Zootaxa 5493 (4): 345–370
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5493.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:93ED2E82-3AFA-4410-8155-F2753F52C89D

A revision of the subgenus *Limnaeoperyphus* Nakane, 1963 (Coleoptera: Carabidae, *Bembidion*), with the description of a new species

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Abstract

The subgenus *Limnaeoperyphus* Nakane, 1963, genus *Bembidion* Latreille, 1802, has been revised. It presently includes two species: *B. quadriimpressum* (Motschulsky, 1860) and *B. petromarinum* **sp. nov.**, both inhabiting the littoral zones of the northwestern Pacific. A revised diagnosis of *Limnaeoperyphus* is presented, the lectotype of *B. quadriimpressum* is redescribed, and the new species is described, which, unlike *B. quadriimpressum*, lives in rocky areas of the coasts. The possible origins and distribution of the subgenus are hypothesized, based on the system of sea currents in the North Pacific.

Key words: ground beetles, new species, key, littoral fauna, taxonomy, distribution, origins hypothesized

Introduction

The subgenus *Limnaeoperyphus* Nakane, 1963, genus *Bembidion* Latreille, 1802, established for *Bembidion quadriimpressum* (Motschulsky, 1860), which was described from Kamchatka and the Kuril Islands more than 180 years ago (Nakane 1963), has hitherto been considered monotypic. Our studies on the ground beetle fauna of the southern Kuril Islands in 2008–2022 unexpectedly showed that two closely related species of this subgenus co-occur on these islands. The diagnosis of *Limnaeoperyphus* is refined, a redescription of the *B. quadriimpressum* given, and the description of *B. petromarinum* **sp. nov.** presented.

Materials and methods

Standard methods were applied for treating the material. Genitalia were mounted on permanent slides using Hoyer's medium with a Solackryl mounting medium. External characters were studied with the help of MBS-1 and Leica M165C stereo microscopes, the genitalia examined under Zeiss Axio Scope A.1 microscope. Pictures were taken using a Canon EOS 5D Mark III camera with a Canon MP-E 65 mm objective lens and a Canon EOS 60D, while the extended focus images by means of Zerene Stacker software.

The abbreviations used in the text are as follows:

EL—greatest length of elytra;
EW—greatest width of elytra;
HL—length of head, measured along the median line from fore margin of clypeus to rear edge of the temples;
HW—greatest width of the head with eyes;
PA—width of pronotal apex;
PB—width of pronotal base;

Accepted by D. Seldon: 5 Jun. 2024; published: 13 Aug. 2024

PL—length of pronotum, measured along the median line;
PW—greatest width of pronotum;
TL—length of body from apex clypeus to apex of elytra;
M—arithmetic mean.

Designations of the sclerotized parts of the aedeagus are given after Maddison (1993), and Neri and Vigna Taglianti (2010). Female reproductive tract characters follow the terminology of Maddison (1993), and Liebherr and Will (1998). The abbreviations given in the illustrations are as follows:

AG—apical gonocoxite;
aFS—apical part of flagellar sheath;
BC—bursa copulatrix;
BS—basal sclerite;
DP—dorsal plate (= lateral sclerite);
Fl—flagellum;
RB—ribbon brush;
SD—spermathecal duct;
SG—spermathecal gland;
SP—spermatheca;
VS—ventral sclerite (spinules?).

Statistical analysis was performed using PAST v4.0 software (Hammer *et al*. 2001). The significance was determined by two-sample tests (t-test, F-test, Mann-Whitney test and Kolmogorov-Smirnov test) and Tukey's pairwise test for independent variables, with a 95% confidence level.

The material has been shared between the collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZISP), Zoological Museum, M.V. Lomonosov Moscow State University, Moscow (ZMMU), Moscow State Pedagogical University, Moscow (MSPU), Federal Scientific Center of East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok (FEB), private collection of I.A. Belousov and I.I. Kabak, St. Petersburg (cBK) (all Russia) and Natural History Museum (former British Museum, Natural History), London, United Kingdom (NHM).

Systematics

Subgenus *Limnaeoperyphus* Nakane, 1963

Limnaeoperyphus Nakane, 1963: 23. Type species: *Lymnaeum quadriimpressum* Motschulsky, 1860, original designation.
Lymnaeoperyphus auct.

Diagnosis. Small (length 3.5–5.0 mm), slightly convex beetles, with distinct microsculpture over entire dorsal surface; colour of upper parts with metallic sheen over entire dorsal surface or elytra brown. Head rather large, not punctured; eyes bulging; posterior supra-orbital pore located at posterior edge of eye; frontal grooves wide, parallel, not bifurcated; mandibles rather narrow, with apices slightly curved inward; antennae with light basal segments. Pronotum small, distinctly cordiform, slightly wider than head; bases near the basal foveae is slanted forward; posterior angles rectangular, with pointed apices; midline very narrow; basal foveae small, not punctate; laterobasal carina weak. Elytra small, oval, moderately convex; shoulders strongly rounded, not protruding; basal border very short, smoothly passing into lateral margin, reaching of 5th stria; striae complete up to apex; third interval with two discal pores lying on 3rd stria. Hind wings reduced. Legs slender and relatively short. Underside: not punctate; metasternal process with a thin, often indistinct border; metepisternum short; abdominal sternites simple, with neither pubescence nor additional setae.

Aedeagus elongate (5.0–5.6 times longer than wide), penis tube almost straight, lamella short, wide, rounded and rather strongly bent ventrally. Complex of central sclerites with a developed flagellum, ribbon brush small, slightly larger than basal sclerite. Lateral sclerite small, without processes.

Endophallus straight, with two lateral tubercles at base and two small tubercles at apex.

Tergite IX of female weakly sclerotized, transverse, with sparse setae at apical margin. Basal gonocoxite subtriangular, with a convex outer margin and 1–4 ventral subapical setae. Apical gonocoxite falcate, 1.8–2.1 times

as long as wide at base, with a pair of thin subapical setae. In addition to the dorsal spine, apical gonocoxite bearing two or three lateral ones.

Spermatheca sclerotized, spermathecal duct moderately long, not coiled, and a vaginal sclerite (annulus receptaculus) absent. Spermathecal gland developed, its subbasal part thickened and bearing ring folds, weakly sclerotized distally.

Species composition. The subgenus presently includes two species, *Bembidion quadriimpressum* (Motschulsky, 1860) and *B. petromarinum* **sp. nov.**, both distributed on the coastal areas of the northwestern Pacific.

Notes. For more than a century, *B. quadriimpressum* was considered within the genus/subgenus *Lymnaeum* Stephens, 1828 [= *Limnaeum* auct.] (Motschulsky 1860; Netolitzky 1935, 1943; Jedlička 1965; Kryzhanovskij *et al*. 1975; *etc*.), although doubts were expressed already by F. Netolitzky (1943: 100/72). In 1963, T. Nakane established the monotypic subgenus *Limnaeoperyphus* Nakane, 1963 for this particular species, pointing out in a short diagnosis the combination of a habitus characteristic of *Cillenus* and the structure of the genitals typical of *Peryphus* (Nakane 1963: 23). The new subgenus was not immediately accepted by specialists. For example, A. Jedlička (1965: 160), in his monograph of the Bembidiini of East Asia, considered *Limnaeoperyphus* as a junior synonym of *Lymnaeum*.

From species of the Western Palaearctic subgenus *Lymnaeum*, which for a long time included *B. quadriimpressum*, *Limnaeoperyphus* species differ in having large eyes, very short temples, the location of the posterior supra-orbital pore at the level of the posterior edge of the eye, relatively short oval elytra and completely rounded shoulders.

The structure of the genitalia allows *Limnaeoperyphus* to be attributed to the *Ocydromus* Series, within which it shows some similarities to the Nearctic *Ocydromus* Clade (*sensu* Maddison 2012). The relative size and shape of the aedeagus sclerites resemble those of the Nearctic species of the subgenus *Ocydromus*, members of the '*striola'* group (*sensu* Lindroth 1963). This is consistent with the results of a phylogenetic analysis using seven genes (Maddison & Maruyama 2019).

Bembidion (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860)

(Figures 1–17, 31–36, 50–53, 58–77, 98–105)

Lymnaeum quadriimpressum Motschulsky, 1860: 90–91, pl. vi, fig. 8. Type locality: "les bords de l'Océan pacifique dans la baie d'Avatcha au Kamtschatka et sur les iles Kourilles" (original citation), Avacha Bay on the east coast of Kamchatka and the Kuril Islands, Russian Far East.

Lectotype, ♂ with labels: illegible text [red rectangle; handwritten], "*Lymnaeum 4 impressum* Motsch. Kamtschatka" [white rectangle; handwritten], "Holotypus *Bembidion* (*Limnaeum*) *quadriimpressum* Motsch. 73 Lafer det." [red rectangle; handwritten], "LECTOTYPUS *Lymnaeum quadriimpressum* Motschulsky, 1860 design Yu.Sundukov et K.Makarov, 2024." [red rectangle; printed] [ZMMU].

Paralectotype, ♀ with labels "Ins. Kuril." [folded white rectangle; printed], "Scher (illegible text) 2.19." [white rectangle; handwritten], "*Phila 4 impressum* Menet. Urupa." [white rectangle; handwritten], "Holotypus *B*. (*Limnaeum*) *quadriimpressum* Mot." [red rectangle; handwritten], "PARALECTOTYPUS *Lymnaeum quadriimpressum* Motschulsky, 1860 design Yu.Sundukov et K.Makarov, 2024." [red rectangle; printed] [ZISP]. The specimen is severely damaged: 4–11 left antennomeres, the left fore and right hind legs are missing, the right elytra is split in the middle.

Others material. RUSSIA: *Kuril Archipelago*: Zelyonyi Island [Khabomai Arch.], western coast 1.5 km N of Glushnevsky Cape, single-sand beach under wracks, 6.VIII.1994, leg. K. Eskov, 1 ex [MSPU]; Tanfiliev Island, Zorkaya Bay, sandy beach between the sea and a freshwater lake, 7.VI.2017, leg. Yu. Sundukov, 14 ex [FEB, MSPU]; Yuri Island, western bay of Shirokaya Bay, sand and pebble beach, 26.VIII.2016, leg. Yu. Sundukov & L. Sundukova, 9 ex [FEB]; ibid, 1.IX.2016, Yu. Sundukov & L. Sundukova, 2 ex [FEB]; Yuri Island, Katernaya Bay, sand and pebble beach, 28.VIII.2016, Yu. Sundukov & L. Sundukova, 8 ex [FEB]; Yuri Island, eastern bay of Shirokaya Bay, sand and pebble beach, 30.VIII.2016, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; Yuri Island, ocean coast, sand and pebble beach, 31.VIII.2016, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; Polonsky Island, Chasovaya Bay, sandy beach, 30.VIII.2017, leg. Yu. Sundukov & L. Sundukova, 27 ex [FEB, MSPU]; Polonsky Island, Moryakov Bay, sandy beach, 2.IX.2017, leg. Yu. Sundukov & L. Sundukova, 41 ex [FEB]; Polonsky Island, coast near Cape Yazykovy, sandy beach, 5.IX.2017, leg. Yu. Sundukov & L. Sundukova, 19 ex [FEB]; Polonsky Island, Udobnaya Bay, sand-pebble beach, 6.IX.2017, leg. Yu. Sundukov & L. Sundukova, 48 ex

