPE; 1 ♀ [ZISP]; Dolinsky district, biological station “Sokol”, 1–30.vi.2005, leg. Yu. Melnikova; 2 ♂♂; trail to Chekhov Mountain, 46°58’52”N 142°49’14”E, 26.vi.2011, leg. K. Makarov; 1 ♂; south slope of Bolshevik mountain, 46°57’15”E 142°48’41”N, 31.vii.2017, leg. K. Makarov; 2 ♀♀; near Khomutovo, 46°52’39”N 142°43’56”E, 25.vi.2008, leg. K. Makarov; 1 ♀; same, 46°52’39”N 142°43’56”E, 27.viii.2008, leg. K. Makarov; 1 ♀; same, 46°52’39”N

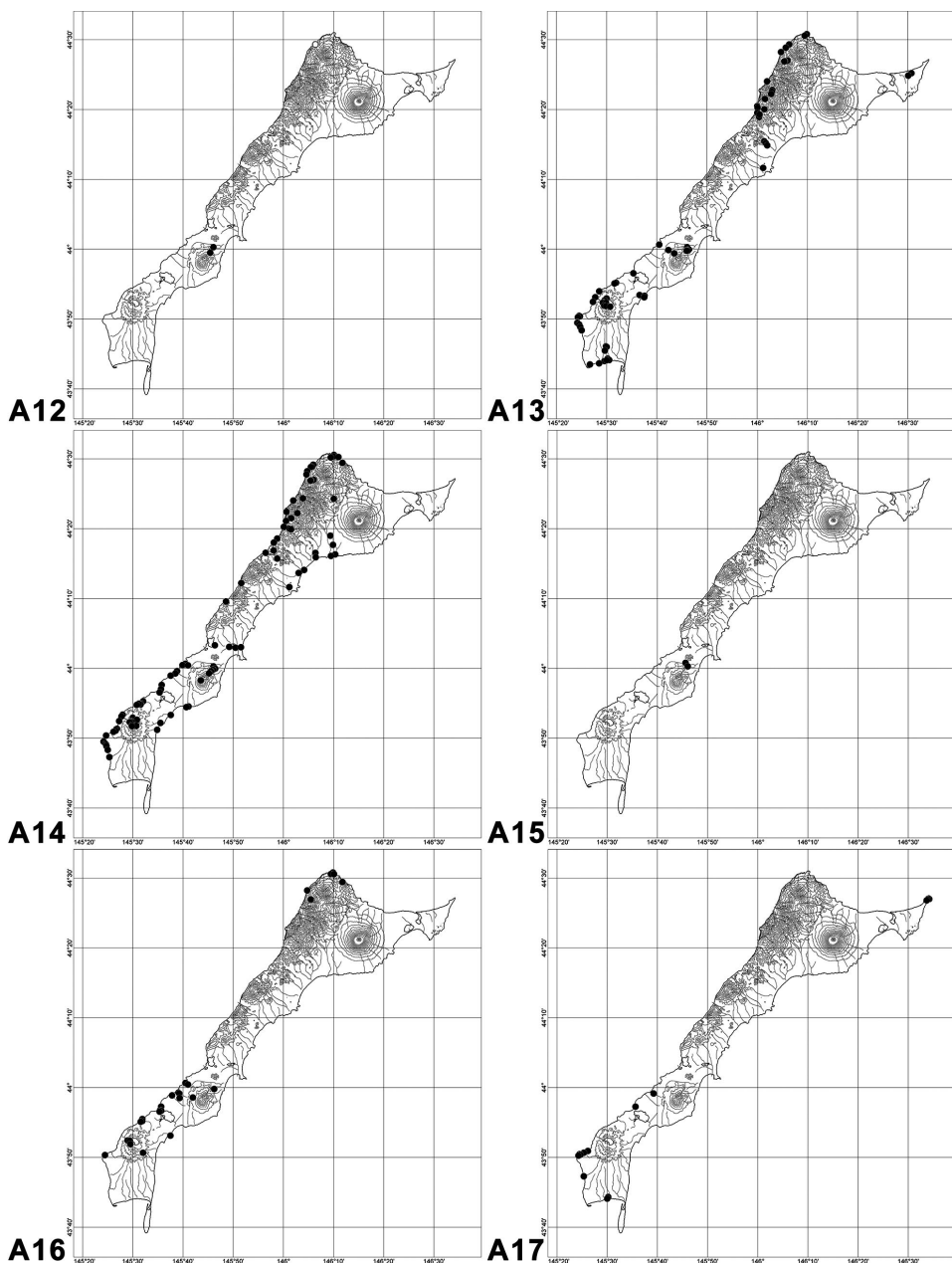
142°43'56"E, 17.vii.2011, leg. K. Makarov; 1 ♀ 1 ♂; 3 km southeast of Novikovo, 46°18'46"N 143°30'40"E, 10.vi.1990, leg. K. Makarov; 3 ♂♂; Aniva, 09.vii.1953; 2 ♂♂; valley of Uglovoy Stream, 5-6.vii.2003, leg. I. Melnik; 2 ♀♀; Korsakovskiy Kon., v.1902, leg. Pilsutsky; 1 ♀; near Yuzhno-Sachalinsk, 25.viii.1991, leg. I. Melnik; 1 ♀; Pravda vill., south of Kholmsk, 25.v.1973, leg. Kerzhner; 1 ♂.

Iturup Isl.: Pioneer, 19.ix.1981, leg. Kabakov; 1 ♀ 1 ♂.

Kunashir Isl.: Dokuchaeva Cape, 44°30'47E 146°09'54E, 30.vii.2013, leg. K. Makarov; 3 ♂♂; same, 6.viii.2013, leg. K. Makarov; 4 ♀♀; Dokuchaeva Ridge, hot spring south of Vodopadnoe Lake, 44°27'1"N 146°6'4"E, 6.viii.2017, leg. K. Makarov; 8 ♀♀; Dokuchaeva

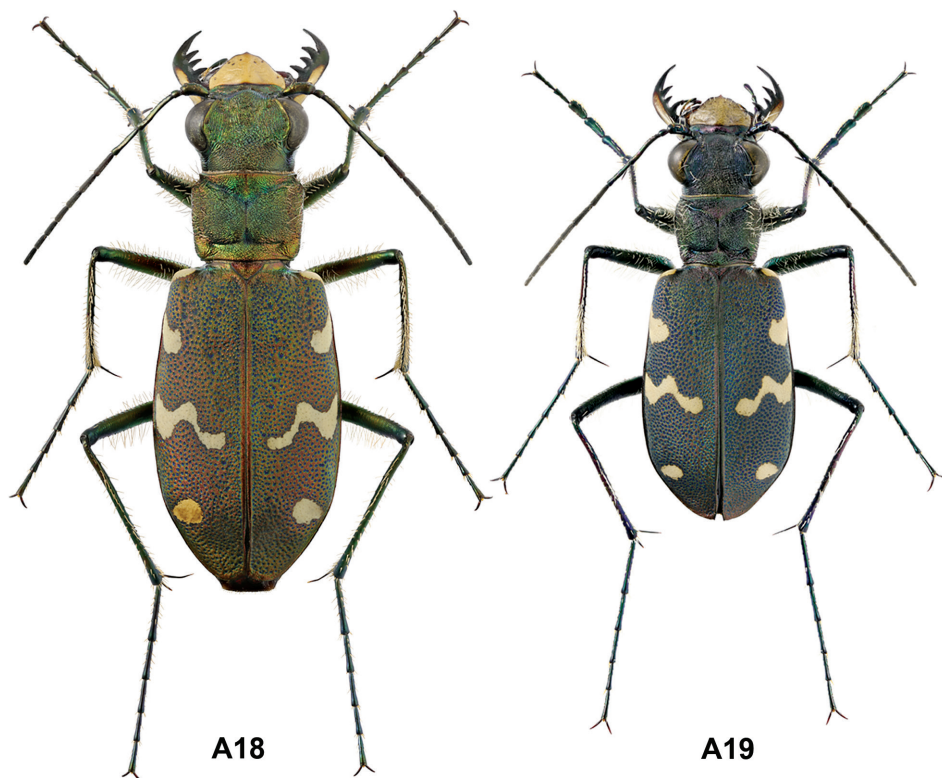


Figs A8–A11. Ground beetles on the fumarole fields of Kunashir Isl.: A8 = *C. sachalinensis* (Kunashir Isl., caldera of Golovnin Volcano, Kipyashcheye Lake); A9 = *C. elisae elisae* (Kunashir Isl., Ruruy Volcano, Neskuchenskie Streams); A10–A11 = *B. dolorosum* (Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field "Bolshoye")



