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DNA-barcode and endophallus morphology delimit congruent species in a systematic revision of the oxyporine rove beetles of Russia (Coleoptera: Staphylinidae: Oxyporinae)

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Abstract

Rigorous species delimitation is a challenge in biology and systematics in particular. In insects, male genitalia traditionally, and the barcoding region of the CO1 gene recently, are the main markers to identify species, even though a standalone use of CO1 for that is often criticized. In our systematic revision of the mycophagous and in other ways peculiar oxyporine rove beetles of Russia, the legacy alpha-taxonomy could not be improved by traditional investigation of genitalia as they are unusually character-poor in this group. Using phylogenetic inference and ancestral state reconstruction, we demonstrate that CO1 and endophallus are useful markers for species delimitation in Oxyporus. We also show that many
morphological traits previously used for species delimitation in Oxyporus are in fact highly variable and thus inconsistent. We hypothesize that in Oxyporus diversification of the endophallic structures is driven by intense intra- and inter-species interactions of multiple individuals co-occurring in narrow spaces inside fungal bodies during mating. Our results encourage broader use of both markers, especially easy-to-generate DNA barcodes, for the desired alpha-taxonomical work in Oxyporinae globally. The revision revealed 10 species of Oxyporus in the fauna of the Russian Federation; eliminated erroneous species records; established two new synonyms, *Oxyporus (Oxyporus) basicornis* Cameron, 1930 = *O. (O.) aequicollis* Bernhauer, 1935, *syn. nov.* = *O. (O.) parvus* Lee et al., 2020, *syn. nov.*; and raised the hypothesis that *O. (O.) aokii* Dvořák, 1956, *O. (O.) basiventris* Jarrige, 1948 and *O. (O.) kobayashi* Hayashi, 2015 are conspecific with *O. (O.) maxillosus* Fabricius, 1793. Lectotypes are designated for *O. (O.) basicornis* Cameron, 1930, *O. (O.) germanus* Sharp, 1889, *O. (O.) niger* Sharp, 1889, and *O. (O.) triangulus* Sharp, 1889. Comprehensive taxonomic treatment and an identification key are provided for all species.

**Keywords**

*Oxyporus* s. str. – *Pseudoxyporus*, Palaeartic – aedeagus – inner sac – taxonomy – new synonyms – CO1

**Introduction**

*Oxyporus* Fabricius, 1775, taken in its broad sense with *Oxyporus* s. str. and *Pseudoxyporus* Nakane and Sawada, 1956 as subgenera, is the only extant genus of Oxyporinae, a rove beetle subfamily that is noteworthy for many reasons. Oxyporinae are a relatively small lineage of at least 110 described, peculiar looking extant species that are confined to Eurasia and the Americas (Herman, 2001; Newton et al. 2001; Löbl & Löbl, 2015 and papers after). The subfamily is strictly mycophagous, tightly associated with fungal fruiting bodies and, due to its largely unique morphological and biological traits that must be quite ancient (Cai et al., 2017), it does not have a clearly established sister group within the family Staphylinidae (Tokareva et al., 2020).

Poor knowledge of the global species diversity of Oxyporus is the first and most important obstacle to the broad scientific study of this genus, a common manifestation of the now so-called “Linnean shortfall” (Possingham et al., 2007). This shortfall is further amplified by the properties of the genus itself. *Oxyporus* are relatively large, mostly colorful and attractive beetles that are active in short-lived, patchily distributed fruiting bodies of fungi. As a result, they are popular among taxonomists but are also rather rarely-collected insects, where large comprehensive series of specimens are available only for some species. As most *Oxyporus* are strikingly colored, taxonomists have tended to focus on differently colored, easy to distinguish singletons, resulting in a number of species described based on color patterns without a detailed consideration of other characters. Makranczy (2012) strongly cautioned against taxonomy based on external characters (mainly coloration) alone, which has led to an alarming overestimation of species diversity in *Oxyporus*, especially in the fauna of the Old World. Following earlier examples (Campbell, 1969; Smetana, 1989; Hwang & Ahn, 2000), Makranczy also stressed the importance of the morphological variation in the complex endophallus, which compensates for the very simple and thus poorly informative shape of the median lobe of the aedeagus in this genus. This structure is promising for species delimitation within
Oxyporus, but it is also known to be notoriously difficult to evert (dissect) for study and is thus under-explored.

Our own attempts to identify species of Oxyporus from Russia, especially from its more diverse Far Eastern fauna using for example a recent review work by Shabalin (2012), raised the same concerns of Makranczy (2012). Several ‘species’ that Shabalin (2012) had recognized in the Russian Far East using the state-of-the-art taxonomic literature for the region, differed from each other almost entirely by coloration alone.

The overall shape of the aedeagus is usually considered as sufficiently diagnostic for species in entomology. Its documentation (outline drawings, later photos) is the mainstream in the taxonomy of beetles, and rove beetles in particular, for many decades. The endophallus also has been noted as a species-specific marker and used for precise identification of pest beetle species long ago (Barber, 1935). A more regular use of the endophallus in beetle taxonomy started to increase after the 1970s (Denis Kassatkin, pers. comm.). In the contemporary literature, endophallic characters are frequently used for species diagnostics and in many cases they are believed to be even more informative in this capacity than the external aedeagal structures (e.g., Petitpierre & Anichtchenko, 2018). However, compared to the external structure of the aedeagus, the endophallus is used much less commonly and much less consistently for species diagnostics because of its hidden position inside the median lobe of the aedeagus. The examination of these hidden structures demands a special technique for their eversion. The above considerations urged us here to thoroughly examine the fully everted endophallus of Oxyporus, to ensure accurate comparison of homologous structures among species.