[FEB]; Polonsky Island, Cape Severnyi, sandy beach, 9.IX.2017, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; Shikotan Island, in nests Larus sp. 14.VIII.56, leg. Violovich, 11 ex [ZISP]; Shikotan Island, mouth of Vesolyy Stream, 43°49’36’’N 146°54’02’’E, 26.VI.2011, leg. I. Melnik, 16 ex [MSPU]; Shikotan Island, Malaya Tserkovnaya Bay, peat shore in the high tide zone, 16.VIII.2022, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; Shikotan Island, Tserkovnaya Bay, sand-pebble beach at the mouth of the stream, 25.V.2012, leg. Yu. Sundukov, 3 ex [FEB]; ibid, 3.VI.2012, leg. Yu. Sundukov, 52 ex [FEB, MSPU]; ibid, 7.VI.2012, leg. Yu. Sundukov, 11 ex [FEB]; ibid, 26.VIII.2012, leg. Yu. Sundukov & L. Sundukova, 2 ex [FEB]; ibid, 12.VIII.2016, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; ibid, 18.VIII.2022, leg. Yu. Sundukov & L. Sundukova, 46 ex [FEB]; Shikotan Island, mouth of the Anama River, muddy shore in the high tide zone, 13.VIII.2022, leg. Yu. Sundukov & L. Sundukova, 14 ex [FEB]; Shikotan Island, Malokurilskaya Bay, sand-pebble beach, 20.VIII.2016, leg. Yu. Sundukov, 1 ex [FEB]; Kunashir Island, Veslo Cape, 43°39’12”N 145°32’22”E, 21.VII.2008, leg. I. Melnik, 3 ex [MSPU]; Kunashir Island, Veslovsky Peninsula, muddy shore in the high tide zone, 27.VII.2017, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; Kunashir Island, Veslovsky Peninsula 1.5 km north of Veslo Cape, 43°39’57”N 145°32’12”E, 20–22.VII.2008, leg. K. Makarov, 1 ex [MSPU]; Kunashir Island, Belozerskie lakes, sandy beach, 19.VIII.2017, leg. Yu. Sundukov, 1 ex [FEB]; ibid, 23.VIII.2017, leg. Yu. Sundukov, 8 ex [FEB]; Kunashir Island, mouth of the Ricorda River, muddy shore in the high tide zone, 19.VIII.2017, leg. Yu. Sundukov, 1 ex [FEB]; Kunashir Island, env. Golovnino, 43°44’05”N 145°31’15”E, 14.VII.2008, leg. I. Melnik, 1 ex [MSPU]; Kunashir Island, Golovnino, on the seashore under seaweed, 8.IX.1976, leg. V. Kuznetsov, 1 ex [FEB]; Kunashir Island, mouth of the Golovnina River, sandy beach, under seaweed, 20.VIII.2017, leg. Yu. Sundukov, 1 ex [FEB]; ibid., leg. K. Makarov, 11 ex [MSPU]; Kunashir Island, interfluve of the Golovnin and Khlebnikov rivers, fine gravel beach, under seaweed, 7. VI.2015, leg. Yu. Sundukov, 12 ex [FEB]; ibid, 30.IX.2015, leg. Yu. Sundukov, 5 ex [FEB]; Kunashir Island, mouth of the Khlebnikov River, under the algae, 16.VI.2015, leg. Yu. Sundukov, 12 ex [FEB]; Kunashir Island, mouth of the Khlebnikov River, 4 km east of Paltusovo, 43°43’59’’N 145°29’33’’E, 11.VIII.2011, leg. K. Makarov, 5 ex [MSPU]; Kunashir Island, mouth of Sennaya River ca. 2.5 km eastern Paltusovo, 43°43’44”N 145°28’34”E, 11.VIII.2011, leg. K. Makarov, 11 ex [MSPU]; Kunashir Island, env. Paltusovo, 43°43’31”N 145°26’48”E, 15.VI.2011, leg. A. Matalin, 4 ex [MSPU]; Kunashir Island, mouth of the Bystry Creek, sandy beach, 10.VII.2013, leg. L. Sundukova, 2 ex [FEB]; Kunashir Island, mouth of the Bystry Stream, 43°47’18’’N 145°25’19’’E, 18.VIII.2011, leg. K. Makarov, 3 ex [MSPU]; Kunashir Island, mouth of the Temnaya River, sandy beach, 6.VI.2015, leg. Yu. Sundukov, 5 ex [FEB]; Kunashir Island, ca. 2 km north of Bolotny Stream, 43°49’13’’N 145°24’32’’E, 18.VIII.2011, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, 3 km south of Ivanovsky Cape, mouth of the stream, 43°48’53’’N 145°24’44’’E, 15.VI.2011, leg. I. Melnik, 2 ex [MSPU]; Kunashir Island, mouth of the Vodopadny Stream south of Ivanovsky Cape, 43°48’20’’N 145°24’59’’E, 11.VI.2011, leg. A. Matalin, 13 ex [MSPU]; ibid, 18.VIII.2011, leg. K. Makarov, 9 ex [MSPU]; Kunashir Island, cliff betweeh Ivanovsky Cape and Vodopadny Stream, 43°48’55”N 145°24’41”E, 15.VI.2011, leg. A. Matalin, 32 ex [MSPU]; Kunashir Island, small stream 2 km south of Grozovoye, sandy beach, 2.VI.2015, leg. Yu. Sundukov, 8 ex [FEB]; Kunashir Island, Cape Ivanovsky, sandy beach, 25.V.2013, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; ibid, 16.VI.2013, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; ibid, 14.VII.2013, leg. Yu. Sundukov & L. Sundukova, 3 ex [FEB]; ibid, 2.IX.2013, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; ibid, 4.IX.2013, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; Kunashir Island, mouth of the Krivonozhka River, sandy beach, 28.V.2013, leg. Yu. Sundukov & L. Sundukova, 5 ex [FEB]; Kunashir Island, sea coast north of the Krivonozhka River, sandy beach, 11.VII.2013, leg. Yu. Sundukov & L. Sundukova, 2 ex [FEB]; Kunashir Island, stream north of the Krivonozhka River, pebble beach, 19.IX.2013, leg. Yu. Sundukov & L. Sundukova, 10 ex [FEB]; Kunashir Island, mouth of stream, 1.3 km north of Krivonozhka River, 43°50’55’’N 145°26’08’’E, 16.VIII.2011, leg. K. Makarov, 5 ex [MSPU]; Kunashir Island, mouth of stream, southern of Blizhny Island, 43°51’05’’N 145°26’37’’E, 26.VII.2011, leg. K. Makarov, 4 ex [MSPU]; Kunashir Island, mouth of stream, 1 km north of Blizhny Island, 43°51’22’’N 145°26’51’’E, 16.VIII.2011, leg. K. Makarov, 8 ex [MSPU]; Kunashir Island, mouth of the Ozernaya River, 43°53’07”N 145°27’44”E, 7.VII.2008, leg. K. Makarov, 1 ex [MSPU]; Kunashir Island, 1.5 km south-west mouth of the Ozernaya River, sea coast, 43°52’27”N 145°27’16”E, 26.VII.2011, leg. K. Makarov, 3 ex [MSPU]; Kunashir Island, 6 km SW of Alekhin Cape, 43°53’58’’N 145°28’31’’E, 20.VIII.2009, leg. I. Melnik, 1 ex [MSPU]; Kunashir Island, bay south-west of the Odinoky Creek, 43°54’36”N 145°30’25”E, 1.VI.2009, leg. I. Melnik, 2 ex [MSPU]; ibid, 1.VI.2011, leg. A. Matalin, 3 ex [MSPU]; Kunashir Island, mouth of Odinoky Stream 1.5 km south of Alekhino, 43°54’47”N 145°30’46”E, 3.VIII.2011, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, mouth of the Odinokiy Creek, sandy bank of the stream, 10.IX.2014,

leg. Yu. Sundukov, 2 ex [FEB]; Kunashir Island, 1 km south-west of Alekhino, coastal rockery, 43°54’58’’N 145°31’00’’E, 4.VIII.2011, leg. K. Makarov, 5 ex [MSPU]; Kunashir Island, near Alekhino, fumarole, 6.VIII.1970, leg. Loktin, 1 ex [ZISP]; Kunashir Island, near Alekhino, sea shore under algae, 3.VIII.1970, leg. Loktin, 32 ex [ZISP]; Kunashir Island, near Alekhino, sandy beach, 14.IX.2014, leg. Yu. Sundukov, 1 ex [FEB]; ibid, 5.VII.2015, leg. L. Sundukova, 3 ex [FEB]; ibid, 7.VII.2015, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; ibid, 23.VII.2015, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; Kunashir Island, mouth of Alekhina River, 43°55’15”N 145°31’59”E, 2.VIII.2011, leg. K. Makarov, 5 ex [MSPU]; Kunashir Island, flood-plain of the Alekhina River near mouth, 43°55’14’’N 145°32’09’’E, 2.VIII.2011, leg. K. Makarov, 1 ex [MSPU]; Kunashir Island, Cape Puzanov, sandy beach, 16.VIII.2014, leg. Yu. Sundukov & L. Sundukova, 6 ex [FEB]; ibid, 26.VIII.2014, leg. Yu. Sundukov & L. Sundukova, 8 ex [FEB]; Kunashir Island, north coast of Puzanova Cape, 43°52’23’’N 145°36’23’’E, 21.VIII.2011, leg. K. Makarov, 5 ex [MSPU]; Kunashir Island, northern coast of Chetverikova Cape, 43°53’01”N 145°37’30”E, 10.VII.2008, leg. K. Makarov, 14 ex [MSPU]; Kunashir Island, mouth of the Andreevka River, sandy beach, 9.VIII.2014, leg. Yu. Sundukov & L. Sundukova, 5 ex [FEB]; Kunashir Island, mouth of the Andreevka River, sandy river bank, 22.VIII.2014, leg. Yu. Sundukov, 1 ex [FEB]; Kunashir Island, mouth of Andreevka River, 43°53’13.9”N 145°37’32.6”E, 7.VII.2008, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, mouth of the Belkina River, 43°53’26’’N 145°37’39’’E, 20.V.2011, leg. I. Melnik, 5 ex [MSPU]; Kunashir Island, eastern shore of Glukhoe Lake, 43°54’11”N 145°38’12”E, 9.VII.2008, leg. I. Melnik, 7 ex [MSPU]; Kunashir Island, mouth of Tyurina River, 43°54’33’’N 145°41’06’’E, 22.VIII.2011, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, south coast of Vodopadny Cape, 43°54’39’’N 145°39’31’’E, 22.VIII.2011, leg. K. Makarov, 6 ex [MSPU]; Kunashir Island, Vodopadny Cape, 43°54’27”N 145°40’40”E, 22.VIII.2011, leg. K. Makarov, 5 ex [MSPU]; Kunashir Island, Krugly Cape, ca. 1.5 km NE of Tretyakovo, 44°00’16”N 145°39’21”E, 26.VIII.2017, leg. K. Makarov, 3 ex [MSPU]; Kunashir Island, coast of Okhotsk Sea, south of Znamenka Cape, 43°56’10”N 145°33’13”E, 4.VIII.2009, leg. K. Makarov, 12 ex [MSPU]; ibid, 22.VIII.2009, leg. K. Makarov, 4 ex [MSPU]; Kunashir Island, shore of Peshchanoe Lake, 43°56’36”N 145°35’22”E, 5.VI.2011, leg. A. Matalin, 4 ex [MSPU]; Kunashir Island, western shore of Lake Peshchanoe, sandy shore of the lake, 4.IX.2014, leg. Yu. Sundukov, 10 ex [FEB]; ibid, 7.IX.2014, leg. Yu. Sundukov, 24 ex [FEB]; ibid, 6.VIII.2011 leg. K. Makarov, 2 ex [MSPU]; ibid, 8.VIII.2008 leg. K. Makarov, 2 ex [MSPU]; ibid., 30.VII.2011, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, south-west shore of Peshchanoe Lake, 43°56’33”N 145°33’20”E, 22.VIII.2009, A. Zaitsev, 26 ex [MSPU]; Kunashir Island, north-west shore of Peshchanoe Lake, 43°56’41”N 145°35’39”E, 6.VIII.2011, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, Danilovo Natural Boundary, sea shore, 43°57’15”N 145°35’29”E, 7.VIII.2011, leg. K. Makarov, 9 ex [MSPU]; Kunashir Island, cordon Alekhinsky, 43°57’17”N 145°35’34E, 17–18.IX.2009, leg. I. Melnik, 5 ex [MSPU]; Kunashir Island, mouth of the Asin Stream, 43°58’59’’N 145°37’33’’E, 8.VIII.2009, leg. K. Makarov, 2 ex [MSPU]; Kunashir Island, Tretjakovo, 10.VIII.1973, leg. Kerzhner, 3 ex [ZISP]; Kunashir Island, mouth of Valentiny Stream, 43°59’34”N 145°38’47”E, 10.VIII.2011, leg. K. Makarov, 21 ex [MSPU]; Kunashir Island, mouth of Zmeiny Stream, 44°00’40”N 145°40’27”E, 27.VII.2008, leg. I. Melnik, 3 ex [MSPU]; Kunashir Island, mouth of the Stolbovskoy Stream, 44°00’39’’N 145°40’29’’E, 9.VI.2011, leg. A. Matalin, 2 ex [MSPU]; Kunashir Island, Pervukhina Bay, 44°03’18”N 145°44’36”E, 15.VIII.2011, leg. K. Makarov, 4 ex [MSPU]; ibid, 23.VII.2013, leg. K. Makarov, 4 ex [MSPU]; Kunashir Island, env. Yuzhno-Kurilsk, ocean shore, 15–19.VI.1990, leg. K. Makarov, 6 ex [MSPU]; Kunashir Island, env. Yuzhno-Kurilsk, 44°01’49”N 145°51’13”E, 17–18.IX.2009, leg. I. Melnik, 5 ex [MSPU]; Kunashir Island, Yuzhnokurilsky Cape, 44°01’14’’N 145°51’52’’E, 22.VII.2013, leg. K. Makarov, 4 ex [MSPU]; Kunashir Island, env. Yuzhno-Kurilsk, Golovnina Bay, 44°02’29”N 145°51’50”E, 28.VIII.2009, leg. I. Melnik, 3 ex [MSPU]; Kunashir Island, southern coast of Serebryanoe Lake, 44°03’05”N 145°49’12”E, 11.IX.2009, leg. A. Zaitsev, 1 ex [MSPU]; Kunashir Island, shore of Mikhaylovskoye Lake, 44°18’01”N 145°58’07”E, 14.VIII.2017, leg. K. Makarov, 23 ex [MSPU]; Kunashir Island, mouth of the Filatova River, sand-pebble beach, 26.VI.2013, leg. Yu. Sundukov, 10 ex [FEB]; Kunashir Island, Filatova River, 16.VIII.1981, leg. O. Kabakov, 1 ex [ZISP]; Kunashir Island, sea coast between Filatova River and Rogacheva Cape, 44°11’11”N 146°01’57”E, 10.IX.2009, leg. I. Melnik, 5 ex [MSPU]; Kunashir Island, mouth of the Medny Creek, seaside sandy beach, 16.VIII.2017, leg. Yu. Sundukov, 26 ex [FEB]; ibid, 27.VI.2008, leg. K. Makarov, 3 ex [MSPU]; Kunashir Island, sea coast near Valentina Lake, 44°16’34”N 145°56’27”E, 16.VIII.2017, leg. K. Makarov, 24 ex [MSPU]; Kunashir Island, mouth of the Saratovskaya River, sandy river bank, 2.VII.2014, leg. Yu. Sundukov, 17 ex [FEB]; ibid, 12.VII.2014, leg. Yu. Sundukov & L. Sundukova, 17 ex [FEB]; ibid, sandy beach, 4.VII.2014, leg. Yu. Sundukov & L. Sundukova, 7 ex [FEB]; Kunashir Island, lower reaches of the Saratovskaya River, swampy river bank in the high tide zone, 14.VII.2014, leg. Yu.