Figs A12–A17. Distribution of ground beetles on Kunashir Isl.: A12 = *C. elisae* (black points = *C. e. kunashirensis*; white point = *C. e. elisae*); A13 = *C. sachalinensis*; A14 = *B. dolorosum*; A15 = *B. sanatum*; A16 = *P. samurai*; A17 = *P. fortipes*

va Ridge, fumarole field "Bolshoye", h~400, 44°26'57"N 146°5'28"E, 08.viii.2017, leg. K. Makarov; 2♀ 4 ♂♂; stream near Moristyi Island, 44°23'45"N 146°01'47"E, 17.viii.2013, leg. K. Makarov; 1 ♀; western spur of the Morozov Mount, 550 m, 44°22'34" 146°02'56", 19.viii.2013, leg. K. Makarov; 3 ♀; mouth of the Zolotaya River, 44°20'48"N 146°00'10"E, 15.vii.2013, leg. K. Makarov; 1 ♀; hills between Severyanka and Zolotaya rivers, 44°20'29"N 146°00'01"E, 1.vii.2008, leg. K. Makarov; 2 ♂♂; right slope of Severyanka River valley, 44°19'53"N 146°01'33"E 27.vii.2013 leg. K. Makarov; 1 ♂; road from Rudnyi to pass 44°19'32"N 146°00'03" E h~200; 44°18'20"N 146°00'46", h~431, 2.vii.2008, leg. K. Makarov, I. Melnik; 18 ♀♀; cordon Filatovsky, 44°11'38"N 146°01'11"E, 3.ix.2009, leg. A. Zaitzev; 2 ♂♂; 2 km north of Bolotny Stream, 44°02'32"N 145°51'6"E, 17.viii.2011, leg. K. Makarov; 2 ♀♀; near Yuzhno-Kurilsk, 28.viii.1981, leg. S. Saluk; 2 ♂♂; 7 km south-west from Yuzhno-Kurilsk, 44°00'53"N 145°45'44"E, 17.vi.1990, leg. K. Makarov; 1 ♀; Yuzhno-Kurilsk, 28.viii.1985, leg. B. Aristov; 1 ♀; south of Yuzhno-Kurilsk, 28.viii.1981, leg. Kabakov; 2 ♀♀; SW from Goryachyi Plyazh, 27.vii.1981, leg. Kabakov; 1 ♂; Mendeleevo vill., vi.1973, leg. Kerzhner; 1 ♂; Mendelev Volcano, 11.viii.1973, leg. Kerzhner; 1 ♂; Kislyi Stream, 44°00'36"N 145°46'04"E; 43°59'56"N 145°46'02"E, 24.viii.2009, leg. I. Melnik; 19 ♂♂; Mendelev Volcano, fumarole field, 43°59'40"N 145°43'06"E h~239; 43°59'08"N 145°43'53"E h~455, 7.viii.2008, leg. I. Melnik; 10 ♀♀; trail on Stolbovskiy hot springs, 44°00'38"C 145°40'41"E, 9.v.2011, leg. A. Matalin; 2 ♀♀; Stolbovskoy Stream, below hot springs,



Figs A18–A19. *Cicindela sachalinensis*, typical (A18) and melanistic (A19) forms

44°00'32"N 145°40'47"E, 26.viii.2017, leg. K. Makarov; 4 ♀♀; valley of the Valentiny Stream, lower sulfur springs, 44°00'36"N 145°46'04"E; 43°59'56"N 145°46'02"E, 24.ix.2009, leg. I. Melnik; 3 ♀♀; valley of the Valentiny Stream, thermal springs, 43°59'30"N 145°45'25"E, 18.vi.2011, leg. A. Matalin; 15 ♂♂; Daniloovo Natural Boundary, 43°57'17"N 145°35'34"E, 9.viii.2011, leg. K. Makarov; 1 ♀; same, 22.viii.2009, leg. K. Makarov; 1 ♀; western shore of Peshchanoe Lake, 43°56'33"N 145°35'20"E, 31.vii.2011, leg. K. Makarov; 3 ♀♀; northern slope of Alekhina Cape, 43°55'41"N 145°32'41"E, 4.vi.2011, leg. A. Matalin; 10 ♂♂; south of Alekhino Outpost, Sernaya bay, on thermal, 43°54'37"N 145°30'28"E, 1.vi.2011, leg. A. Matalin; 1 ♀; 4.5 km SW of Alekhino, 27.vii.2011, leg. K. Makarov; 1 ♂; mouth of the Ozernaya River, 43°53'07"N 145°27'44"E, 27.v.2011, leg. A. Matalin; 1 ♀; same, 27.vii.2011, leg. K. Makarov; 2 ♀♀; 1.5 km south-west from mouth of the Ozernaya River, 43°52'27"N 145°27'16"E, 26.vii.2011, leg. K. Makarov; 2 ♂♂; northern shore of Goryacheye Lake, hot springs, 43°52'39"N 145°30'48"E, 24.vii.2011, leg. K. Makarov; 5 ♀♀; eastern shore of Goryacheye Lake, 43°51'47"N 145°30'42"E, 24.vii.2008, leg. K. Makarov; 5 ♀♀; southern shore of Goryacheye Lake, fumarolas, 43°52'19"N 145°29'45"E, 13.vii.2008, leg. K. Makarov; 16 ♀♀; caldera of Golovnin Volcano, 43°51'57"N 145°29'26"E, 26.v.2011, leg. A. Matalin; 4 ♂♂; sea shore near cordon Ivanovskiy, 43°50'23"N 145°24'40"E, 11.vi.2011, leg. A. Matalin; 6 ♀♀; near Ivanovskiy cordon, 43°50'20"N 145°24'27"E, 15.vi.2011, leg. A. Matalin; 1 ♀; Ivanovskiy Cape, 43°50'20"N 145°24'27"E, 17.viii.2011, leg. K. Makarov; 1 ♀; 2 km north of Dubovoe, 43°46'44"N 145°29'44"E, 24.viii.2017, leg. K. Makarov; 4 ♀♀; near Paltusovo, 43°44'19"N 145°25'25"E, 16.vi.2011, leg. A. Matalin; 3 ♂♂; watershed of the Golovnin and Khlebnikova streams, 43°44'51"N 145°30'10"E, 20.viii.2017, leg. K. Makarov; 1 ♂.

Shikotan Isl.: Sikotan, A. Diakonov, 9.ix.1949; 1 ♂; valley of the Otrada River, 43°51'10"N 146°50'54"E, h~45, 22.vi.2011, leg. I. Melnik; 2 ♂♂; hills along the valley of the Vesely stream, 43°50'00"N 146°52'36"E, h~185; 43°49'36"N 146°54'02"E, h~11, 26.vi.2011, leg. I. Melnik; 11 ♀♀; northern outskirts of the village of Krabozavodskoe, 43°49'56"N 146°44'47"E, h~63, 28.vi.2011, leg. I. Melnik; 1 ♂; pass the Tserkovnaya bay; source of the Gorobets River, 43°45'15"N 146°41'54"E, 25.v.2012, leg. Yu. Sundukov; 2 ♂♂; middle course of a stream in Tserkovnaya Bay, 43°44'59"N 146°41'40"E, 25.v.2012, leg. Yu. Sundukov; 1 ♀; road Malaya Tserkovnaya Bay; Tserkovnaya Bay, 43°44'10"N 146°41'09"E, 31.v.2012, leg. Yu. Sundukov; 1 ♀, 1 ♂; road to the Tserkovnaya Bay, leg. A. Strelkov, 08.ix.1949; 2 ♀♀ 1 ♂; the Tserkovnaya Bay, Anufriev, 25.vii.1976; 2 ♀♀ 2 ♂♂; the Tserkovnaya Bay, Brusilov Mountain, 43°44'20"N 146°40'27"E, 8.vi.2012, leg. Yu. Sundukov; 2 ♂♂; slopes of the hills north of Anama (Krabovaya) Bay, A. Strelkov, 5.viii.1949; 1 ♀; upper reaches of the Gorobets River, 43°46'34"N 146°42'43"E, 28.ix.2012, leg. Yu. Sundukov; 1 ♂.

Cylindera (Eugrapha) elisae (Motschulsky, 1859)

C. elisae elisae:

China: North China, 6-7.viii.14, leg. Yu. Vasiliev; 1 ♂; Manchuria, Langashi, 20.vi-11.vii.905, leg. A. Yakovlev; 2 ♂♂; Pekin; 1 ♀ 1 ♂; Peking, Staud., 1889; 2 ♀♀; Peking, Herz; 2 ♂♂; Canton, Herz; 3 ♂♂; Kan-ssu, G. Potanin, 1886; 1 ♀; Gansu, Min Shan Mt. R., 70 km NW Wudu, h ~ 2100 m, 1-10.vi.1997, leg. A. Gorodinski; 1 ♀.

Russian Far East: Amur Area, near Blagoveshensk, left bank of Zeya River, 21.vii.1997, leg. A. A. Kuzmin; 1 ♂; Korsakovo na Amure, 100 km W Svobodnoe, 7.viii.1959, leg. Falkovich; 1 ♀ 2 ♂♂; fl. Sungari; 4 ♀♀ 7 ♂♂; Ussuri, Juni-Juli 1857, Rod.; 1 ♂; Sidemi, near Vladivostok, 86, Jankowskiy; 21 ♀♀ 27 ♂♂; Lazo Nat. Res., Proselochnyi (Ta-Chingouza), beach,

43°00'34"N 134°07'43"E, 17–22.viii.2007, leg. K. Makarov, A. Zaitsev; 1 ♀; Kedrovaya Pad' Nat. Res., 7.viii.1978, leg. Stepanov; 1 ♂.

Sachalin Isl.: Susuya River, near Lugovoe vill., 26.viii.2010, leg. A. Vertyankin; 2 ♀♀ 2 ♂♂.

Kunasir Isl.: Ruruy Volcano, thermal fields, ~ 1 km N of the Dalnie Streams, 44°29'19"N 146°06'24"E, 8.viii.2013, leg. K. Makarov, Yu. Sundukov; 23 ♀♀, 12 ♂♂.

C. elisae novitia:

Japan: Okinawa Met., Ishigaki Isl., Maehama, vi.1974, leg. S. Nakamura; 1 ♀ 1 ♂.

C. elisae mikurana:

Japan: Tokyo Met., Hacnijoima Isl., Sueyoshi-Noboru Pass., 18–22.vii.1985, leg. M. Nishimura; 1 ♂; Tokyo Met., Konzushima Isl., near Tsuzukido, 31.vii.1983, leg. M. Nishimura; 1 ♂; Tokyo, Bodemeyer – 2 ♀♀.