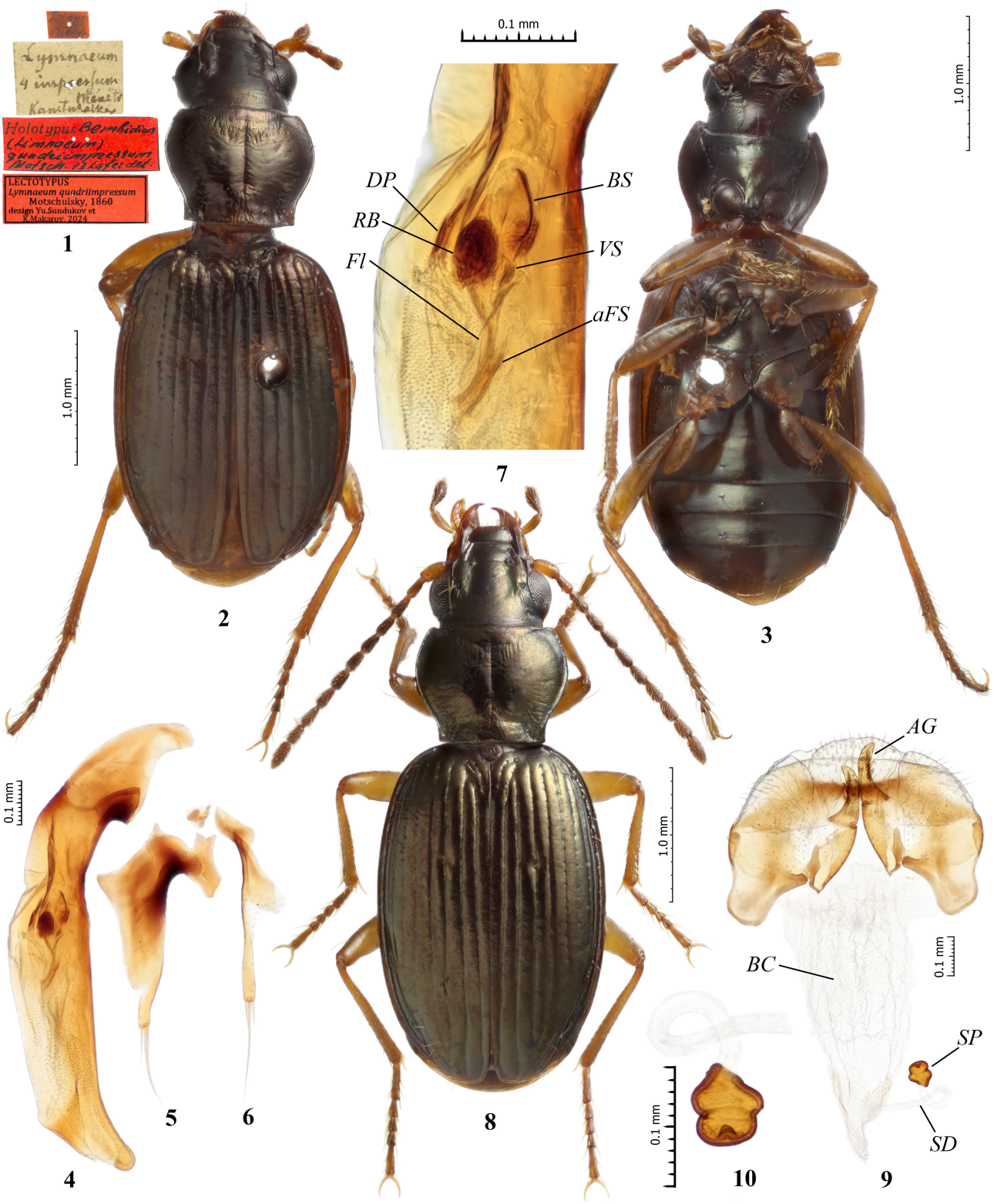
Sundukov & L. Sundukova, 4 ex [FEB]; Kunashir Island, mouth of the stream ~250 m north of the mouth of the Saratovskaya River, sand and pebble beach, 16.VI.2016, leg. Yu. Sundukov, 7 ex [FEB]; Kunashir Island, env. cordon Tyatinsky, 44°16’20”N 146°10’20’’E, 3.VII.2011, leg. I. Melnik, 1 ex [MSPU]; Kunashir Island, mouth of the Tyatina River, pebble river bank, 21.VII.2014, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; Kunashir Island, Lovtsova Peninsula, Spokoiny Bay, sandy beach, 21.VIII.2015, leg. Yu. Sundukov, 1 ex [FEB]; Kunashir Island, tip of Cape Lovtsov near Pico Island, sandy beach, 12.VIII.2015, leg. Yu. Sundukov & L. Sundukova, 17 ex [FEB]; Iturup Island, Burevestnik—Iodny, stream mouths, 26.VIII.1975, leg. S. Storozhenko, 18 ex [FEB]; Iturup Island, Medvezhyi Peninsula, Slavnaya Bay near the Slavnaya River mouth, 20.VIII.1994, leg. K. Eskov, 2 ex [MSPU]; Urup Island, Natalia Bay, Irina Bay, 46°05’43”N, 150°09’49”E, rocks in the tidal zone, 22.VIII.2021, leg. D.R. Zhigir, 5 ex [ZMMU]; Urup Island, Natalia Bay, Irina Bay, 46°05’45”N, 150°10’04”E, rocks in the tidal zone, 23.VIII.2021, leg. D.R. Zhigir, 1 ex [ZMMU]; Paramushir Island, Krasheninnikov Bay, 4.VIII.1997, leg. A. Lelej & S. Storozhenko, 1 ex [FEB]; Paramushir Island, Shelikhovo, 13.VIII.1997, leg. A. Lelej & S. Storozhenko, 1 ex [FEB]; Paramushir Island, near Severo-Kurilsk, 10.VIII.1997, leg. Yu. Marusik, 1 ex [FEB]. *Sakhalin Island*: Kuznetsova Cape, 22.VIII.1988, leg. S. Korolev, 2 ex [MSPU]; Aniva Bay, Taranai, sea shore, 7.VII.1947, leg. E. Guryanova, 6 ex [ZISP]; Aniva district, ca 1.8 km SE from Novikovo, Evstafiya Cape, 8.VI.1990, leg. K. Makarov, 2 ex [MSPU]; Ptichye Lake, 16.VIII.1974, leg. M. Kuporosov, 5 ex [ZISP]; Solovyovka, muddy seashore in the high tide zone, 7.VIII.2018, leg. Yu. Sundukov & L. Sundukova, 5 ex [FEB]; Okhotskoe, mouth of the Krasnoarmeysky channel, muddy shore in the high tide zone, 1.VIII.2022, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; Yasnomorsky north of Nevelsk, mouth of the Yasnomorka River, 21.VII.2019, leg. M. Sergeev, 1 ex [FEB]. *Primorsky Territory*: Vityaz Bay, Andreevka, 11.IV.1974, leg. A.B. Egorov, 1 ex [FEB]; Khasansky district, Vityaz Bay, intertidal zone, 14.VII.1959, leg. R.A. Vasiliev, 4 ex [ZISP]; Khasansky district, sea shore, 9.VII.1959, leg. R.A. Vasiliev, 1 ex [ZISP]; Khasansky district, Gorshkov Bay, sandy beach at the mouth of the stream, 28.V.2022, leg. Yu. Sundukov, K. Makarov & A. Matalin, 25 ex [FEB, MSPU]; Ryazanovka, sandy sea beach, 7.VII.1985, leg. G. Lafer, 8 ex [FEB]; Ryazanovka, sea beach, 4.X.1998, leg. B. Kataev, 1 ex [ZISP]; Khasansky district, coast between the mouths of the Zaklyuchennaya and Ryazanovka rivers, sandy beach, 21.V.2023, leg. Yu. Sundukov, 4 ex [FEB]; Khasansky district, Kedrovy Cape, shore of the Amur Bay, 43°04’04’’N 131°36’17’’E, 27.V.2015, leg. A. Matalin, 5 ex [MSPU]; Khasansky district, mouth of the Kedrovaya River, sandy beach, 43°04’47’’N 131°36’47’’E, 25.V.2015, leg. K. Makarov & A. Matalin, 16 ex [MSPU]; Khasansky district, Melkovodnaya Bay, beach, 19.VII.1973, leg. G. Lafer, 9 ex [ZISP]; Khasansky district, mouth of the Kedrovaya River, sandy beach, 22.VIII.2018, leg. Yu. Sundukov, 15 ex [FEB, MSPU]; Vladivostok, Shamara Bay, VII.1976, leg. G. Lafer, 8 ex [FEB]; Vladivostok env., 28.VIII.1969, leg. O. Kryzhanovskij, 4 ex [ZISP]; near Bolshoi Kamen, Andreeva Bay, 27.V.2023, leg. M. Sergeev, 6 ex [FEB]; Lazovsky district, Sudzukhe, 25.VIII.1961, leg. Tryapitsyn, 1 ex [ZISP]; Lazovsky district, Lake Chekhunenko at the mouth of the Kievka River, pebble beach, 1.VII.2022, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; Lazovsky Reserve, Petrov Bay, sandy beach, 16–19.VI.2008, leg. V. Shokhrin, 2 ex [FEB]; Lazovsky Reserve, env. cordon Petrova, 1th Olenevod, 20.IX.1998, leg. B. Kataev, 2 ex [ZISP]; Lazovsky district, Sokolovka Bay, seaweed discharges at the mouth of the stream, 14.VII.2002, leg. Yu. Sundukov, 7 ex [FEB]; ibid, 28.VII.2005, leg. Yu. Sundukov, 7 ex [FEB]; ibid, leg. K. Makarov, 1 ex [MSPU]; Lazovsky Reserve, mouth of the Proselochnaya River, sandy river bank, 14.VII.2005, leg. Yu. Sundukov & V. Shokhrin, 1 ex [FEB]; ibid, 12.VII.2005, leg. K. Makarov, 2 ex [MSPU]; Olginsky district, mouth of the Avvakumovka River, sandy beach at the mouth of the river, 30.VII.2004, leg. Yu. Sundukov & L. Sundukova, 4 ex [FEB]; ibid, 1.IX.2019, leg. Yu. Sundukov & L. Sundukova, 1 ex [FEB]; *Kamchatka*: river Kireun [=Kirevna], valley of Kamchatka River, 9.VIII.1929, leg. Novograblenov, 1 ex [ZISP].

*92 specimens were measured, and 29 preparations made.

Redescription of the lectotype. The body is slightly convex. Length 3.9 mm, width 2.3 mm.

Head and pronotum dark bronze, elytra dark brown with faint bronze tint. Appendages of head: basal antennal segment red-brown, the rest partially blackened (one basal segment of the left antenna and three basal segments of right antenna preserved); palps and mandibles more or less uniformly brown (left maxillary palp absent); labrum dark brown. Underparts dark brown with barely noticeable greenish tint. Epipleurae of elytra and pronotum brownish yellow. Legs light brown, coxae and trochanters slightly darker, brown.

Dorsal side without punctures. Microsculpture of dorsal side of head (including clypeus and labrum), pronotum and most of elytra isodiametric, very weakly transverse around basal foveae of pronotum and on the 1st to the 6th inner intervals of elytra.



FIGURES 1–10. *Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860): 1–7—male, lectotype, 8–10—female (Tanfiliev Island, Zorkaya Bay): 1—labels of the lectotype; 2, 8—habitus, dorsal view, 3—habitus, ventral view, 4—median lobe of aedeagus, 5—left paramere, 6—right paramere, 7—sclerite of endophallus, 9—female genitalia, 10—spermatheca. Abbreviations see in text.

Standard sizes (in mm): lectotype—HW 0.90; HL 0.60; PA 0.87; PW 1.11; PB 0.78; PL 0.86; EW 1.57; EL 2.30; TL 3.9; paralectotype—HW 0.95; HL 0.60; PA 0.89; PW 1.17; PB 0.83; PL 0.91; EW 1.73; EL 2.53; TL 4.2.

Head large, moderately convex, its width with eyes 1.56 times its length. Eyes normal, moderately convex. Mandibles rather narrow, elongate, with pointed apices slightly curved inward. Labrum trapezoidal, with six setae along anterior margin. Clypeus trapezoidal, with two lateral setae, distant from anterior edge by 1/3 length of clypeus. Tooth of mentum large, broadly triangular, rounded at apex, with two small setae at base. Submentum with two large setae each side. Gula in basal third with a narrow longitudinal groove. Temples very short, ~ 1/5 eye diameter. Two supra-orbital setae, one each at the middle of eye and at its posterior margin. Frontal grooves not bifurcated, parallel, widely groove-shaped, expressed from the middle of posterior half of eye to clypeus; from posterior edge of clypeus to its setae, grooves narrow and less deep; immediately behind clypeal suture, a pore-like formation on each groove. Space between frontal groove and lateral edge of forehead convex, weakly keeled; space between anterior and posterior supra-orbital pores with three oblique wrinkles. Antennae: one basal segment of left antenna and three basal segments of right antenna preserved.

Pronotum moderately convex, distinctly cordate, weakly transverse (PW/PL = 1.28), slightly wider than head (PW/HW = 1.21), with the maximum width of 2/3 from base. Anterior margin very weakly and regularly concave, very finely edged at anterior angles. Front angles almost not protruding forward, their apices narrowly rounded. Base slightly concave in the middle, at basal foveae clearly sloping forward, without clear edging, slightly narrower than anterior margin (PB/PA = 0.92). Posterior corners almost not protruding, rectangular, slightly skewed forward, pointed at apex. Sides moderately convex and regularly rounded, slightly concave in front of posterior angles. Lateral edges narrowly bordered entire. Two lateral setae each side: one in front of the maximum width and the other in posterior angle. Midline very narrow, distinct, reaching both anterior and posterior transverse impressions, these being weak. Basal foveae relatively small, externally delimited by an indistinct carina; their short central impression arched from posterior angles to anterior edge. Area between foveae distinctly and longitudinally rugose.

Elytra oval, moderately convex, short (EL/EW = 1.34, EL/PL = 2.73, EW/PW = 1.56), with the maximum width approximately at middle. Shoulders broadly rounded, not protruding. Basal border very short, gradually turning into lateral margin, reaching the apex of 5th stria. Lateral edge flattened, uniformly narrow all along; an outer apical angle not expressed, gradually turning into lateral margin. Striae complete, moderately deep (deeper in anterior half), finely punctured; 2nd stria at apex clearly connected to 1st stria; 7th stria developed all along; apical stria moderately deep, continuous, connected to the apex of 5th stria, and bearing two setigerous pores: one at apex, the second opposite the junction of 4th and 5th striae. Intervals in anterior half moderate, in posterior half slightly convex. A subscutellar striola absent. Prescutellar pore is located on top of fused 1st and 2nd striae. Third interval with two clearly visible discal pores lying inside 3rd stria: anterior approximately 1/3 of base, posterior approximately 1/3 of apex. Lateral series (series umbilicate) consisting of eight setae: four in humeral group, two in the middle, and two at apex. Wings reduced to a small and narrow plate.

Legs relatively short, slender; middle tibia 1.10 times as long as middle tarsus; hind tibia 1.04 times as long as hind tarsus.

Underside of body not punctured. Metasternal process weakly and indistinctly bordered. Metepisternae short. Hind coxae with three setae. Hind trochanters each with one seta, in the middle. Abdominal sternites simple, with neither pubescence nor additional setae; apical sternite with two setae at apex.

Penis (Fig. 4) thin, 5.6 times longer than thick, ventral margin almost straight, slightly curved in front of apex, lamella short and rounded.

Left paramere (Fig. 5) wide, with three setae at apex: middle one 2.5 times as long as lateral ones; right paramere (Fig. 6) narrow, with three setae at apex, a subapical seta absent.

Endophallus armament (Fig. 7) well-developed. Dorsal plate (DP) small and without processes. Ribbon brush (RB) rounded and slightly shorter than dorsal plate. Flagellum (Fl) short, approximately twice as long as ribbon brush. The sclerotized part of the flagellar sheath (aFS) is approximately half as long as the flagellum. Basal sclerite (BS) longer than ribbon brush, rather weakly and symmetrically curved in profile. Ventral sclerite (VS) short, without spines.

Additional morphological information (based on non-type specimens).

Wing reduced down to a narrow triangular plate with visible remains of costal and subcostal veins at base and faint traces of 1–2 longitudinal veins distally, these probably corresponding to radial and medial veins.

Everted endophallus (Figs 33–36) asymmetrical, with large, clearly defined, laterobasal tubercles, unpaired

dorso-apical tuberosity small, all tubercles covered with spines. Two small apical tubercles in front of central sclerite complex.

In female, apical gonocoxite crescent-shaped, shorter than basal one (Fig. 9). In juveniles, apex slightly expanded laterally; in beetles that have laid eggs, apex strongly worn out and devoid of its characteristic shape. Subapical setae thin, dorsal spine short, lateral spines large, usually two, rarely three (three spines usually found on only one, left or right, gonocoxite). Spermatheca almost symmetrical, short, 1.1–1.5 times as long as wide. Basal part of spermatheca conical, separated from distal part by a deep groove (Fig. 10).

Variability. Body length 3.40–4.45, width 1.38–1.75 mm (Table 1). Sexual dimorphism well-expressed, females larger than males in all measurements ($p<0.01$). Colouration from light to dark bronze, sometimes with greenish or bluish sheen (Figs 58–77). Legs always lightly coloured, only knees slightly darkened. Antennae always darkened colouration from 3rd segment; in most specimens, 2nd segment also partially darkened. Anterior depression of pronotum well-expressed, rarely (in approximately 10% beetles) smoothed. Subscutellar striola always developed, rather long (not shorter than width of scutellum), usually with several punctures, rarely without punctures. Discal pores of elytra large; in approximately every fifth beetle they interrupt adjacent intervals. Sutural stria at apex of elytra usually connected with 2nd stria and noticeably deepened there; less often ending up freely.

TABLE 1. Morphometric variability of *Limnaeoperyphus*. The cells indicate the range of values (top line) and the arithmetic mean ± error of the mean (bottom line). All values are in mm.

species	sex	*n*	HW	HL	PW	PL	EW	EL	TL
B. petromarinum	♂	39	0.80–1.00 (0.92±0.006)	0.56–0.73 (0.63±0.006)	1.04–1.26 (1.141±0.007)	0.80–0.98 (0.88±0.006)	1.56–1.93 (1.73±0.011)	2.23–2.80 (2.53±0.016)	3.80–4.68 (4.27±0.025)
	♀	31	0.85–1.00 (0.93±0.007)	0.58–0.70 (0.63±0.005)	1.06–1.26 (1.16±0.010)	0.83–0.98 (0.89±0.008)	1.63–1.90 (1.78±0.012)	2.40–2.83 (2.61±0.022)	4.03–4.58 (4.37±0.029)
B. quadriimpressum	♂	41	0.79–0.96 (0.89±0.007)	0.50–0.65 (0.58±0.006)	0.95–1.20 (1.07±0.009)	0.73–0.93 (0.83±0.008)	1.39–1.75 (1.57±0.015)	2.08–2.58 (2.32±0.020)	3.44–4.45 (3.96±0.032)
	♀	50	0.78–0.98 (0.85±0.005)	0.53–0.63 (0.57±0.004)	0.93–1.18 (1.04±0.008)	0.71–0.89 (0.80±0.006)	1.38–1.73 (1.50±0.011)	1.95–2.50 (2.17±0.017)	3.40–4.23 (3.75±0.025)

Populations from different islands of the Kuril Archipelago fail to differ in colouration, size or proportions ($p<0.05$).

Structure of spermatheca constant in different parts of the range. Shape of aedeagus and armament of endophallus little variable.

Diagnosis. It differs from *B. petromarinum* **sp. nov.** in the light colouration of the legs, the lightened integument, the relatively narrow elytra, the short spermatheca, the strongly extended laterobasal lobe of the endophallus (see below), and the short flagellum (Table 2, Figs 119–122).

TABLE 2. Morphometric differences in the genitalia of male *Limnaeoperyphus*. The cells indicate the range of values (top line) and the arithmetic mean ± error of the mean (bottom line).

species	*n*	EdL/EdW	EdL/FiL	EdW/FiL
B. petromarinum	13	3.67–3.97 (3.80±0.025)	4.00–4.80 (4.42±0.080)	1.07–1.26 (1.16±0.018)
B. quadriimpressum	7	3.99–4.45 (4.20±0.056)	7.00–8.34 (7.60±0.178)	1.63–2.05 (1.82±0.053)

Abbreviations: EdL—length of the aedeagus, EdW—width of the aedeagus, FiL—length of flagellum.

Note. *Bembidion quadriimpressum* was first mentioned by V.I. Motschulsky (1850) under the name *Phila quadriimpressa* in his catalogue of ground beetles, indicating the authorship of E. Ménétriés. At the same time, he pointed out (Motschulsky 1850: 14) that four specimens were known: one from Kamchatka and three from the Urup Island, Kuril Islands. Ten years later, Motschulsky published a description of this species, without indicating the number of specimens, but mentioning material from Kamchatka and the Kuril Islands: "... habite les bords de l'Océan pacifique dans la baie d'Avatcha au Kamtschatka et sur les îles Kourilles" (Motschulsky 1860: 91). Thus,

it can well be assumed that Motschulsky had several syntypes at his disposal. Subsequently, some of the specimens were lost or moved, and only one specimen is mentioned from Motschulsky's collection in the Moscow Museum, i.e., a male labeled "Holotypus. Kamtschatka" (Keleinikova 1976). The second specimen, a significantly damaged female, is kept in the collection of ZISP RAS, St. Petersburg. As lectotype, we designate the male from the ZMMU collection in accordance with the recommendations of Art. 74 ICZN. The type area, according to clause 76.2 of the ICZN, is the Kamchatka Peninsula.

Distribution. Northwestern Pacific: the coasts of the Sea of Okhotsk and the Sea of Japan from Kamchatka to the Korean Peninsula, as well as the Kuril Islands (all), Sakhalin, Moneron Island, Hokkaido and Honshu.

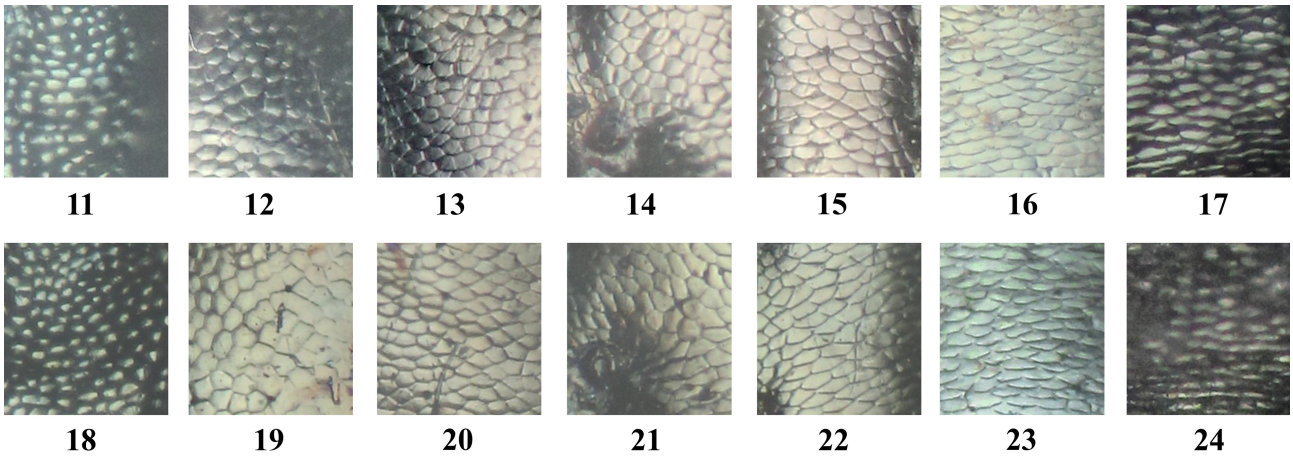
Habitat. Coastal areas: sandy and pebble beaches, muddy shores of the tidal zone, river mouths (Figs 123, 125, 127, 129). Beetles are found under discarded algae, boards, logs and other objects in the supra-littoral zone; more abundant near fresh waters discharging into the sea.

Bembidion (*Limnaeoperyphus*) *petromarinum* Sundukov et Makarov, sp. n.

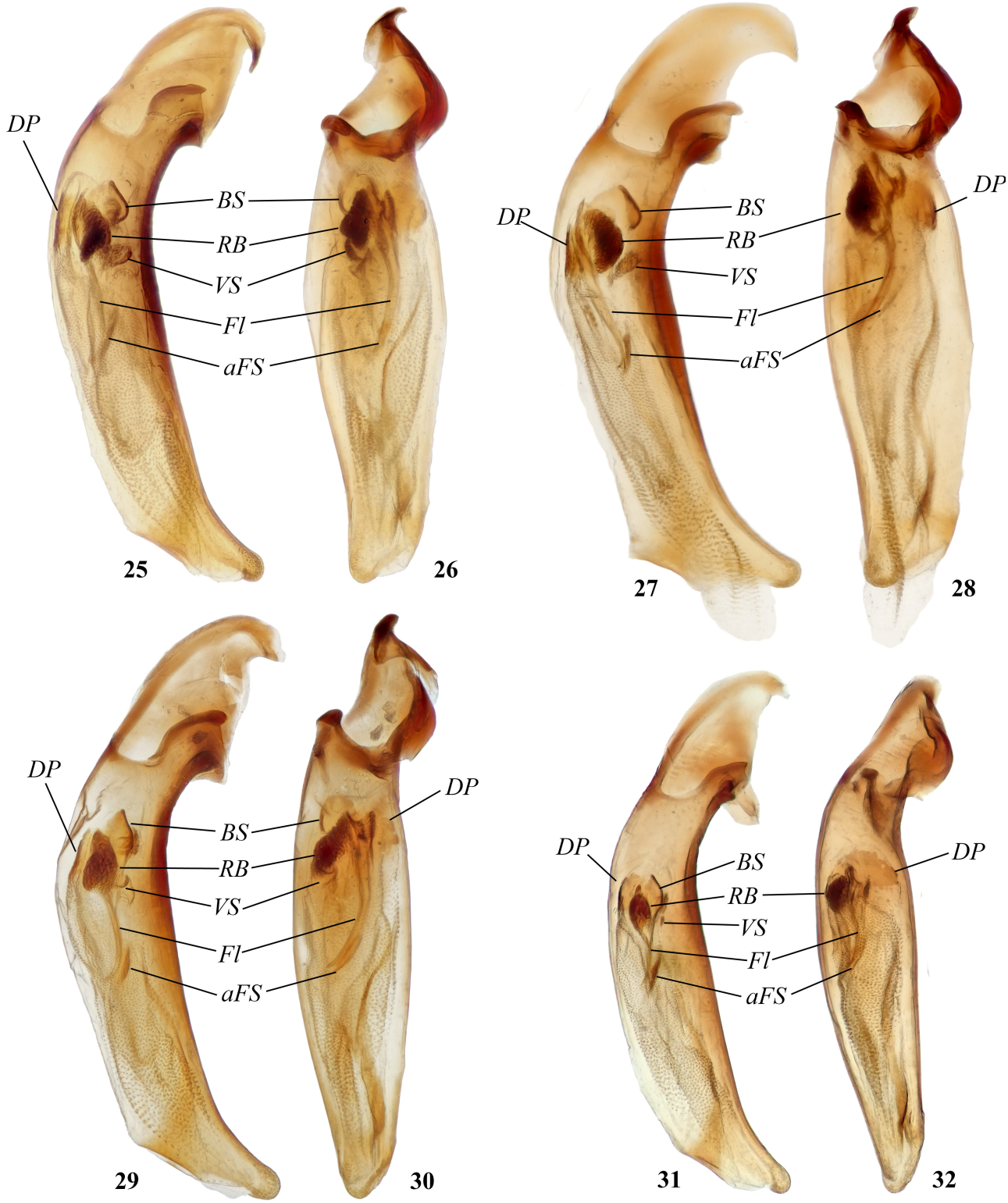
(Figures 18–30, 37–49, 54–57, 78–97, 106–118)

Holotype ♂ with labels: "Kunashir, Cape Prasolov, south coast, rocks, 44°21'15"N 146°00'19"E, 11.VIII.2017, leg. K. Makarov & Yu. Sundukov" [ZISP].

Paratypes. 8♂ 2♀, Southern Kuril Islands, Tanfiliev Island, Zorkaya Bay, seaside rocky cliffs, 7.VI.2017, leg. Yu. Sundukov [FEB, ZMMU, NHM, MSPU]; 1♂ 2♀, Southern Kuril Islands, Polonsky Island, Moryakov Bay, 2.IX.2019, leg. Yu. Sundukov & L. Sundukova [cBK, MSPU]; 1♂ 1♀, Southern Kuril Islands, Shikotan Island, Tserkovnaya Bay, seaside rocks, 27.V.2012, leg. Yu. Sundukov [MSPU]; 6♂ 2♀, ibid, 18.VIII.2022, leg. Yu. Sundukov & L. Sundukova [FEB]; 5♂ 2♀, Shikotan Island, in nests Larus sp. 14.VIII.56, leg. Violovich, [ZISP]; 18♂ 13♀, Southern Kuril Islands, Rogachev Island near Kunashir Island, seaside rocks, 28–29.VI.2017, leg. Yu. Sundukov [FEB, ZMMU, ZISP, MSPU, cBK]; 1♀, Southern Kuril Islands, Kunashir Island, mouth of the Ozernaya River, 43°53'07"N 145°27'44"E, 11.VIII.2009, leg. K. Makarov [MSPU]; 1♂ 2♀, Southern Kuril Islands, Kunashir Island, mouth of Tyatina River, 44°16'06"N 146°09'30"E, 6.IX.2009, leg. I. Melnik [MSPU]; 1♀, Southern Kuril Islands, Kunashir Island, sea coast between Filatova River and Rogacheva Cape, 44°11'11"N 146°01'57"E, 10.IX.2009, leg. I. Melnik [MSPU]; 1♂, Southern Kuril Islands, Kunashir Island, mouth of the Vodopadny Stream south of Ivanovsky Cape, 43°48'20"N 145°24'59"E, 11.VI.2011, leg. I. Melnik [MSPU]; 1♂ 2♀, Southern Kuril Islands, Kunashir Island, 0.3 km south-west from mouth of the Ozernaya River, 43°52'55"N 145°27'38"E, 21.VII.2011, leg. K. Makarov [MSPU]; 2♂, Southern Kuril Islands, Kunashir Island, Bely Utes Cape, seaside cliffs, 11.VIII.2013, leg. Yu. Sundukov [MSPU]; 1♂ 2♀, Southern Kuril Islands, Kunashir Island, Prasolov Cape, south coast, rocks, 44°21'15"N 146°00'19"E, 11.VIII.2017, leg. K. Makarov & Yu. Sundukov [ZISP, NHM, MSPU]; 3♂ 1♀, Southern Kuril Islands, Kunashir Island, shore of Mikhaylovskoye Lake, 44°18'01"N 145°58'07"E, 14.VIII.2017, leg. K. Makarov [ZISP, MSPU].