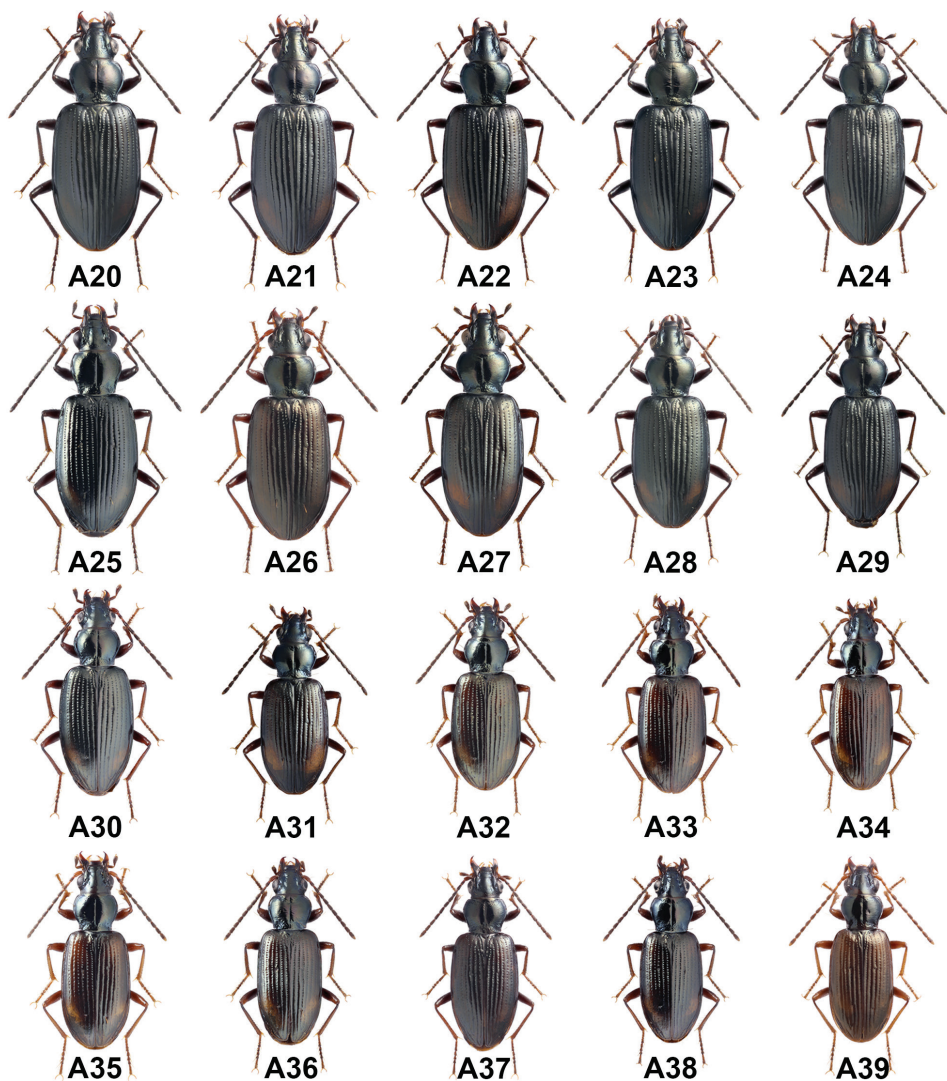
C. elisae kunashirensis:

Kunasir Isl.: Mendelev Volcano, source of Kislyi Stream, 43°59'46"N 145°45'54"E, 19.vi.1990, leg. I. Melnik, K. Makarov; 4 ♀♀, 2 ♂♂; Mendelev Volcano, Kislyi Stream, 2–3.ix.1992, leg. A. Sokolov; 2 ♀♀, 1 ♂; Mendelev Volcano, Kislyi Stream below hot springs, 44°00'36"N 145°46'04"E, 43°59'56"N 145°46'02"E, 24.ix.2009, leg. I. Melnik; 1 ♀; Mendelev Volcano, Kislyi Stream below hot springs, 44°00'36"N 145°46'04"E, 43°59'56"N 145°46'02"E, 18.vi.2011, leg. A. Matalin; 4 ♀♀, 8 ♂♂; Mendelev Volcano, source of Kislyi Stream below the solfatara field, 43°59'46"N 145°45'54"E, 15.vii.2017, leg. Yu. Sundukov, L. Sundukova; 7 ♀♀, 9 ♂♂.

Bembidion (Ocydromus) dolorosum (Motschulsky, 1860):

Urup Isl.: Ukromnaya Bay, seashore rocky debris, 20.viii.1996, leg. K. Eskov; 2 ♂♂.

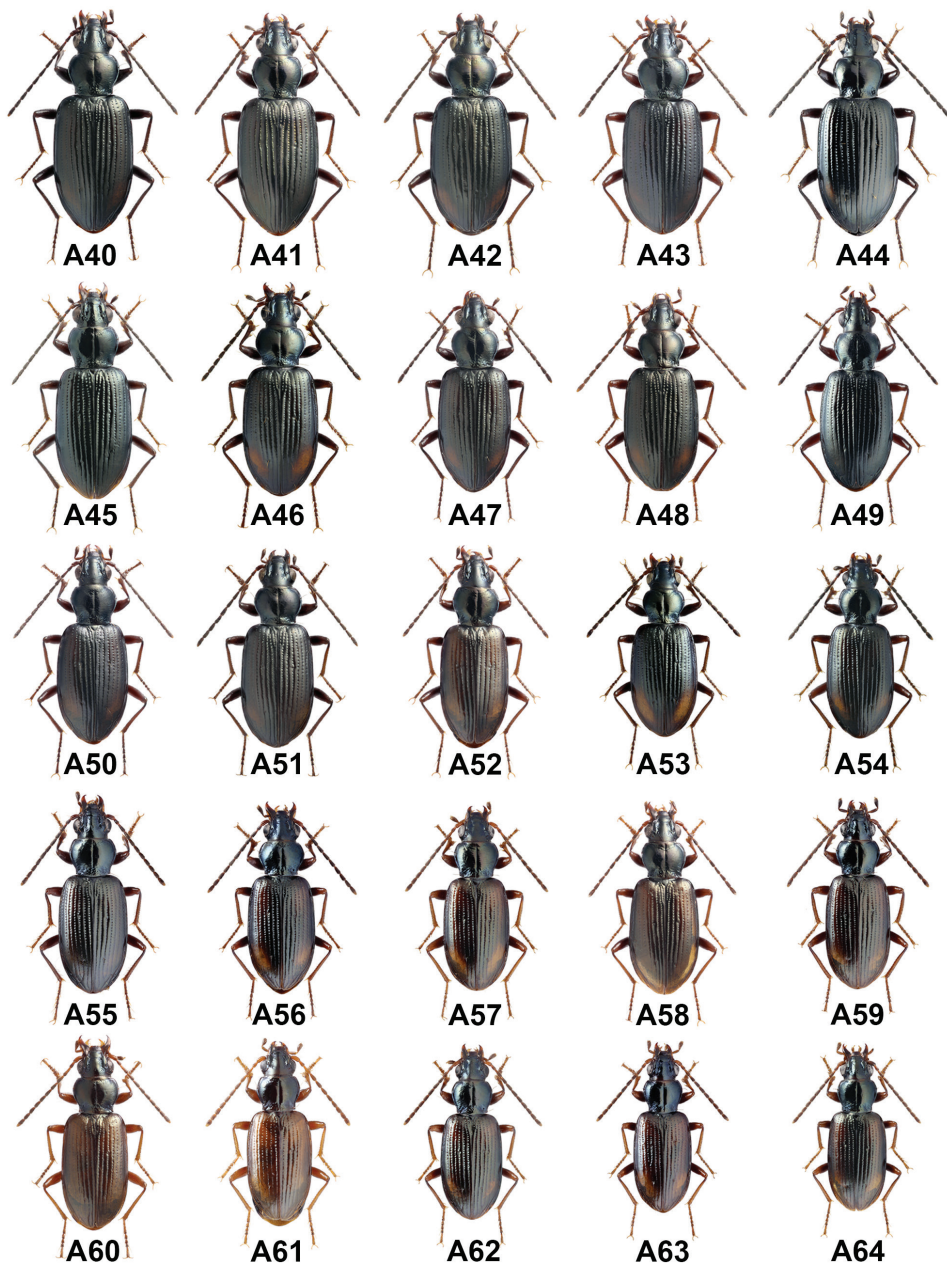
Kinashir Isl.: 2.5 km NW of Cape Nelyudimyi, 44°29'26"N 146°11'47"E, 2.viii.2013, leg. K. Makarov; 10 ♀♀ 5 ♂♂; same, 4.viii.2013, leg. K. Makarov; 2 ♀♀; mouth of the Dokuchaev River, 44°30'16"N 146°10'58"E, 30.vii.2013, leg. K. Makarov; 2 ♀♀ 1 ♂; Cape Belyy Utos, 44°28'14"N 146°04'45"E, 11.viii.2013, leg. Yu. Sundukov; 1 ♀ 1 ♂; Dokuchaeva Ridge, Dal'niye springs, acid lake, 500–530 m, 44°27'01"N 146°06'04"E, 23.vi.2017, leg. Yu. Sundukov; 6 ♀♀ 5 ♂♂; same, 6.viii.2017, leg. K. Makarov; 9 ♀♀ 2 ♂♂; same, 6.viii.2017, leg. Yu. Sundukov, L. Sundukova; 3 ♀♀ 7 ♂♂; Dokuchaeva Ridge, solfatara field "Bolshoye", h~400, 44°26'57"N 146°5'28"E, 4.viii.2017, leg. Yu. Sundukov; 9 ♀♀ 11 ♂♂; same, 8.viii.2017, leg. K. Makarov; 20 ♀♀ 6 ♂♂; Dokuchaeva Ridge, Dal'niye springs, solfatara field Dlinnoye, 400 m, 44°26'54"N 146°5'24"E, 21.vi.2017, leg. Yu. Sundukov; 3 ♀♀ 2 ♂♂; Dokuchaeva Ridge, E slope, Williams Lake, 535 m, 44°24'10"N 146°10'06"E, 23.ix.2017, leg. Yu. Sundukov; 6 ♀♀ 3 ♂♂; stream southern of the Moristyi Island, 44°23'45"N 146°01'47"E, 17.viii.2013, leg. K. Makarov; 1 ♀ 1 ♂; rocky brook south of Prasolov Cape, 44°21'15"N 146°0'19"E, 18.vi.2017, leg. Yu. Sundukov; 3 ♀♀ 3 ♂♂; lower course of the Zolotaya River, 44°21'06"N 146°00'31"E, 30.vi.2008, leg. I. Melnik; 1 ♂; same, 24.vii.2013, leg. K. Makarov; 4 ♀♀ 11 ♂♂; same, 12.viii.2017, leg. Yu. Sundukov, K. Makarov; 8 ♀♀ 9 ♂♂; mouth of the Zolotaya River, 44°20'48"N 146°00'10"E, 1.vii.2008, leg. I. Melnik; 1 ♀ 2 ♂♂; same, 18.vi.2017, leg. Yu. Sundukov; 2 ♀♀ 1 ♂; same, 11.viii.2017, leg. K. Makarov; 1 ♂; mouth of the Severyanka River, 44°19'58"N 146°01'15"E, 15.vi.2017, leg. Yu. Sundukov; 2 ♀♀ 3 ♂♂; lower course of the Severyanka River, 44°19'58"N 146°01'15"E, 17.vi.2014, leg. Yu. Sundukov; 3 ♀♀ 3 ♂♂; right slope of Severyanka River valley, 44°19'53"N 146°01'33"E, 23.vii.2013, leg. K. Makarov; 2 ♀♀ 1 ♂; mouth of Tyatina River, 44°16'06"N 146°09'30"E, 6.ix.2009, leg. A.