FIGURES 11–24. Microsculpture: 11–17—*Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860), 18–24—*Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.**, 11, 18—frontal furrow, 12, 19—forehead, 13, 20—disk of pronotum, 14, 21—3rd elytral interval near discal pore, 15, 22—4th elytral interval, 16, 23—first visible sternite, 17, 24—last visible sternite.



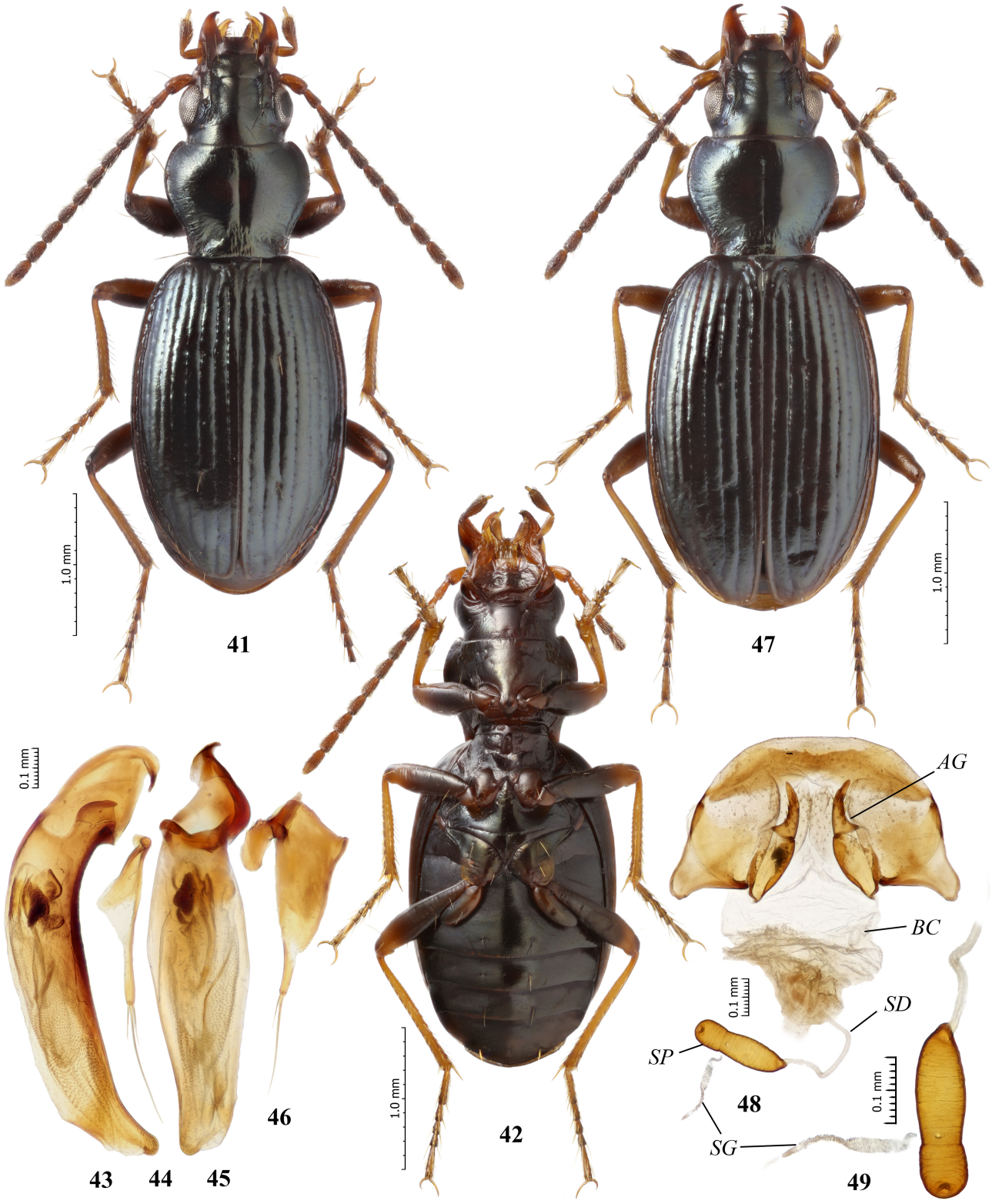
FIGURES 25–32. Median lobe of aedeagus: 25–30—*Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.** (25–26—holotype, Kunashir Island, Prasolov Cape, 27–28—Tanfiliev Island, Zorkaya Bay, 29–30—Khasansky district, Ostrovok Falshivy Peninsula), 31–32—*Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860), from Kunashir Island, Serebryanoe Lake, 25, 27, 29, 31—right view, 26, 28, 30, 32—ventral view. Abbreviations see in text.

FIGURES 33–40. Everted endophallus: 33–36—*Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860), Kunashir Island, Sennaya River, 37–40—*Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.**, Shikotan Island, Tserkovnaya Bay, 33, 37—ventral view, 34, 38—right view, 35, 39—left view, 36, 40—dorsal view.

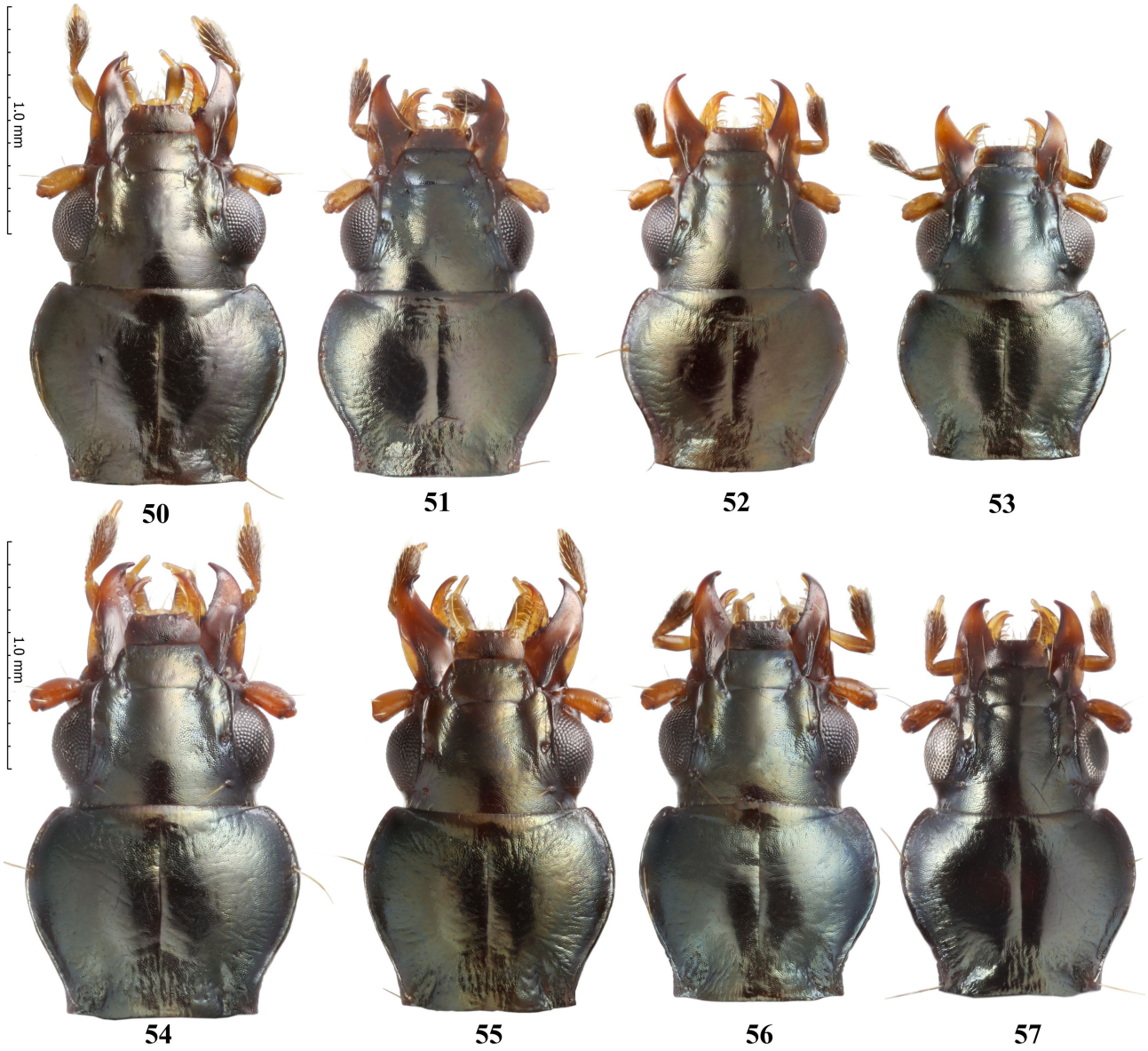
72 specimens were measured (including all types), and 26 preparations made.

Type locality. RUSSIA, Kuril Archipelago: Kunashir Island, Cape Prasolov.

Material not included in the typical series. RUSSIA: *Kuril Archipelago*: 2♂ 2♀, Yuri Island, western bay of Shirokaya Bay, sand and pebble beach, 26.VIII.2016, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♀, ibid, 1.IX.2016, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♂ 2♀, Polonsky Island, Chasovaya Bay, seaside rocky cliffs, 30.VIII.2017, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♀, Polonsky Island, Moryakov Bay, seaside rocky cliffs, 2.IX.2017, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♀, Polonsky Island, coast near Cape Yazykovy, seaside rocky cliffs, 5.IX.2017, leg. Yu. Sundukov & L. Sundukova [FEB]; 5♂ 5♀, Polonsky Island, Udobnaya Bay, seaside rocks, 6.IX.2017, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♀, Polonsky Island, Cape Severny, seaside rocky cliffs, 9.IX.2017, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♂, Shikotan Island, Tserkovnaya Bay, seaside rocks, 25.V.2012, leg. Yu. Sundukov [FEB]; 2♂, Kunashir Island, rocks at Cape Prasolov, 11.VIII.2017, leg. Yu. Sundukov [FEB]; 1♀, Kunashir Island, mouth of the Tyatina River, river bank with large boulders, 21.VII.2014, leg. Yu. Sundukov & L. Sundukova [FEB]; 1♂, Kunashir Island, Cape Bely Utes, seaside cliffs, 11.VIII.2013, leg. Yu. Sundukov [FEB]. *Primorsky Territory*: 1♂ 1♀, Khasansky district, Ostrovok Falshivy Peninsula, seaside rocks, 23.V.2022, leg. Yu. Sundukov [FEB].



FIGURES 41–49. *Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.** (41, 43–49—Kunashir Island, Prasolov Cape, 42—Tanfiliev Island, Zorkaya Bay): 41–46—male, holotype, 47–49—female, paratype, 41, 47—habitus, dorsal view, 42—habitus, ventral view, 43—median lobe of aedeagus, right view, 44—right paramere, 45—median lobe of aedeagus, ventral view, 46—left paramere, 48—female genitalia, 49—spermatheca.



FIGURES 50–57. Variation of the head and pronotum: 50–53—*Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860), 54–57—*Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.**, 50–51, 53–57—male, 52—female, 50—Khasansky district, Gorshkov Bay, 51—Khasansky district, Kedrovaya River, 52, 53—Polonsky Island, Moryakov Bay, 54—Rogachev Island near Kunashir Island, 55—Tanfiliev Island, Zorkaya Bay, 56—Khasansky district, Ostrovok Falshivy Peninsula, 57—Kunashir Island, Prasolov Cape.

Description of the holotype. Body slightly convex. Length 3.80 mm, width 1.55 mm.

Dorsal side black with a distinct bluish or bluish-greenish tint (Fig. 41). Appendages of head: 2.5 basal antennal segments red-brown, the rest partially blackened; palps red-brown with slightly blackened apical segments; mandibles red-brown with blackened apices and ribs at base; labrum red-brown (Figs 41, 57). Ventral side black or brownish black (Fig. 42). Epipleurae of elytra barely paler than body venter. Legs red-brown with pale brown tibiae and blackened trochanters, femora and tarsi; most of hind coxae black.

Dorsal side without punctures. Microsculpture of dorsal side of head (including clypeus and labrum) and along lateral margins of pronotum distinct, but not coarse, and consisting of more or less isodiametric meshes (Figs 18, 19); on pronotal disc (Fig. 20) and elytra (completely or 6–7 internal intervals) weakly transverse (Figs 21, 22). Microsculpture on abdominal sternites is transverse (Fig. 23), especially coarse on anal sternite (Fig. 24).

Standard sizes (in mm): HW 0.8; HL 0.56; PA 0.75; PW 1.04; PB 0.73; PL 0.80; EW 1.54; EL 2.23; TL 3.80.

Head quite large, moderately convex, its width with eyes is 1.42 times its length. Eyes moderately convex (Figs 41, 57). Mandibles rather narrow, elongate, with pointed apices slightly curved inward. Labrum trapezoidal, with six setae along anterior margin. Clypeus trapezoidal, with two lateral setae removed from anterior edge by 1/3 length of clypeus (Fig. 57). Tooth of mentum large, broadly triangular, rounded at apex, with two small setae at base. Submentum with two large setae each side, outer setae shorter. Gula in basal part with a short longitudinal depression. Temples short, slightly shorter than 1/4 longitudinal diameter of eye. Two supraorbital setae: one at the middle of eye and the other at its posterior margin. Frontal grooves parallel, widely groove-shaped, reaching the middle of posterior half of eye; grooves narrow and less deep on clypeus (Fig. 57). Anterior tentorial pits quite deep. Space between frontal groove and lateral edge of forehead convex, weakly keeled; space between anterior and posterior supra-orbital pores with oblique wrinkles (Fig. 57). Antennae long, reaching 2/5 length of elytra (Fig. 41).

Pronotum moderately convex, distinctly cordate, weakly transverse (PW/PL = 1.30), slightly wider than head (PW/HW = 1.30), with the maximum width of 3/5 of base (Figs 41, 57). Anterior margin slightly and regularly concave, very finely edged at anterior angles. Anterior angles almost not protruding forward, their apices narrowly rounded. Base slightly concave in the middle, slightly sloping forward at basal foveae, without clear edging, slightly narrower than anterior margin (PB/PA = 0.97). Posterior angles not protruding to sides, rectangular, slightly skewed forward, their apices pointed. Sides moderately convex and regularly rounded, slightly concave in front of posterior angles. Lateral edges narrowly bordered all along. Two lateral setae each side: one in front of the maximum width and the other in posterior angles. Midline very narrow, reaching both anterior and posterior transverse impressions, these being weak. Basal foveae relatively small, delimited externally by a weak carina; their short central impression arcuate and concave from posterior angles to anterior edge. Area between foveae distinctly longitudinally rugose; weaker transverse wrinkles present along lateral margins in basal half of pronotum and longitudinal wrinkles present on disc along anterior depression.