Figs A20–A39. Variability *B. dolorosum*, females: A20 = Kunashir Isl., mouth of the Ozer-naya River; A21 = Kunashir Isl., mouth of the Mednyi Stream; A22 = Sakhalin Isl., near Khomutovo; A23 = Sakhalin Isl., Rogatka River; A24 = Kunashir Isl., caldera of Golovnin Volcano, near cordon Ozernyi; A25 = Yuriy Isl., Shirokaya Bay; A26 = Kunashir Isl., Mendelev Volcano, mouth of Kislyi Stream; A27, A31 = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field "Bolshoye"; A28, A29 = Shikotan Isl., Tserkovnaya Bay; A30, A32–A34, A36, A37 = Kunashir Isl., caldera of Golovnin Volcano, solfatara field "Cherepakhovoye"; A35, A39 = Kunashir Isl., Mendelev Volcano, source of Kislyi Stream; A38 = Kunashir Isl., caldera of Golovnin Volcano, Kipyashcheye Lake (loc. typ. *B. kuznetsovi*)

Prosvirov; 3 ♀♀ 1 ♂; same, leg. I. Melnik; 3 ♀♀ 9 ♂♂; same, 3.vii.2011, leg. I. Melnik; 1 ♂; valley of the Tyatina River, 1–2 km upstream of mouth, 44°19'30"N 146°09'17"E, 7.vi.2016, leg. Yu. Sundukov; 1 ♀ 4 ♂♂; valley of the Tyatina River, 10–18 km upstream of mouth, 44°19'27"N 146°09'11"E, 22–24.ix.2017, leg. Yu. Sundukov; 2 ♀♀ 1 ♂; lower reaches of the Saratovskaya River, riverside, 44°15'46"N 146°06'13"E, 15.vi.2016, leg. Yu. Sundukov; 5 ♀♀ 5 ♂♂; Saratovskaya River, 44°15'55"N 146°06'27"E, 4.ix.2009, leg. A. Prosvirov; 1 ♀; lower reaches of the Saratovskaya River ca. 3 km upstream of mouth, 44°15'46"N 146°06'13"E, 16.vii.2014, leg. Yu. Sundukov, L. Sundukova; 4 ♀♀, 6 ♂♂; valley of the Filatov River, 44°11'38"N 146°01'11"E, 2.ix.2009, leg. I. Melnik; 1 ♂; same, 10.ix.2009, leg. I. Melnik; 1 ♀; Mikhaylovskoye Lake, 44°18'01"N 145°58'07"E, 14.viii.2017, leg. Yu. Sundukov, K. Makarov; 5 ♀♀ 2 ♂♂; mouth of the Medny Stream, 44°16'34"N 145°56'27"E, 16.viii.2017, leg. K. Makarov; 10 ♀♀ 6 ♂♂; lower course of the Medny Stream, 44°16'34"N 145°56'27"E, 16.viii.2017, leg. Yu. Sundukov; 3 ♀♀ 2 ♂♂; lower reaches of the Polynova stream, 44°15'43"N 145°58'46"E, 15.viii.2017, leg. K. Makarov; 9 ♀♀ 3 ♂♂; Mostovaya River, 44°13'14"N 146°03'03"E, 9.ix.2009, leg. A. Prosvirov; 1 ♀ 2 ♂♂; mouth of the Nazarova River, 44°12'13"N 145°51'36"E, 5.vii.2008, leg. K. Makarov; 2 ♂♂; Il'inskoye Lake, 44°9'35"N 145°48'34"E, 17.viii.2017, leg. K. Makarov; 6 ♀♀; same, 17.viii.2017, leg. Yu. Sundukov; 6 ♂♂; mouth of Petrova River, 44°4'13"N 145°52'07"E, 25.viii.2017, leg. K. Makarov; 5 ♀♀ 5 ♂♂; shore of Serebryanoye Lake, 44°03'05"N 145°49'12"E, 11.ix.2009, leg. A. Zaitzev; 2 ♂♂; same, 12.ix.2009, leg. I. Melnik; 2 ♀♀ 1 ♂; same, 12.ix.2009, leg. A. Prosvirov; 1 ♀ 1 ♂; Mendeleev Volcano, source of Lechebnyi hot spring, 43°59'52"N 145°46'03"E, 24.vi.2016, leg. Yu. Sundukov, L. Sundukova; 1 ♀ 1 ♂; same, 16.vii.2017, leg. Yu. Sundukov, L. Sundukova; 2 ♀♀ 1 ♂; Mendeleev Volcano, Kislyi Stream below hot springs, 44°00'36"N 145°46'04"E – 43°59'56"N 145°46'02"E, 18.vi.2011, leg. I. Melnik; 1 ♀; Mendeleev Volcano, source of Kislyi Stream below the solfatara field, 43°59'46"N 145°45'54"E, 15.vii.2017, leg. Yu. Sundukov, L. Sundukova; 5 ♀♀ 5 ♂♂; same, 3.viii.2016, leg. Yu. Sundukov, L. Sundukova; 7 ♀♀ 8 ♂♂; same, 22.ix.2016, leg. Yu. Sundukov; 9 ♀♀ 10 ♂♂; Mendeleev Volcano, mouth of Kislyi Stream, 44°00'48"N 145°46'37"E, 17.viii.2009, leg. A. Prosvirov; 2 ♀♀ 2 ♂♂; riverside of Lesnaya River, 44°00'48"N 145°46'37"E, 17.viii.2009, leg. A. Prosvirov; 1 ♂; mouth of Lesnaya River, 44°00'47"N 145°48'34"E, 17.viii.2009, leg. K. Makarov; 1 ♂; mouth of the Tyurina River, 43°54'33"N 145°41'06"E, 22.viii.2011, leg. K. Makarov; 9 ♀♀ 25 ♂♂; bay south of Puzanov Cape, 43°52'11"N 145°35'30"E, 21.viii.2011, leg. K. Makarov; 7 ♀♀ 1 ♂; cliffs 2–4 km south of Cape Puzanov, 43°51'44"N 145°35'06"E – 43°50'37"N 145°34'33"E, 21.viii.2011, leg. K. Makarov; 5 ♀♀ 6 ♂♂; Zmeinyy (Stolbovskoy) Stream, 44°00'31"N 145°40'49"E, 9.vi.2011, leg. A. Matalin; 5 ♀♀ 1 ♂; same, leg. I. Melnik; 1 ♀; same, 21.vii.2013, leg. Yu. Sundukov, L. Sundukova; 3 ♀♀ 3 ♂♂; same, 26.viii.2017, leg. K. Makarov; 10 ♀♀ 6 ♂♂; stream north of Cape Krugly, 44°00'33"N 145°40'13"E, 12.viii.2011, leg. K. Makarov; 10 ♀♀ 3 ♂♂; valley of the Valentiny Stream near Tretyakovo, 44°00'36"N 145°46'04"E, 17.viii.2008, leg. I. Melnik; 1 ♂; same, 21.viii.2013, leg. K. Makarov; 3 ♀♀; mouth of the Valentiny Stream, 43°59'33"N 145°38'50"E, 10.viii.2011, leg. K. Makarov; 1 ♀ 1 ♂; Tretyakov Stream near Tretyakovo outpost, 43°59'05"N 145°38'46"E, 22.viii.2013, leg. K. Makarov; 2 ♀♀ 2 ♂♂; same, 30.vi.2018, leg. Yu. Sundukov, L. Sundukova; 6 ♀♀ 5 ♂♂; mouth of Tretyakov Stream, 43°59'17"N 145°38'33"E, 30.v.2011, leg. A. Matalin; 1 ♀ 2 ♂♂; lower course of the Asin Stream, 43°58'57"N 145°37'31"E, 16.ix.2009, leg. I. Melnik; 1 ♂; same, 28.vii.2015, leg. Yu. Sundukov, L. Sundukova; 4 ♀♀ 3 ♂♂; Danilovo Natural Boundary, 43°57'17"N 145°35'34"E, 29.vii–6.viii.2008, leg. I. Melnik; 1 ♀; western shore of Peshchanoe Lake, 43°56'33"N 145°35'20"E, 6.viii.2008, leg. I. Melnik; 3 ♀♀ 2 ♂♂; mouth of the Alekhina River, 43°55'17"N 145°32'03"E, 19.viii.2009, leg. K. Makarov; 1 ♀ 4 ♂♂; same, 2.viii.2011, leg.

K. Makarov; 3 ♀♀ 3 ♂♂; same, 19.viii.2009, leg. K. Makarov; 1 ♀ 2 ♂♂; same, 19.ix.2009, leg. A. Prosvirov; 5 ♂♂; warm thermal hollow next to the hot stream "Imperial spring" south of Alekhino outpost, 43°54'58"N 145°31'16"E, 1–2.vii.2011, leg. A. Matalin; 20 ♀♀ 21 ♂♂; same, 10.ix.2014, leg. Yu. Sundukov; 6 ♀♀ 6 ♂♂; Odinkiy Stream, 43°54'41"N 145°30'56"E,



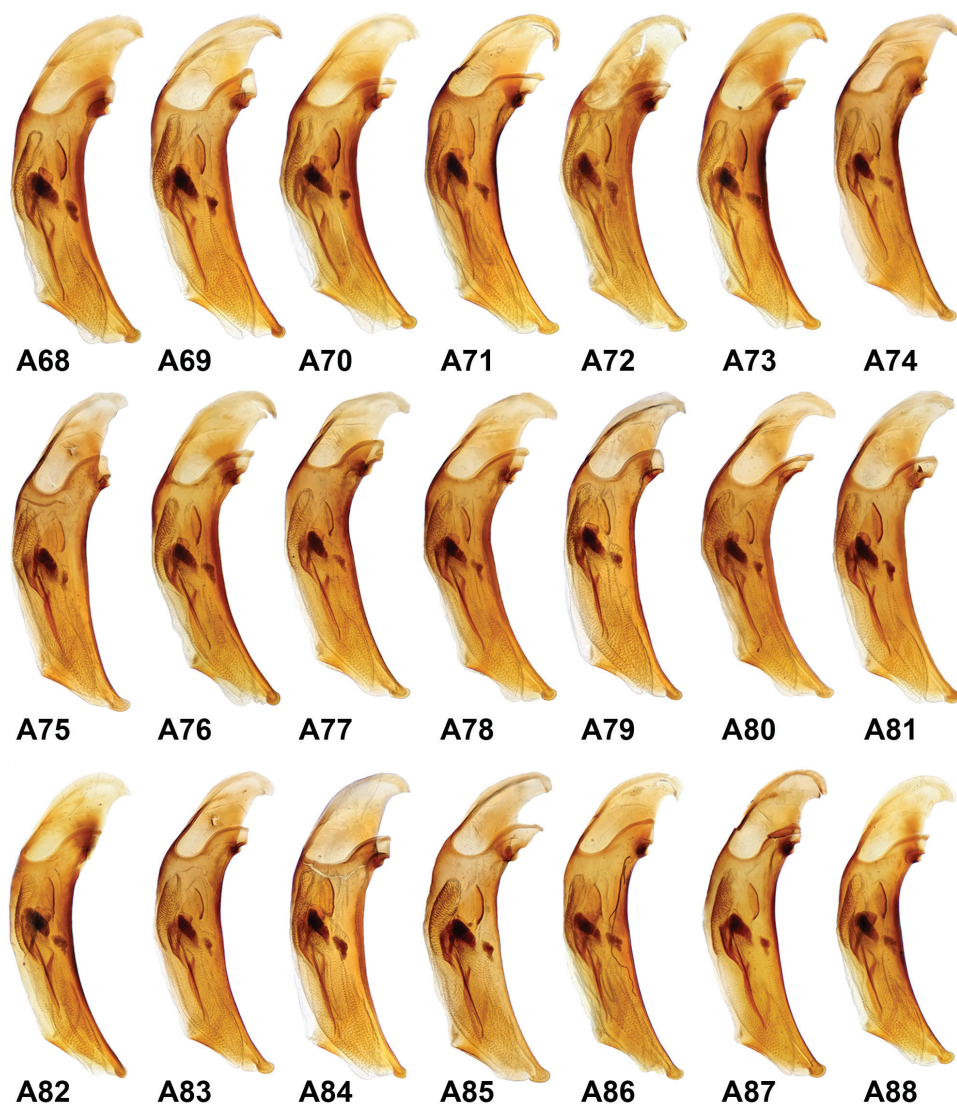
3.viii.2011, leg. K. Makarov; 1 ♂; mouth of Odinkoy Stream, 43°54'47"N 145°30'49"E, 3.viii.2011, leg. K. Makarov; 13 ♀♀ 21 ♂♂; south of Alekhino Outpost, Sernaya bay, on thermal, 43°54'37"N 145°30'28"E, 1.vi.2011, leg. A. Matalin; 3 ♀♀ 5 ♂♂; ca. 6 km south of Alekhino Outpost, 43°53'58"N 145°28'31"E, 20.viii.2009, leg. K. Makarov; 2 ♂♂; caldera of Golovnin Volcano, eastern shore of Goryacheye Lake, 43°51'47"N 145°30'42"E, 24.vi.2008, leg. I. Melnik; 1 ♀ 5 ♂; same, 26.v.2011, leg. I. Melnik; 5 ♀♀ 14 ♂♂; same, 13.viii.2009, leg. K. Makarov; 1 ♀ 16 ♂♂; caldera of Golovnin Volcano, northern shore of Goryacheye Lake,



Figs A65–A67. The tarsi of *B. dolorosum* inhabiting solfatara fields (A66, A67) and ordinary habitats (A65): A65 = Kunashir Isl., mouth of the Ozernaya River; A66 = Kunashir Isl., caldera of Golovnin Volcano, solfatara field “Cherepakhovoye”; A67 = Kunashir Isl., caldera of Golovnin Volcano, eastern shore of Goryacheye Lake

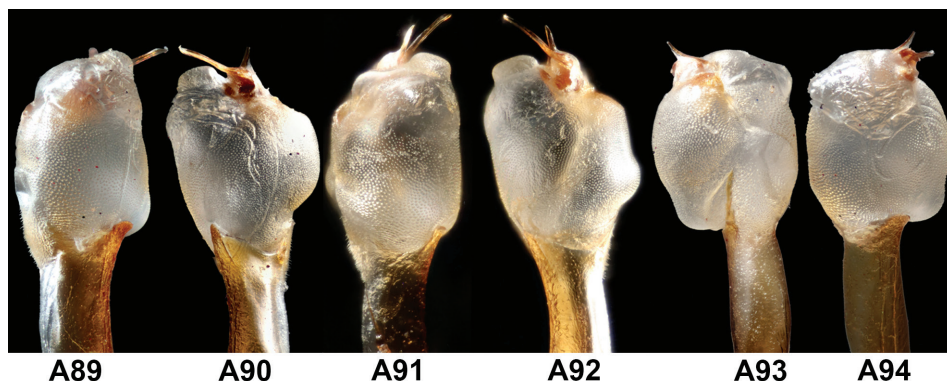


Figs A40–A64. Variability *B. dolorosum*, males: A40 = Sakhalin Isl., Rogatka River; A41 = Kunashir Isl., mouth of the Ozernaya River; A42, A51 = Sakhalin Isl., near Khomutovo; A43 = Kunashir Isl., Mendelev Volcano, mouth of Kislyi Stream; A44 = Kunashir Isl., Zmeinyy (Stolbovskoy) Stream; A45 = Kunashir Isl., mouth of the Mednyi Stream; A46, A53, A54 = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field “Bolshoye”; A47 = Sakhalin Isl., near Khomutovo; A48 = Kunashir Isl., caldera of Golovnin Volcano, near cordon Ozernyi; A49, A50, A52 = Yuriy Isl., Shirokaya Bay; A55, A56, A57, A59, A62–A64 = Kunashir Isl., caldera of Golovnin Volcano, solfatara field “Cherepakhovoye”; A58 = Kunashir Isl., caldera of Golovnin Volcano, Kipyashcheye Lake (loc. typ. *B. kuznetsovi*); A60, A61 = Kunashir Isl., Mendelev Volcano, source of Kislyi Stream



Figs A68–A88. Variability of the shape and size of the aedeagus *B. dolorosum*: A68, A73 = Shikotan Isl., Tserkovnaya Bay; A69 = Kunashir Isl., Zmeinyy (Stolbovskoy) Stream; A70 = Kunashir Isl., mouth of the Ozernaya River; A71 = Sakhalin Isl., Rogatka River; A72, A74, A75, A77, = Kunashir Isl., Mendelev Volcano, mouth of Kislyi Stream; A79, A83, A84 = Kunashir Isl., Mendelev Volcano, source of Kislyi Stream; A76 = Kunashir Isl., caldera of Golovnin Volcano, Kipyashcheye Lake (loc. typ. *B. kuznetsovi*); A78, A80, A81 = Yuriy Isl., Shirokaya Bay; A82, A86, A88 = Kunashir Isl., caldera of Golovnin Volcano, solfatara field “Cherepakhovoye”; A85 = Kunashir Isl., mouth of the Mednyi Stream; A87 = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatara field “Bolshoye”