Elytra oval (Fig. 41), moderately convex, rather short (EL/EW = 1.43, EL/PL = 2.78, EW/PW = 1.50), with the maximum width approximately at middle. Shoulders broadly rounded, not protruding. Basal border very short, gradually turning into lateral margin, reaching the apex of 5th stria. Lateral edge flattened and uniformly narrow all along; an outer apical angle not expressed, gradually turning into lateral margin. Striae complete, moderately deep, with shallow punctures; 2nd stria at apex widely depressed; 7th stria well-developed all along; apical striole moderately deep, continuous, connected to apex of 5th stria and bearing two setigerous pores: one at apex, the second opposite the junction of 4th and 5th striae. Intervals moderately convex. Subscutellar striole short, marked by 3 points on right elytron; located inside 1st interval. Prescutellar pore located on top of fused 1st and 2nd striae. Third interval with two clearly visible discal pores lying at 3rd stria: anterior approximately 1/3 of base, posterior one approximately 1/3 of apex. Lateral series (series umbilicate) consisting of seven setae: four in the humeral group, one in the middle, and two at apex.

Wing in the form of a narrow triangular plate, 9–10 times shorter than elytra. Bases of costal and subcostal veins and traces of longitudinal veins visible on wing.

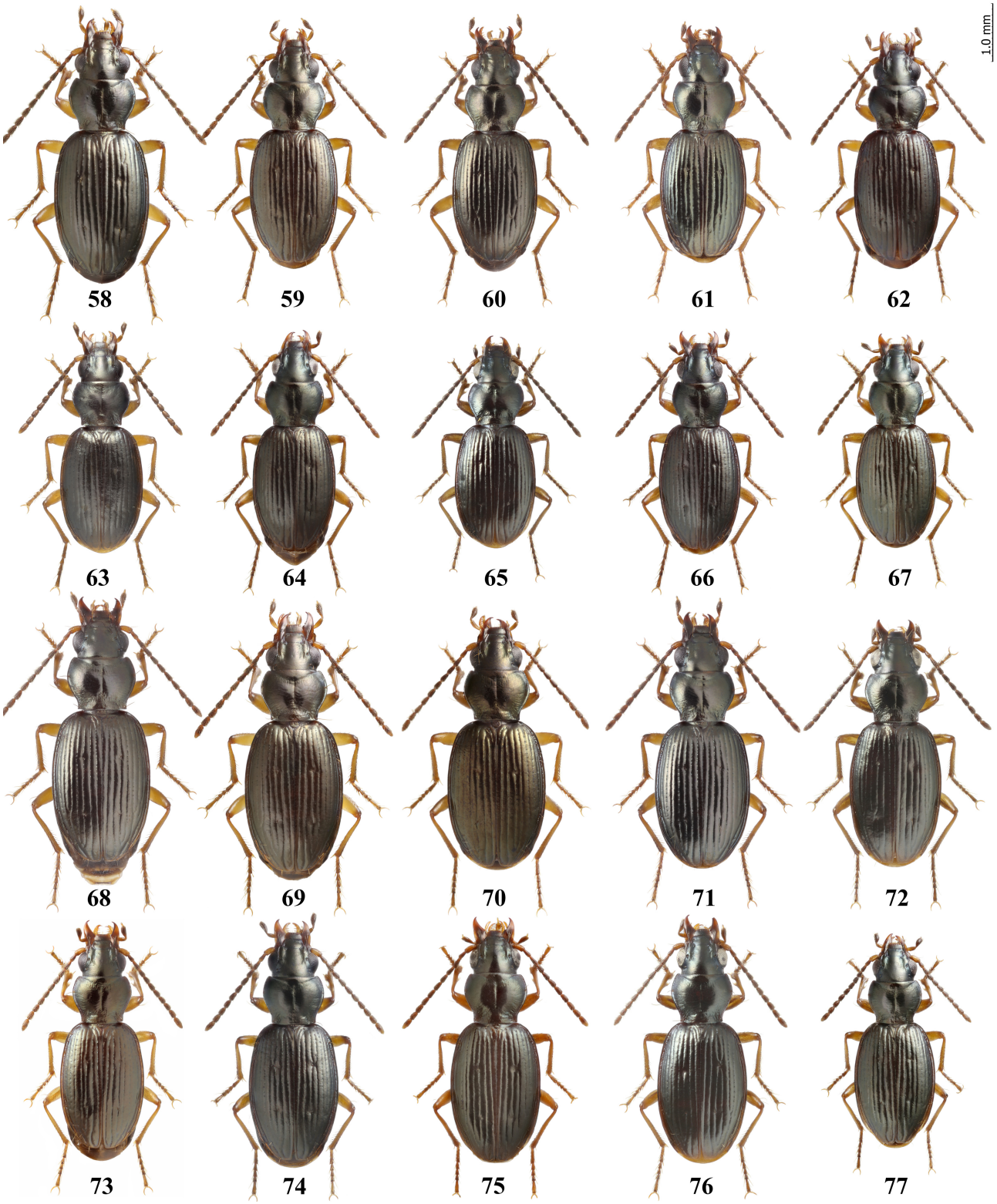
Legs relatively short, slender; middle tibia 1.21 times as long as middle tarsus; hind tibia 1.16 times as long as hind tarsus.

Underside of body not punctured. Metasternal process bordered by a thin line smoothed anteriorly. Metepisternum shortened: 1.6 times longer along outer margin than width along anterior margin. Hind coxae with three setae. Metatrochanters each with one seta, in the middle. Abdominal sternites simple, with neither pubescence nor additional setae; apical sternite with two setae at apex.

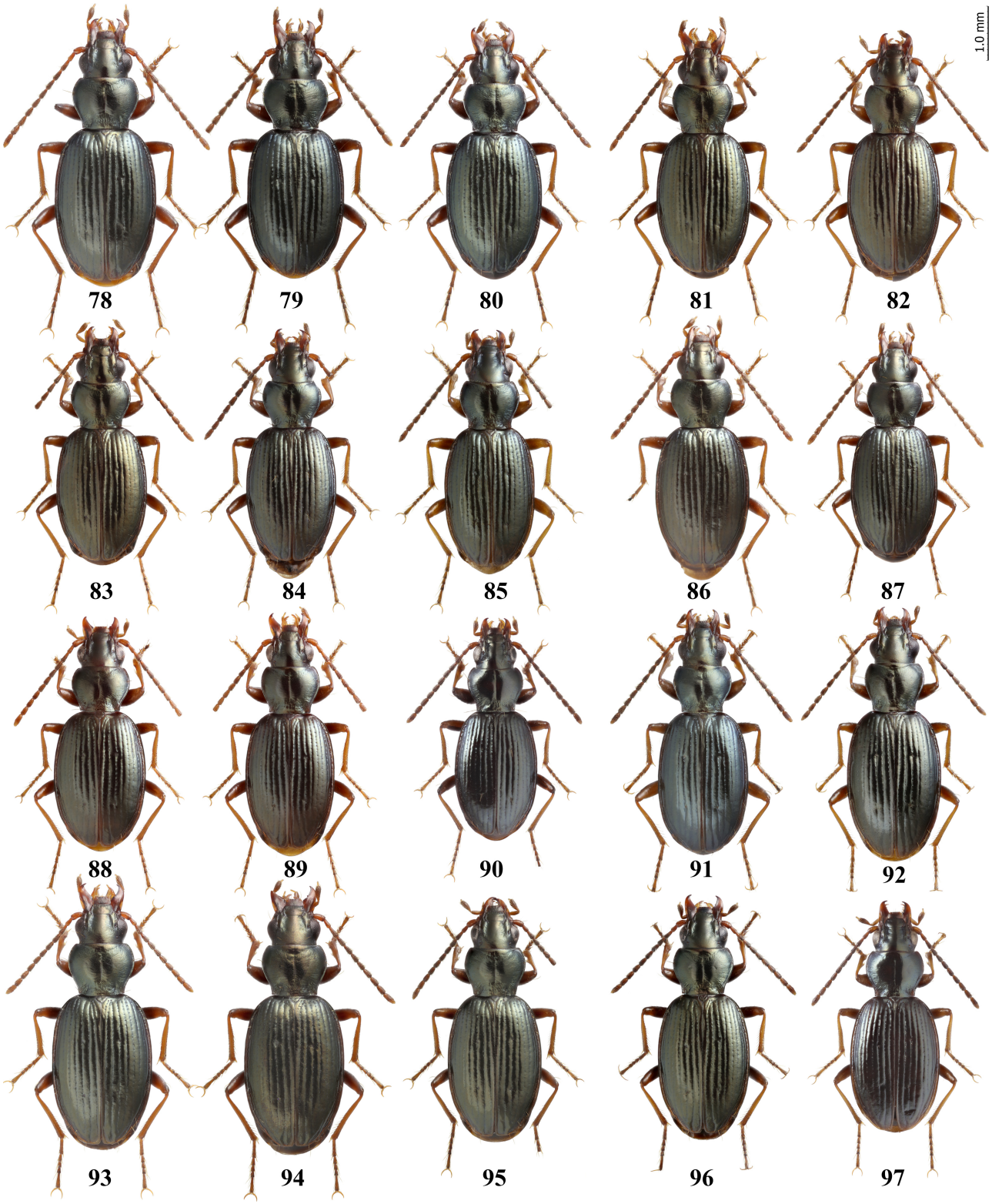
Penis (Figs 43, 45) thin and long, its ventral edge very slightly curved, lamella being short and widely rounded.

Left paramere (Fig. 46) wide, with three setae at apex: middle one very long, 3–3.5 times as long as both lateral ones; right paramere (Fig. 44) narrow, with three setae at apex (middle one very long, 3–3.5 times as long as lateral ones) and one short subapical seta on ventral side.

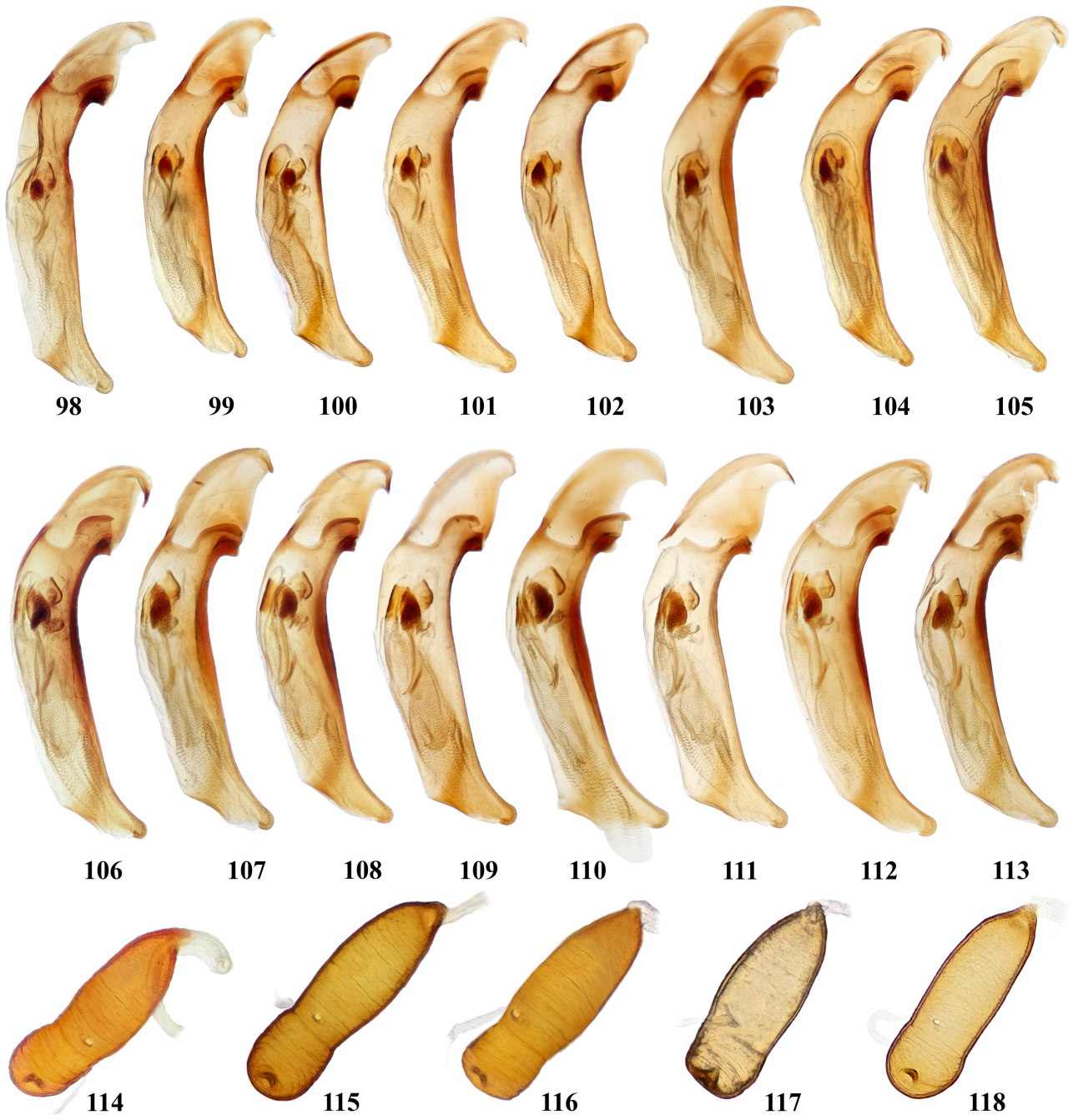
Endophallus armament (Figs 25, 26) typical of *Ocydromus*. Dorsal plate (DP) short, without processes. Ribbon brush (RB) compact, subequal in length to dorsal plate. A flagellum (Fl) originating from left part of the central complex of sclerites, its length being subequal to diameter of penis tube. A sclerotized part of flagellar sheath (aFS) visible near apex of flagellum. Basal sclerite (BS) slightly shorter than ribbon brush, being strongly and asymmetrically curved in profile. Ventral sclerite (VS) small, with an oblong field of spines next to it.



FIGURES 58–77. Variability of *Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860): 58–67—male, 68–77—female, 58, 69—Khasansky district, Gorshkov Bay, 59, 67, 73, 77—Polonsky Island, Moryakov Bay, 60, 61, 68, 71—Khasansky district, Kedrovaya River, 62, 74—Kunashir Island, Sennaya River, 63—Kunashir Island, Serebryanoe Lake, 64, 66—Shikotan Island, Tserkovnaya Bay, 65, 72, 76—Kunashir Island, Krugly Cape, 70—Tanfiliev Island, Zorkaya Bay, 75—Kunashir Island, Medny Creek.