solfatarata field "Bezmyannoye", 43°52'38"N 145°30'48"E, 6.vii.2016, leg. Yu. Sundukov, L. Sundukova; 12 ♀♀ 10 ♂♂; caldera of Golovnin Volcano, solfatarata field "Cherepakhovoye", 43°52'51"N 145°30'01"E, 28.vii.2011, leg. K. Makarov; 3 ♀♀ 8 ♂♂; same, 30.vi.2016, leg. Yu. Sundukov, L. Sundukova; 1 ♀, 4 ♂♂; caldera of Golovnin Volcano, solfatarata field of the Western Central dome, 43°52'19"N 145°29'45"E, 30.vi.2016, leg. Yu. Sundukov, L. Sundukova; 3 ♀♀ 4 ♂♂; caldera of Golovnin Volcano, shore of Kipyashcheye Lake, 43°51'47"N 145°30'04"E, 24.vi.2008, leg. K. Makarov; 1 ♀ 1 ♂; caldera of Golovnin Volcano, south-west shore of Kipyashcheye Lake, 43°51'52"N 145°29'54"E, 7-9.vi.2013, leg. Yu. Sundukov, L. Sundukova; 7 ♀♀ 5 ♂♂; same, 15.vii.2015, leg. Yu. Sundukov, L. Sundukova; 5 ♀♀ 6 ♂♂; same, 5.ix.2015, leg. Yu. Sundukov; 3 ♀♀ 4 ♂♂; caldera of Golovnin Volcano, southern shore of Goryacheye Lake western of the Central West Dome, 43°52'17"N 145°29'26"E, 7.vii.2017, leg. Yu. Sundukov, L. Sundukova; 2 ♀♀ 2 ♂♂; same, 7.ix.2015, leg. Yu. Sundukov; 1 ♀; same, 11.ix.2015, leg. Yu. Sundukov; 1 ♀ 1 ♂; caldera of Golovnin Volcano, near Goryacheye Lake, Central Western Solfatarata field, 43°52'19"N 145°29'45"E, 11.ix.2015, leg. Yu. Sundukov; 2 ♀♀ 2 ♂♂; caldera of Golovnin Volcano, southern shore of Goryacheye Lake near the Central Western Solfatar Field, 43°52'17"N 145°29'26"E, 16.vii.2015, leg. Yu. Sundukov, L. Sundukova; 5 ♀♀ 6 ♂♂; caldera of Golovnin Volcano, near cordon Ozernyi, 43°52'26"N 145°28'56"E, 11.viii.2009, leg. K. Makarov; 1 ♀ 1 ♂; same, 26.v.2011, leg. A. Matalin; 19 ♀♀ 21 ♂♂; mouth of the Ozernaya River, 43°53'07"N 145°27'44"E, 19.vii.2008, leg. K. Makarov; 3 ♀♀ 5 ♂♂; same, 11.viii.2009, leg. K. Makarov; 3 ♀♀ 4 ♂♂; same, 20.viii.2009, leg. K. Makarov; 1 ♀ 1 ♂; same, 21.vii.2011, leg. K. Makarov; 4 ♀♀ 4 ♂♂; 1.5 km south-west mouth of the Ozernaya River, 43°52'27"N 145°27'16"E, 26.vii.2011, leg. K. Makarov; 13 ♀♀ 9 ♂♂; same, 4.viii.2013, leg. Yu. Sundukov; 4 ♀♀ 6 ♂♂; ravine north of Blizky Island, 43°51'22"N 145°26'51"E, 16.viii.2011, leg. K. Makarov; 7 ♀♀ 4 ♂♂; mouth of the stream opposite Blizky Island, 43°51'17"N 145°26'41"E, 16.viii.2011, leg. K. Makarov; 1 ♀ 3 ♂♂; near cordon Ivanovskiy, 43°50'20"N 145°24'27"E, 8-15.viii.2008, leg. I. Melnik; 1 ♀ 1 ♂; stream mouth 2 km south of Ivanovskiy Cape, 43°48'53"N 145°24'44"E, 18.viii.2011, leg. K. Makarov; 1 ♀; waterfall 2.5 km south of Ivanovskiy Cape, 43°49'04"N 145°24'40"E, 18.viii.2011, leg. K. Makarov; 1 ♂; stream south of Vodopadny Stream, 43°49'31"N 145°24'09"E, 11.vi.2011, leg. A. Matalin; 7 ♀♀ 1 ♂; Vodopadny Stream south of Ivanovskiy Cape,



Figs A89–A94. Variability of the endophallus (shape of the sac and distal parts of the main sclerite and lamina 2) *B. dolorosum*: A89, A90 = Kunashir Isl., 2.5 km NW of Cape Nelyudimiy; A91, A92 = Kunashir Isl., caldera of Golovnin Volcano, solfatarata field "Cherepakhovoye"; A93, A94 = Kunashir Isl., Dokuchaeva Mt. Ridge, solfatarata field "Bolshoye"

43°49'20"N 145°24'56"E, 13.viii.2008, leg. I. Melnik; 3 ♀♀ 1 ♂; same, 15.v.2011, leg. A. Matalin; 1 ♀ 1 ♂; same, 27–28.v.2013, leg. Yu. Sundukov, L. Sundukova; 4 ♀♀ 3 ♂♂; stream 2 km north of Bolotny Stream, 43°49'13"N 145°24'32"E, 18.viii.2011, leg. K. Makarov; 1 ♂; near Dubovoe Vill., 43°45'58"N 145°29'38"E, 21.viii.2017, leg. K. Makarov; 1 ♀.

Sakhalin Isl.: Chekhov Mountain, 1.vii.1986, leg. E.Nesterov; 1 ♂; Aniva district, Lyutoga River, 24.vi.1988, leg. E.Nesterov; 3 ♀♀ 3 ♂♂; Naiba River 10 km upstream of Bykovo, 6–10.viii.1991, leg. V. Grachev; 1 ♂; the Khondasa river 15 km to the North-West of Honor, 11.viii.1992, leg. A. Napolov; 1 ♀ 1 ♂; near Khomutovo, 46°52'39"N 142°43'56"E, 23.vi.2008, leg. I. Melnik; 3 ♂♂; same, 25.vi.2008, leg. I. Melnik; 1 ♀ 1 ♂; same, 24.vi.2011, leg. A. Matalin; 1 ♂; same, 14–16.vii.2011, leg. K. Makarov; 3 ♀♀ 8 ♂♂; valley of the Rogatka River, 46°58'03"N 142°46'24"E, 18.vii.2011, leg. K. Makarov; 1 ♀ 4 ♂♂; Vakhrushevka River near the Troitskoe Vill., 46°55'48"N 142°39'10"E, 4.viii.2018, leg. Yu. Sundukov, L. Sundukova; 3 ♀♀ 6 ♂♂; Srednyaya River near the Troitskoe Vill., riverside, 46°53'15"N 142°38'25"E, 17.vi.2018, leg. Yu. Sundukov; 9 ♀♀ 11 ♂♂; village Solovyovka, riverside, 46°43'24"N 142°44'05"E, 7.viii.2018, leg. Yu. Sundukov, L. Sundukova; 6 ♀♀ 4 ♂♂; bank of the Susuya River near Lugovoe vill., 25.vi.2011, leg. A. Matalin; 2 ♂♂.

Tanfil'ev Isl.: Zorkaya Bay, 43°25'57"N 145°53'55"E, 7.vi.2017, leg. Yu. Sundukov; 1 ♀.

Shikotan Isl.: the Tserkovnaya Bay, stream bank, 43°44'59"N 146°41'40"E, 24.v.2012, leg. Yu. Sundukov; 1 ♀ 2 ♂♂; same, 24.v–10.vi.2012, leg. Yu. Sundukov; 1 ♀; same, 29.vi–10.vii.2012, leg. Yu. Sundukov; 2 ♀♀ 2 ♂♂; same, 1.vii.2012, leg. Yu. Sundukov; 1 ♀ 1 ♂; same, 43°44'39"N 146°41'26"E, on seaside rocks, 1.vii.2012, leg. Yu. Sundukov; 3 ♀♀ 4 ♂♂; same, 43°44'51"N 146°41'37"E, middle stream, 12.viii.2016, leg. Yu. Sundukov, L. Sundukova; 12 ♀♀ 9 ♂♂; Melkiy Stream, 43°50'36"N 146°47'01"E, 17.viii.2016, leg. Yu. Sundukov, L. Sundukova; 4 ♀♀ 1 ♂; the hill on the creek valley Vesolyy, 43°50'00"N 146°52'36"E, 26.vi.2011, leg. I. Melnik; 1 ♂; valley of the Otrada River, 43°51'10"N 146°50'54"E, 22.vi.2011, leg. I. Melnik; 6 ♀♀ 4 ♂♂.

Yuriy Isl.: Shirokaya Bay, 43°25'33"N 146°04'08"E, 26–31.viii.2016, leg. Yu. Sundukov, L. Sundukova; 19 ♀♀ 11 ♂♂; same, 2.ix.2016, leg. Yu. Sundukov; 7 ♀♀ 3 ♂♂.

Bembidion (Peryphanes) sanatum Bates, 1883

Honshu Isl.: Mt. Hikageyama Jyoushu Gunma Pref., 18.ix.1993, leg. S. Morita; 2♂♂ 2♀♀.

Kunashir Isl.: Kislyi Stream below hot springs, 44°00'36"N 145°46'04"E – 43°59'56"N 145°46'02"E, 18.vi.2011, leg. A. Matalin; 1♂ 1♀; Mendeleev Volcano source of Kislyi Stream below the solfatara field, 43°59'46"N 145°45'54"E, 3.viii.2016, leg. Yu. Sundukov, L. Sundukova; 1♂ 1♀; same label, 22.ix.2016, leg. Yu. Sundukov; 15♂♂ 17♀♀; same data, 15.vii.2017, leg. Yu. Sundukov, L. Sundukova; 6♂♂ 9♀♀.