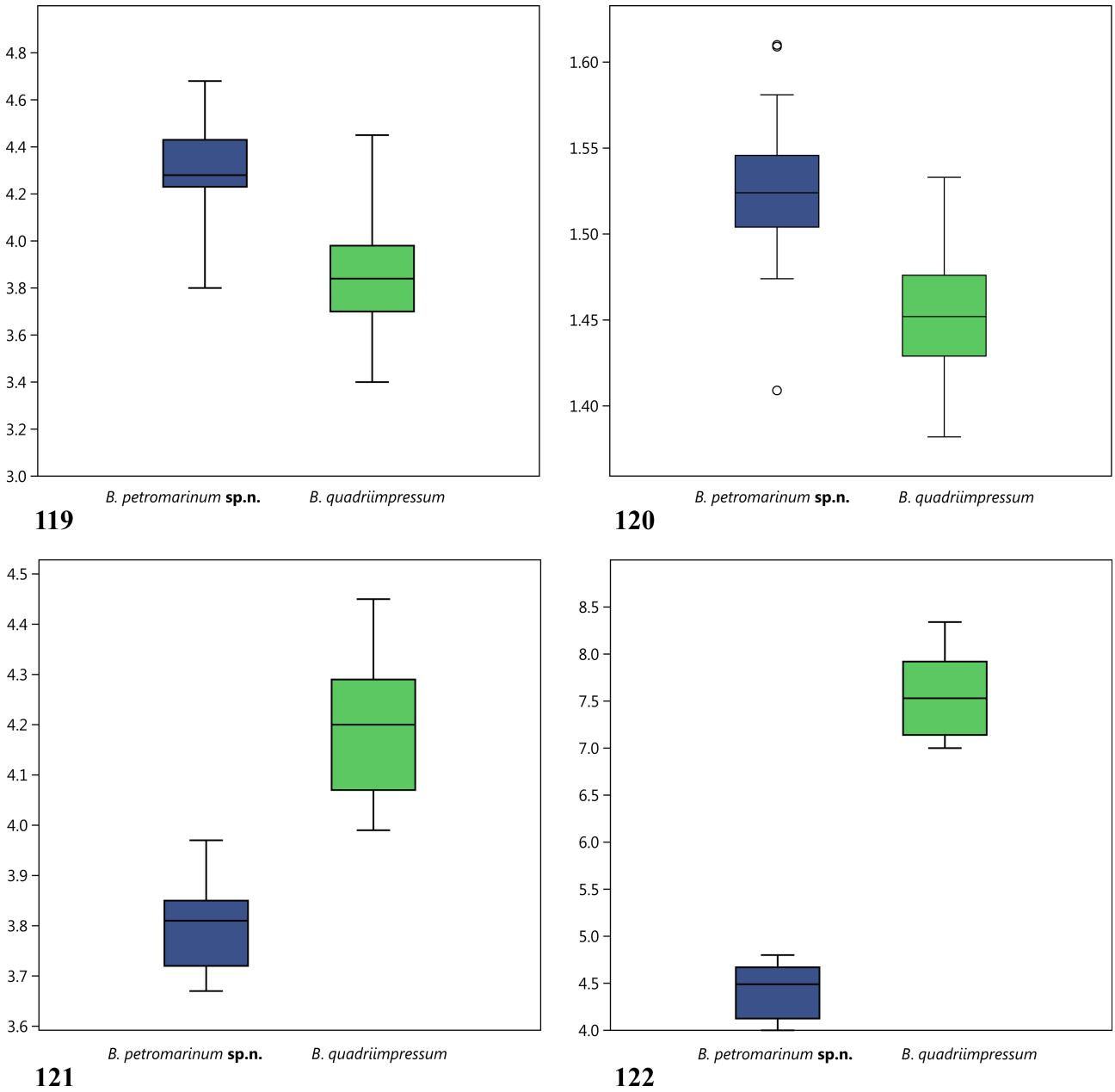


FIGURES 78–97. Variability of *Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.**: 78–91—male, 92–97—female, 78, 80, 93, 94—Rogachev Island near Kunashir Island, 81, 82, 83, 84—Tanfiliev Island, Zorkaya Bay, 85, 95, 96—Polonsky Island, Moryakov Bay, 86, 87—Shikotan Island, Tserkovnaya Bay, 88, 89—Kunashir Island, Bely Utes Cape, 90, 97—Kunashir Island, Prasolov Cape, 91, 92—Khasansky district, Ostrovok Falshivy Peninsula.



FIGURES 98–118. Variation of the genitalia in *Bembidion* (*Limnaeoperyphus*) spp.: 98–105—*Bembidion* (*Limnaeoperyphus*) *quadriimpressum* (Motschulsky, 1860), 106–118—*Bembidion* (*Limnaeoperyphus*) *petromarinum* **sp. nov.**, 98–113—median lobe of aedeagus; 114–118—spermatheca, 98—Kamchatka, lectotype, 99—Kunashir Island, Serebryanoe Lake, 100—Kunashir Island, Krugly Cape, 101, 102, 108, 109, 117—Polonsky Island, Moryakov Bay, 103, 110, 111—Tanfiliev Island, Zorkaya Bay, 104, 105—Khasansky district, Kedrovaya River, 106, 114, 115—Kunashir Island, Prasolov Cape, 107—Kunashir Island, Bely Utes Cape, 112—Shikotan Island, Tserkovnaya Bay, 113, 118—Khasansky district, Ostrovok Falshivy Peninsula, 116—Rogachev Island near Kunashir Island.

Everted endophallus (Figs 37–40) asymmetrical, strongly curved to the left. Both left and right laterobasal lobes small, round, regularly beset with spines (Fig. 37). Unpaired dorso-apical lobe in front of the complex of central sclerites gentle, covered with similar spines (Fig. 39). Two small, conical, apical lobes projecting in front of the complex of central sclerites.

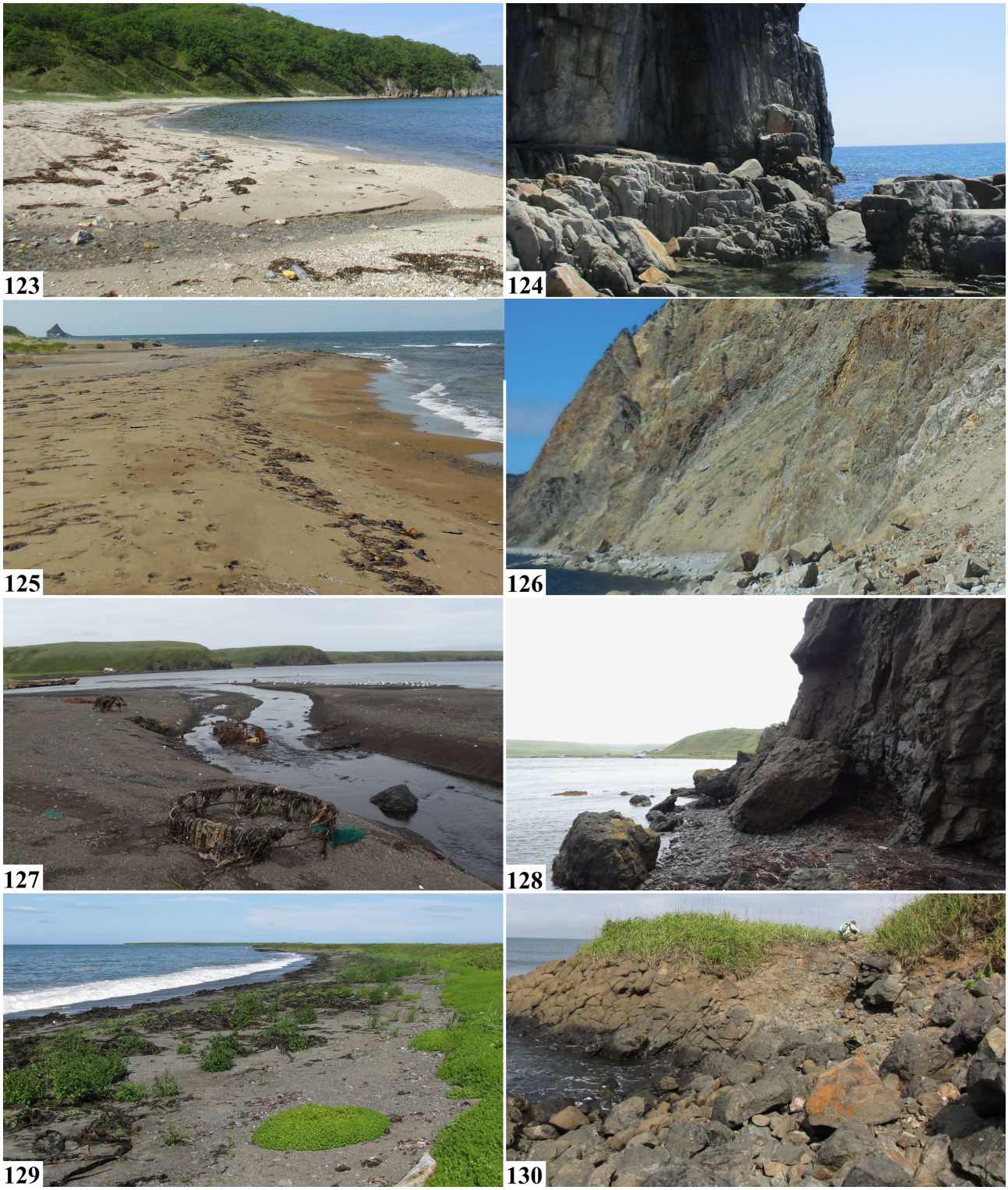


FIGURES 119–122. Morphometric differences between species of the *Limnaeoperyphus*: 119—length of body from clypeus to apex of elytra, 120—elytra length/elytra width ratio, 121—aedeagus length/width ratio, 122—aedeagus length/flagellum length ratio.

Female paratypes. Antennae shorter, up to 1/3 elytra; apical sternite of abdomen with four setae at apex. Apical gonocoxite (Fig. 48) crescent-shaped, slightly shorter than basal one. In young individuals, apex flattened, with a weak rib-like thickening. In addition to a pair of thin subapical setae, bearing a thick dorsal spine and three lateral ones. Spermatheca (Fig. 49) large, fusiform, 2.7–3.5 times as long as wide. Distal part separated by a shallow groove with gentle edges.

Variability. Body length 3.80–4.68, width 1.56–1.93 mm (Table 1). Sexual dimorphism less pronounced than in *B. quadriimpressum*, males are smaller than females, but significant differences ($p<0.05$) found only for total body length, was well as length and width of elytra. Colouration dark bronze, with a more or less strong greenish or bluish sheen (Figs 78–97). 2nd antennomere always light. Gula in basal part with a rather deep longitudinal depression, larger in males (1/3–1/4 gula) and smaller in females (sometimes reduced to a point).

Notch in front of posterior angles of pronotum often very weak; edges of pronotum sometimes narrowed to straight line towards posterior angles.



FIGURES 123–130. Typical habitats of *Limnaeoperyphus* species: 123, 125, 127, 129—*B. quadriimpressum*, 124, 126, 128, 130—*B. petromarinum* **sp. nov.**, 123—Khasansky district, Gorshkov Bay, 124—Khasansky district, Ostrovok Falshivy Peninsula, 125—Kunashir Island, seashore norther Krugly Cape, 126—Kunashir Island, Prasolov Cape, 127—Yuri Island, Shirokaya Bay, 128—Yuri Island, Shiroky Cape, 129—Polonsky Island, Moryakov Bay, 130—Polonsky Island, Udobnaya Bay.

Legs relatively short, slender; mesotibia 1.22–1.29 (M 1.25) times longer than mesotarsus; hind tibia 1.24–1.29 (M 1.26) times longer than hind tarsus. Femora darkened to a greater or lesser extent, but tibiae not darker than the rest of femora.

Intervals moderately or slightly convex. Discal pores small, placed close to 3rd stria, and never interrupting the striae. 2nd stria of elytra deepened in front of apex and ending freely in half of the cases. Prescutellar striola quite long, with several deep points and, less often (in less than 20% cases), shortened.

No statistically significant differences in sizes and proportions are found between populations from the islands of Kunashir, Shikotan, Polonsky, Tanfiliev and Yuri.

No interpopulation differences are found in the structure of the spermatheca (Figs 114–118), but in young individuals it is usually shorter and wider (Fig. 117). The shape of the lamella of the penis is a little variable. The armament of the endophallus is quite constant; there are only minor variations in the length of the dorsal sclerite, but these are found in different parts of the distribution range.

Etymology. The name of the new species comes from the Latinized form of the Greek noun "*πέτρα*" (stone) and the Latin adjective "*marina*" (sea). It reflects the specific habitat of the new species—rocks, cliffs and stones on the seashore.

Distribution. Northwestern Pacific: known from the Kuril Archipelago (Kunashir, Shikotan, Polonsky, Yuri, Tanfiliev, and Rogacheva islands), southern Primorsky Territory, southern Khabarovsk Territory (Sikhote-Alin, Botchinsky Nature Reserve; personal communication from R.Yu. Dudko, Novosibirsk, Russia).

Habitat. Sheer cliffs of the supra-littoral zone (Figs 124, 126, 128, 130). As a rule, during the daytime, beetles are found in rock cracks or rocky-gravel-soil deposits in places where fresh water oozes out (small streams in cracks and small gorges, water streaks on rock slabs), staying close to or directly at the edge of a water stream. Sometimes they are found on large-block or large-pebble seashores, where they have possibly ended up by accident (falling, being washed away by the waves).

Differential diagnosis. The new species differs from *Bembidion quadriimpressum* in its relatively wide elytra (Fig. 120; EW/PW ratio 1.47–1.61, *vs* 1.38–1.53 in *B. quadriimpressum*) with a distinct bluish or bluish-greenish tint; darkened, sometimes almost black hind coxae, trochanters, partly dark femora, and the structure of the genitalia: the female has a large, elongated spermatheca, an apical gonocoxite with three lateral spines; in the male, the medial lobe is wider (Fig. 121), the flagellum is longer (Fig. 122 and Table 2), the ribbon brush and ventral sclerite are more strongly developed, the laterobasal lobes of the endophallus are slightly protruding. *Bembidion petromarinum* **sp. nov.** is on average larger than *B. quadriimpressum* (Fig. 119, Table 1).

Key to the species of the subgenus *Limnaeoperyphus*

1. Larger (TL 3.80–4.68 mm, M 4.27 mm); elytra 1.53 (1.41–1.61) times wider than pronotum. Discal pores of elytra smaller and usually not pitted. Elytra with a distinct bluish or bluish-greenish tint; trochanters, femora and tarsomeres partially blackened, most of hind coxae black; 2nd antennomere always light, reddish. Spermatheca large, elongate; flagellum of endophallus longer . . . . . *Bembidion petromarinum* **sp. nov.**
- Smaller (TL 3.40–4.45 mm, M 3.85 mm); elytra 1.45 (1.38–1.53) times wider than pronotum. Discal pores of elytra larger, usually pitted; pits often occupying 4th interval on one or both elytra. Elytra brown or dull copper, rarely bluish greenish; legs completely, including trochanters, pale brown or yellowish brown; on antennae (in fully coloured individuals) only 1st antennomere light, the rest partially blackened or darkened. Spermatheca small, short; flagellum of endophallus shorter . . . . . *Bembidion quadriimpressum*

Discussion

The subfamily Trechinae is the only group of ground beetles that has widely colonized littoral habitats along the ocean shores (Maddison & Maruyama 2019). Based on an analysis of seven genes, Maddison and Maruyama showed that the tribe Bembidiini entered the intertidal zone at least six times, with the majority of intertidal taxa being distributed in the Western Pacific. One of these evolutionary events has been the appearance of *Limnaeoperyphus* and the related, highly specialized, littoral *Bembidion* (*Sakagutia*) *umi* Sasakawa, 2007 and *B*. (*Leuchydrium*) *tigrinum* LeConte, 1879, all belonging to the Nearctic Clade of *Ocydromus*-complex (Maddison & Maruyama 2019).

Maddison and Maruyama (2019) proposed that *B*. *umi*, *B*. *quadriimpressum* and *B*. *tigrinum* form a common clade with the Nearctic Clade of *Ocydromus* complex based on phylogenetic analysis. It seems noteworthy that, of these species, *B*. *quadriimpressum* shows only part of the characters that are typical of littoral ground beetles (Maddison & Maruyama 2019): this is a general tendency towards depigmentation of the cuticle (light legs and

epipleurae of the elytra, lightened apices of the elytra, brownish colouration) and quite large both head and prothorax. Other characters specific to littoral Bembidiini (increased number of discal setae, changes in the structure of the apex of the elytra, short and wide middle tarsi) are absent from *B. quadriimpressum*. In terms of lifestyle, *B. quadriimpressum* is also moderately specialized, as it lives mainly in the supra-littoral zone and when, the water rises, it retreats to higher areas of the coast. In addition, it is found not only at the sea coast, but also on shores of lagoonal freshwater lakes located near the sea. In the light of what has been said, it seems quite obvious that, of all these species, *B. quadriimpressum*, has a larger set of plesiomorphic characters than the other two species.

Morphology of the new species and the study of the detailed structure of *Limnaeoperyphus*, both confirm this subgenus as belonging to the *Ocydromus*-complex. With so significantly expanding our knowledge of the morphology of the subgenus, this allows for two possible scenarios for its origins to be put forth.

The first is based on the greater similarity of *B. petromarinum* **sp. nov.** to other *Ocydromus* Clairville, 1806: relatively small head and pronotum, normal pigmentation, proportions of legs and antennae. This new species can be considered as a form similar to the ancestor of *Limnaeoperyphus* or as an example of intermediate adaptations that could have ensured the transition to a littoral lifestyle. It seems noteworthy that *B. petromarinum* **sp. nov.** is unusual in living on high coastal cliffs and shows the ability to avoid flooding during tides and storms. In fact, the only character common to *B. petromarinum* **sp. nov.** and the specialized inhabitants of the littoral zone is a thickened head. The basal position of this species is also supported by the more complex armament of the endophallus, reminiscent of some species of the subgenus *Ocydromus*. Previously, we described *B. ruruy* Makarov et Sundukov, 2014, which lives in the cracks of seaside rocks in the north of Kunashir Island and is close to *B. tetraporum* Bates, 1883, which is widespread across that island (Makarov & Sundukov 2014). This pair of species demonstrates the possibility of a rapid specialization to a petrophilic lifestyle. Thus, the cracks of coastal rocks may have served as a transitional environment for the colonization of the littoral zone, and *B. quadriimpressum*, within the framework of this hypothesis, could be considered as a later and more specialized derivative.

An obvious alternative would be hypothesizing the basal position of *B. quadriimpressum* within *Limnaeoperyphus*. It has no such morphological support, but is attractive due to the ecological rationale for the occurrence of *B. petromarinum* **sp. nov.** During sea transgressions, of which there were at least four in the Pleistocene of the Pacific alone (Pushkar *et al*. 1998; Pushkar & Razzhigaeva 2003), populations of *Limnaeoperyphus* could have been displaced from gently sloping beaches onto coastal cliffs. This could have caused the appearance of a specialized petrophilous species. However, repeated sea transgressions of different scales in the Pleistocene and Holocene would have provoked the evolution of several closely related petrophilous taxa, which is not consistent with our data, since *B. petromarinum* **sp. nov.**, although variable, has failed to form local subspecies.

As a result, we consider the first hypothesis more plausible, but its verification requires the accumulation and study of genetic material. It should be pointed out that Maddison and Maruyama assumed the opposite evolutionary scenario: "The sequential relationship of the Nearctic Clade to three ocean-shore species (*B. umi, B. quadriimpressum*, and *B. tigrinum*; Fig. 9) suggests the possibility that the ancestor of this quartet was intertidal or at least restricted to the ocean shore, and that dispersal from the western Pacific to the eastern Pacific and then inland in North America could have been the route the lineage took in populating North America." (Maddison & Maruyama 2019: 54).

Given the current range of *Limnaeoperyphus*, both hypotheses implicitly imply that species of this subgenus are capable of dispersal over significant distances. Suitable habitats are sometimes separated by large spaces unfavourable for the survival of one or the other specialized species, whereas the small islands of the Lesser Kuril Ridge, where both species live together, are known to have repeatedly been flooded in the Holocene, entirely or mostly, with water as a result of catastrophic tsunamis (Razzhigaeva *et al*. 2011). Since both species are wingless, the possible mechanism of their dispersal deserves special comments.

For wingless rove beetles of the genus *Diaulota* Casey, 1893, the possibility of both settling along the coasts of the northern Pacific and crossing the ocean in a longitudinal direction has recently been shown (Ahn *et al*. 2024). High dispersal opportunities are also indicated by the extensive ranges of wingless littoral beetles representing a number of families: *Lyrosoma* Mannerheim, 1853 (Agyrtidae), *Ochthebius* Leach, 1815 (Hydraenidae), *Aegialites* Mannerheim, 1853 (Salpingidae). For example, in the North Pacific, two species of *Lyrosoma* range from the Korean Peninsula throughout the Japanese Archipelago, the Kuril and Aleutian Islands to Kodiak Island (Schawaller 1998; Yoo *et al*. 2013).

Such habitats of wingless littoral Coleoptera suggest the presence of an effective way of dispersal. The most obvious assumption is dispersal with sea currents. This has been proven for the littoral ground beetle, *Thalassoduvalius masidai* (Nakahama *et al*. 2021) and, therefore, it is also possible for *Limnaeoperyphus*. Transfers of beetles with

water are only possible if the animals are capable of withstanding prolonged immersion. Andersen (1968) showed that different species of *Bembidion* were able to float on the surface of the water for a long time. Temperature is of decisive importance in this case: at 18–20°C, beetles remain alive for 2–10 days, while at 6–8°C, most individuals remained alive for 20 days, and some remained viable for more than 40 days. Similar results were obtained by Decleer (2003) and Kolesnikov *et al*. (2012). In seawater, the survival of coastal ground beetles even at 20°C reaches 26 days, indicating that these species are capable of long-range dispersion up to two thousand km (Ueno *et al*. 2020). Beetles with reduced hind wings have, on average, higher survival rate in water than those with full wings (Maulana 2024).

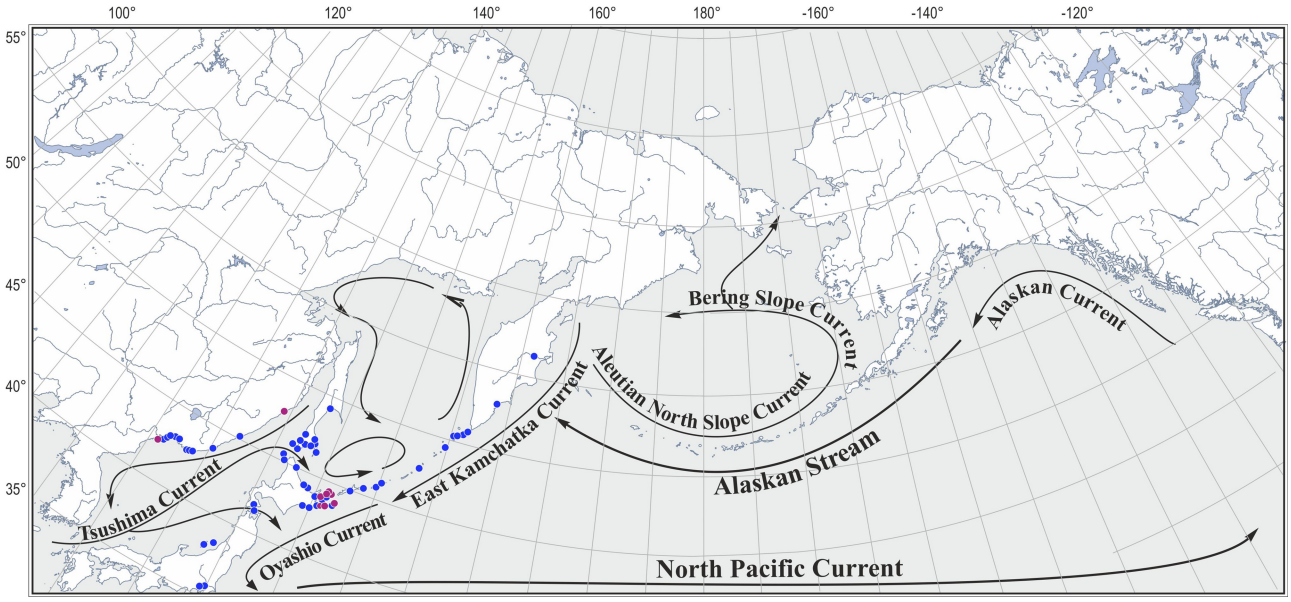


FIGURE 131. Distribution map of *B. quadriimpressum* (blue dots) and *B. petromarinum* **sp. nov.** (purple dots) based on the materials studied and literature data (Jedlička 1965; Lafer & Kuznetsov 1996; Lafer 2002, 2006; Yoshitake *et al*. 2011; Yoshimatsu *et al*. 2018; Maddison & Maruyama 2019; Sundukov & Sergeev 2021; Ohki *et al*. 2022). The scheme of currents of the Northern Pacific is given according to Meyer *et al*. (2016), Sea of Okhotsk according to Dubina *et al*. (2012).

We can assume that the main way of *Limnaeoperyphus* dispersal might have lain in transportation by sea currents, mainly in the cold season. From this consideration, a testable consequence can be drawn: the ranges of wingless littoral beetles in the northern part of the Pacific should be more extensive, and species diversity should be lower than in the south. We do see such a pattern, taking *Diaulota* (Ahn *et al*. 2024), *Bembidion* (*'Cillenus'*) *complex* (Sasakawa 2007; Maddison & Maruyama 2019), *Lyrosoma* (Schawaller 1998; Yoo *et al*. 2013), *Ochthebius 'vandykei'* group (Jach & Delgado 2014) as examples.

As Maddison and Maruyama (2019) showed, morphological features associated with intertidal habitats evolve very rapidly. Structural features associated with a petrophilic lifestyle are also formed in a short time (Makarov & Sundukov 2014). Taken together with the assumption that *Limnaeoperyphus* belongs to the Nearctic clade *Ocydromus*, which is supported both by molecular (Maddison & Maruyama 2019) and our morphological data, this allows us to propose a hypothesis for the origins of this subgenus.

The current system of the Western Pacific in its modern configuration is known to have been formed already in the early Pleistocene (Lam *et al*. 2021), while approximately 1 million years ago, alternating glacial/interglacial cycles were accompanied by an intensification of the North Pacific Gyre (Gallagher *et al*. 2015). Theoretically, one could discuss the possibility of the dispersal of the *Limnaeoperyphus* ancestors in a western direction already at that time. However, the lack of differences between the island populations with significant variability in both species seems to favor their relatively recent formation. We should probably consider options for the penetration of the ancestors of *Limnaeoperyphus* from the Nearctic to the coasts of the northwestern Pacific in the Holocene. According to recent palaeo-reconstructions (Meyer *et al*. 2016), at least after the LGM, the North Pacific was dominated by the Alaskan Stream, which could have transported the coastal petrophilic species of *Bembidion* towards Kamchatka. Repeated regressions of the sea in the Holocene could have led to an area increase in the littoral zone of the Aleutian

Ridge (Baichtal *et al*. 2021; Neplyukhina *et al*. 2021). This could have also contributed to the spread of these ground beetles.

We are unaware of any records of *Limnaeoperyphus* north of 56°30'N, this indicating the impossibility of their existence at low temperatures. This also means that the individuals that arrived to Kamchatka could not have spread north of the Kamchatka Strait, thus excluding their reverse transfer through the Aleutian North Slope Current. For comparison, we point out that the more cryotolerant wingless *Lyrosoma* spp. inhabit most of the islands of the Aleutian Arc. The wide distribution of *Limnaeoperyphus* on the coast of the Sea of Okhotsk seems to be caused by a system of currents (West Kamchatka, North Okhotsk, East Sakhalin) that create a general cyclonic circulation (Dubina *et al*. 2012).

On the contrary, the dispersal of *Limnaeoperyphus* with currents to the south is better to be expected. Thanks to both East Kamchatka Current and Oyashio Current, *Limnaeoperyphus* could have been able to spread south to approximately 38°N (Fig. 131). Further southward expansions are limited as both currents, Oyashio and Kuroshio, leave the coasts into the ocean at approximately 35°N latitude (Gallagher *et al*. 2015), as well as by relatively high temperatures that reduce the survival of beetles in water. The probability of *Limnaeoperyphus* entering the Nearctic in the Holocene with these currents seems low due to the vast distance and high water temperatures.

We consider the above considerations to only be an early hypothesis that needs to be tested and clarified, primarily on the basis of molecular/genetic data.

Acknowledgments

We are grateful to all colleagues who participated in the collection of material or provided material: S.V. Kurbatov, A.V. Matalin, I.V. Melnik, A.A. Zaitsev (all—Moscow). We are grateful to the curators and museum staff, thanks to whose help we were able to study the collection materials: A.A. Gusakov and V.Yu. Savitsky (ZMMU, Moscow), B.M. Kataev (ZISP, St. Petersburg). We wish to thank David Maddison (Corvallis, USA) and Luca Toledano (Verona, Italy) for the critical review and the linguistic revision of the text. Special thanks to S.I. Golovatch for carefully editing an advanced draft.

The research by Yu.N. Sundukov was carried out within the state assignment of the Ministry of Science and Higher Education of the Russian Federation (theme No. 124012400285-7).

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