Poecilus (Poecilus) samurai (Lutshnik, 1916)

Kunashir Isl.: 2.5 km NW of Cape Nelyudimyi, 44°29'26"N 146°11'47"E, 4.viii.2013, leg. Yu. Sundukov; 1 ♀; mouth of the Dokuchaev River, 44°30'16"N 146°10'58"E, 30.vii.2013, leg. K. Makarov; 1 ♂; Dokuchaeva Cape, Dokuchaev [abandoned], 44°30'34"N 146°09'29"E, 31.vii.2013, leg. L. Sundukova; 1 ♀; same label, 3.viii.2013, leg. K. Makarov, Yu. Sundukov; 3 ♀♀; same label, 6.viii.2013, leg. K. Makarov; 3 ♂♂; Dokuchaeva Cape, eastern coast, 44°30'21"N 146°10'01"E, 1.viii.2013, leg. L. Sundukova; 1 ♂; downstream of

the Dalny Stream, 44°28'52"N 146°05'42"E, 9.viii.2013, leg. K. Makarov; 2 ♀♀ 2 ♂♂; Belyy Utos Cape, 44°28'14"N 146°04'45"E, 11.viii.2013, leg. Yu. Sundukov, K. Makarov; 2 ♀♀ 2 ♂♂; stream south of Cape Bely Utos, 44°27'46"N 146°04'37"E, 11.viii.2013, leg. K. Makarov; 1 ♀; Dokuchaeva Ridge, fumarole field "Bolshoye", h~400, 44°26'57"N 146°5'28"E, 8.viii.2017, leg. K. Makarov; 13 ♀♀ 29 ♂♂; middle course of the Zolotaya river, 44°21'44"N 146°01'42"E, 15.viii.2013, leg. K. Makarov; 6 ♀♀ 2 ♂♂; 10 km of the highway Yuzhno-Kurilsk; Golovnnino, 16.vi.1990, leg. K. Makarov; 1 ♂; 18th km of the highway Yuzhno-Kurilsk – Golovnnino, 44°00'39"N 145°42'04"E, 12.vii.2018, leg. Yu. Sundukov, L. Sundukova; 2 ♂♂; lower course of Zmeinyy Stream (Stolbovskoy), 44°00'31"N 145°40'49"E, 3.vii.2013, leg. Yu. Sundukov, L. Sundukova; 1 ♀ 1 ♂; same, 21.vii.2013, leg. Yu. Sundukov, L. Sundukova; 1 ♀ 1 ♂; Mendelev Volcano, GTS [geothermal station] "Tumany", 43°59'48"N 145°46'13"E, 8.vi.2017, leg. Yu. Sundukov; 1 ♂; middle course Tretyakov River, 43°58'30"N 145°39'19"E, 13.viii.2011, leg. K. Makarov; 1 ♀; valley of the Asin Stream south of Tretyakovo, 43°58'52"N 145°37'45"E, 2.viii.2009, leg. K. Makarov; 1 ♀ 1 ♂; near mouth of Andreeva River, 43°53'15"N 145°37'33"E, 22.v.2011, leg. A. Matalin; 1 ♂; Daniloovo Natural Boundary, 43°57'17"N 145°35'34"E, 8–9.viii.2011, leg. K. Makarov; 3 ♀♀; western shore of Peshchanoe Lake, sedge meadow on the slope of the lake, 43°56'33"N 145°35'20"E, 3–5.vii.2015, leg. Yu. Sundukov; 2 ♂♂; mouth of the stream between Cape Znamenka and Cape Alekhina, 43°56'00"N 145°33'12"E, 4.viii.2009, leg. K. Makarov; 1 ♀; northern slope of Alekhina Cape, 43°55'38"N 145°32'34"E, 18.viii.2009, leg. K. Makarov; 1 ♀ 2 ♂♂; caldera of Golovnnin Volcano, near cordon Ozernyi, 43°52'26"N 145°28'58"E, 13–18.vii.2008, leg. K. Makarov; 9 ♀♀ 1 ♂; same label, 2.ix.2015, leg. Yu. Sundukov; 1 ♂; same, 9.ix.2015, leg. Yu. Sundukov; 2 ♂♂; same, 8.vii.2016, leg. Yu. Sundukov, L. Sundukova; 1 ♀; caldera of Golovnnin Volcano, forest road of the Ozerny cordon, 43°51'54"N 145°29'31"E, 14.vii.2015, leg. Yu. Sundukov, L. Sundukova; 2 ♀♀; caldera of Golovnnin Volcano, meadow south of West Central Dome, 43°51'54"N 145°29'53"E, 15.vii.2015, leg. Yu. Sundukov, L. Sundukova; 2 ♂♂; trail from the Golovnnin volcano caldera to 43 km of the route (eastern slope of Golovnnin volcano), 43°49'44"N 145°33'08"E – 43°52'19"N 145°29'43"E, 30.vi.2016, leg. Yu. Sundukov, L. Sundukova; 1 ♂; Ivanovskiy Cape, 43°50'20"N 145°24'27"E, 17.viii.2011, leg. K. Makarov; 1 ♀.

Sakhalin Isl.: env. Yuzhno-Sakhalinsk, 46°57'44"N 142°45'53"E, 27.viii.2008, leg. I. Melnik; 1 ♂; env. Yuzhno-Sakhalinsk. Bolshevik Mountain, 46°57'43"N 142°46'04"E, 15.vii.2011, leg. K. Makarov; 1 ♀; env. Yuzhno-Sakhalinsk, left source of the Elanka River, 46°56'36"N 142°48'19"E, 31.vii.2017, leg. K. Makarov; 1 ♂; near Khomutovo, 46°52'29"N 142°43'55"E, 27.vii.2008, leg. K. Makarov; 4 ♂♂; same label, 1.vii.2009, leg. I. Melnik; 1 ♀; Naiba River 10 km above Bykovo, 6.viii.1991, leg. V. Grachev; 1 ♂; same label, 6–10.viii.1991, leg. V. Zherikhin; 1 ♀; same, 11–17.viii.1991, leg. V. Grachev; 1 ♀.

Appendix 3. GenBank/BOLD accession numbers of COI sequences for each taxon *Bembidion* subgenus *Ocydromus* Clairville, 1806 and outgroup (subgenus *Odontium* LeConte, 1848).

- Bembidion (Ocydromus) decorum subconvexum* K. Daniel et J. Daniel, 1902 – JN171004
- Bembidion (Ocydromus) decorum decorum* (Panzer, 1799) – GU347079, GU347079, GU347080, GU347081, GU347082, GU347083, GU347084, GU347085, GU347086, GU347087, GU347088, HQ953381, HQ954518, HQ954566, KM442982, KM443094, KM444732, KM445300, KM447519, KU876576, KU876611, KU876614, KU876628, KU876759, KU906522, KU910828, KU917526, KU918240, MF170682, MF170683, MF170684, MF170685
- Bembidion (Ocydromus) dolorosum* (Motschulsky, 1860) from solfatar fields – MW240493, MW240494, MW240495, MW240496
- Bembidion (Ocydromus) dolorosum* (Motschulsky, 1860) from other habitats – MW240497, MW240498, MW240499, MW240500, MW240501, MW240502
- Bembidion (Ocydromus) grapii* Gyllenhal, 1827 – BETN4356-19, INRMA1455-14, JF888233, JN171043, KJ964478, KR490216, KR490777, KT959682, KT959846, KT959881, KU874327, KU874328, KU874329, MG056889
- Bembidion (Ocydromus) lugubre* LeConte, 1857 – BBCCA469-12, HM433259, HM433264, JN171062
- Bembidion (Ocydromus) modestum* (Fabricius, 1801) – HQ954512, JF889194, JF889195, JF889196, JF889197, JF889198, JN171071, KM439802, KM442245, KM443902, KM444358, KM447325, KM449092, KM449261, KU876577, KU876677, KU876712
- Bembidion (Ocydromus) sarpedon* Casey, 1918 – JN171106, KU233815, KU233818, KU233823, KU233827
- Bembidion (Ocydromus) saxatile* Gyllenhal, 1827 – KJ962084, KJ962534, KJ962627, KJ962713, KJ962861, KJ962948, KJ966772, KM444848, KU906432, KU907499, KU907637, KU910139, KU914526, KU915056, KU916970
- Bembidion (Ocydromus) scopulinum* (Kirby, 1837) – HQ551623, JN171110, JX259800, KU874366, KU874367
- Bembidion (Ocydromus) transversale* Dejean, 1831 – KJ203568, KU233802, KU233814
- Bembidion (Ocydromus) yukonum* Fall, 1926 – KU874373, KU874374, NEONU1963-13
- Bembidion (Odontium) aenulum* Hayward, 1901 – DNA1622
- Bembidion (Odontium) paraenulum* Maddison, 2009 – DNA1620
- Bembidion (Odontium) persimile* A. Morawitz, 1862 – DNA1288
- Bembidion (Odontium) striatum* (Fabricius, 1792) – BFB_Col_FK_9026

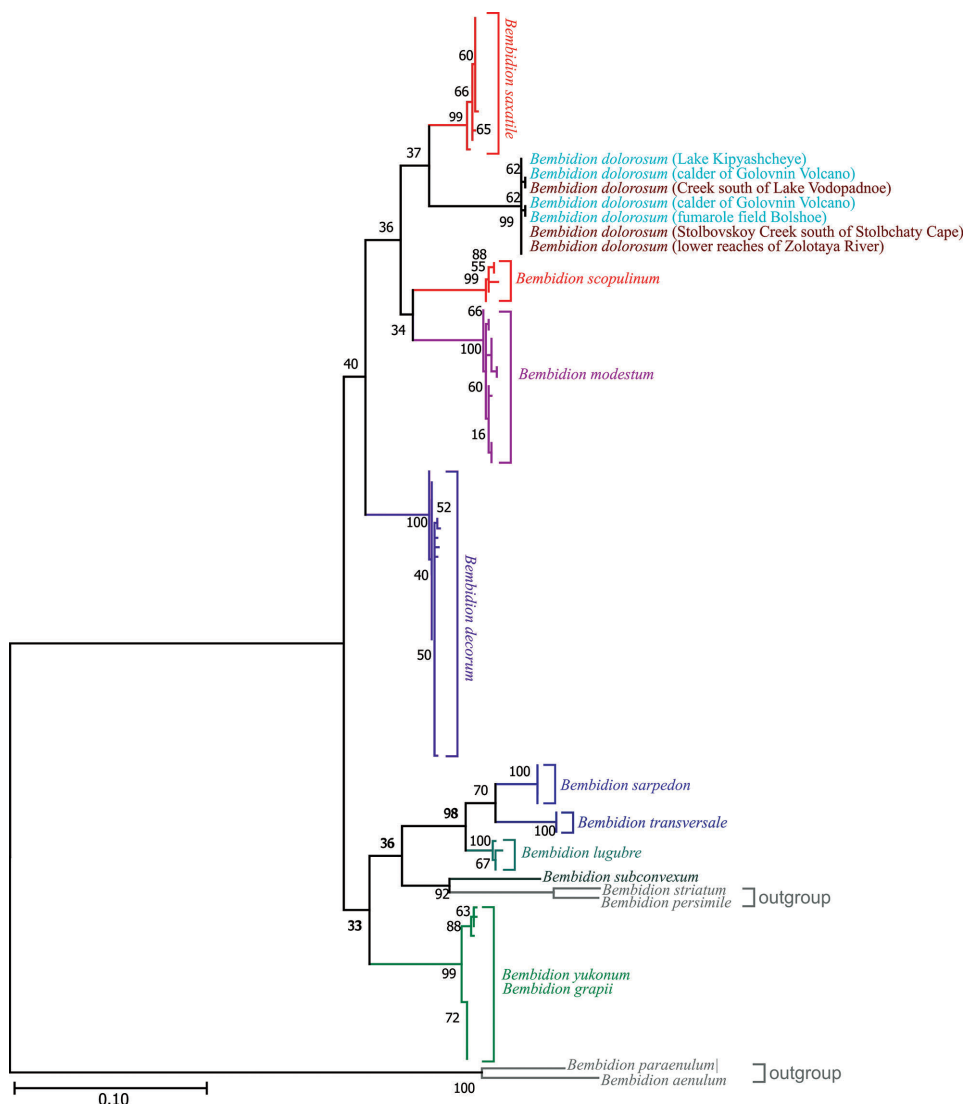
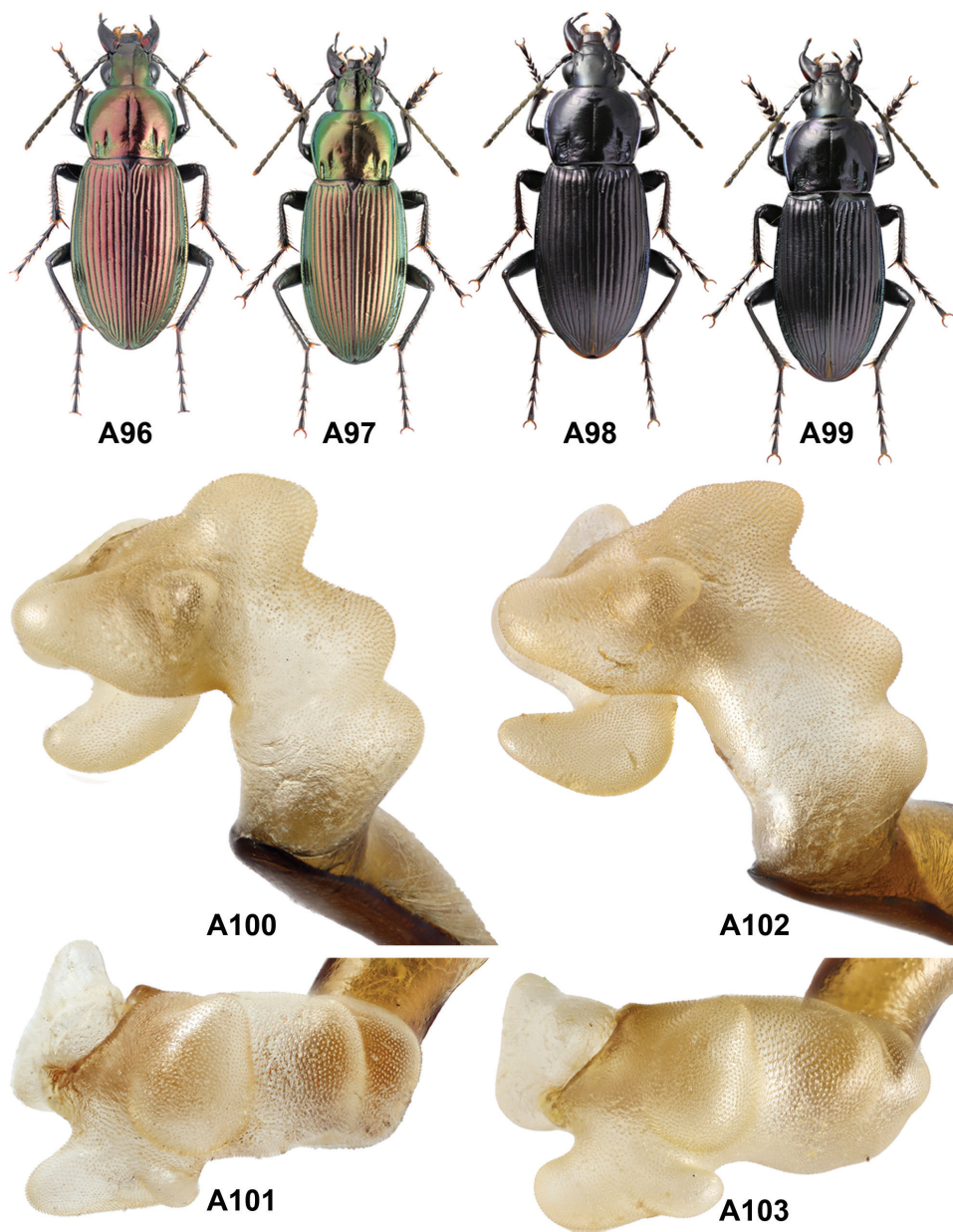


Fig. A95. Position of *B. dolorosum* within *Ocydromus* subgenus. The phylogenetic tree of COI was inferred by the maximum likelihood method (the tree with the highest log likelihood -4576.41 is shown) using 1000 replicates (numbers next to the branching points indicate the relative bootstrap-support). *Bembidion* species are indicated by the color code.

GenBank accession numbers for each isolate indicates in Appendix 3



Figs A96–A103. Variation of *Poecilus samurai* on Kunashir Island: A96, A98 = females, habitus; A97, A99 = male, habitus; A100–A103 = endophallus, lateral (A100, A102) and dorsal (A101, A103); A96–A97, A100–A101 = specimens from common habitats; A98–A99, A102–A103 = specimens, living on solfatara field “Bolshoye”, Dokuchaeva Mt. Ridge

Appendix 4. A list of ground beetles found in the solfatara fields of Kunashir Island

- *Cicindela (Cicindela) sachalinensis* A. Morawitz, 1862
**Cylindera (Eugrapha) elisae* (Motschulsky, 1859)
Nebria (Reductonebria) ochotica R.F. Sahlberg, 1844
Carabus (Carabus) arvensis Herbst, 1784
C. (Leptocarabus) arboreus Lewis, 1882
C. (Megodontus) kolbei aino Rost, 1908
Elaphrus (Elaphrus) riparius (Linnaeus, 1758)
Clivina (Clivina) fossor sachalinica Nakane, 1952
Bembidion (Asioperyphus) bandotaro Morita, 1991
B. (Bembidion) paediscum Bates, 1883
**B. (Ocydromus) dolorosum* (Motschulsky, 1860)
**B. (Peryphanes) sanatum* Bates, 1883
B. (Peryphus) poppii pohlai Kirschenhofer, 1984
B. (Plataphus) tetraporum Bates, 1883
**Poecilus (Poecilus) samurai* (Lutshnik, 1916)
Pterostichus (Bothriopterus) adstrictus Eschscholtz, 1823
Pt. (B.) subovatus (Motschulsky, 1861)
Pt. (Euferonia) thunbergi A. Morawitz, 1862
Pt. (Phonias) diligens (Sturm, 1824)
Pt. (Pseudomaseus) rhaeticus Heer, 1837
Agonum (Europhilus) subtruncatum (Motschulsky, 1860)
Eucolpodes japonicum (Motschulsky, 1861)
Glaucagonum sylphis (Bates, 1873)
Synuchus (Synuchus) arcuaticollis (Motschulsky, 1861)
S. (S.) melantho (Bates, 1883)
Stenolophus (Stenolophus) propinquus A. Morawitz, 1862
Demetrias (Demetrias) amurensis Motschulsky, 1861
Dromius (Klepterus) prolixus Bates, 1883
Lebidia octoguttata A. Morawitz, 1862

*marked species that constantly live here.

Appendix 5. Overall MANOVA results showing the dependence of body length and relative width of the pronotum on temperature and pH of water bodies at the banks inhabited by *B. dolorosum*.

Tests on independent variables						
	Wilks lambda	F	df1	df2	p	
T °C	0.9759	3.67	2	297	0.02665	
pH	0.5765	109.1	2	297	3.007E–36	
Tests on dependent variables						
	R ²	F	df1	df2	p	
EW/PW	0.3181	69.51	2	298	1.672E–25	
L_abs	0.5656	194	2	298	1.104E–54	
Regression coefficients and statistics						
		Coeff.	Std.err.	t	p	R ²
EW/PW	Constant	1.4835	0.014313	103.64	8.4635E–236	
	T °C	–0.00038661	0.00024508	–1.5775	0.11574	0.15846
	pH	0.016147	0.0019331	8.353	2.5487E–15	0.31242
L_abs	Constant	4.4875	0.087028	51.564	1.5588E–150	
	T °C	–0.0038028	0.0014901	–2.552	0.011211	0.27933
	pH	0.16472	0.011754	14.014	1.2665E–34	0.55612

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