As a very significant area of the Palaearctic region with diverse geography and climate, Russia has a sizeable Oxyporus fauna that is suitable for exploring species limits. It is a region that includes very widespread and far more locally distributed species of Oxyporus. By reconciling this general exploratory aspect with the practical goal of a regional taxonomic revision, we aim to demonstrate immediate utility of rigorous species-delimitation tools. Naturally, in the revisionary part, we consider material and data from countries adjacent to Russia as well. This material is especially relevant to the Far East, where the fauna of Oxyporus is more diverse.

The Russian fauna of Oxyporus has never been reviewed in its entirety. Current knowledge on Russian Oxyporus began with single records for the widespread species Oxyporus (Oxyporus) maxillosus Fabricius, 1793, O. (O.) mannerheimii Gyllenhal, 1827 and O. (O.) rufus Linnaeus, 1758, which were earlier described from Europe (according to the extensive literature summarized in Herman, 2001). The first species described from Russia was O. (Pseudoxyporus) dybowskii, (Solsky, 1871) from Baikal region, followed by the large and spectacular O. (O.) procerus described by Kraatz (1879) from the Russian Far East. Decades later, Bernhauer (1935) described O. (O.) aequicollis from the Baikal region while Kirschenblatt (1938) described O. (P.) cyanipennis from Altai and O. (P.) melanocephalus from the Russian Far East. The paper by Kirschenblatt (1938) was an important contribution to the knowledge of Russian Oxyporus because, apart from two newly described taxa, it provided a key to all species of the genus known from the Russian Far East at that time. The peculiar eastern species O. (P.) cyanipennis, O. (P.) melanocephalus and O. (P.) dybowskii were redescribed much later by Makranczy (2012). Apart from these notable two papers, Kryzhanovsky et al. (1973), Ryabukhin (1999) and Shavrin and Gildenkov (2009) published new records for various species of Oxyporus in Russia. Only many decades after Kirschenblatt’s
(1938) summary, a new review of, and an identification key to, *Oxyporus* of the Russian Far East was compiled by Shabalin (2012), who reported 14 species of the genus from that region. Shabalin’s key was essentially a key to all Russian *Oxyporus* because only the three eastern species (*O.* (*O.*) *maxillosus*, *O.* (*O.*) *mannerheimii* and *O.* (*O.*) *rufus*) reach western Russia.

While the data on the more complex fauna of the Eastern Russia were accumulating as shown above, there was a gradual accumulation of new distributional and ecological records from Western and Central Russia, for *O.* (*O.*) *maxillosus*, *O.* (*O.*) *mannerheimii* and *O.* (*O.*) *rufus*. Most of these records are scattered in numerous faunistic accounts of particular nature reserves or areas of similar size, and only some cover larger regions. Of the more inclusive faunistic works covering larger regions, those that provide original detailed occurrence data (e.g., Semenov et al., 2015; Semionenkov et al., 2015) are more informative than generalised area records (e.g., Gusarov, 1989; Solodovnikov, 1998).

Overall, the knowledge of Russian *Oxyporus* is patchy and not well connected to regional works on the same species in the adjacent countries of Eurasia. Available diagnoses and keys for *Oxyporus* of Russia are based mainly on rather polymorphic traits, such as body coloration, shape and size and only rarely involve structural external characters. Problems, caused by the use of such characters are particularly pronounced in the species of the nominative subgenus *Oxyporus* s. str. For example, original descriptions and subsequent literature including keys, discriminate *O.* (*O.*) *maxillosus*, *O.* (*O.*) *aokii*, and *O.* (*O.*) *basiventris* from each other based only on the number of pale segments of abdomen. Dealing with a large amount of specimens, transitional, unidentifiable examples were observed, where it is difficult to decide which abdominal segments are pale and which are dark. Such observations give rise to a hypothesis about the conspecificity of these species. Similarly, we suspected the synonymy of *O.* (*O.*) *aequicollis*, *O.* (*O.*) *basicornis*, *O.* (*O.*) *germanus*, and the most recently described South Korean species *O.* (*O.*) *parvus* Lee et al., 2020, which are supposedly distinguished only by the body size, punctuation of elytra and the number of basal abdominal segments with pale paratergites.

The current taxonomy of Russian *Oxyporus* is also a snapshot of how the complexity of a species problem (Queiroz, 2007) and developing species delimitation methods can intersect to create confusion and uncertainty, especially when only limited individuals are available for study within local faunas, a common practical constraint in systematic entomology. For example, recent progress in algorithm-based, repeatable molecular-based species-delimitation brought a rigorous framework, but also new challenges related to the disparity of this newer phylogenetic approach and the older biological species concepts on which the majority of insect species were based (Lukhtanov, 2019). Another challenge of DNA-based species delimitation stems from unequal evolutionary rates and conflicting gene trees between various loci. A number of methods have been suggested to account for these complications (Talavera et al., 2013) and a general consensus has emerged that no single method is entirely sufficient and that robust species limits are best recognized through the congruence of multiple sources of evidence, even if they are few (Pante et al., 2015). Modern integrative revisions in systematic entomology show that single-locus DNA markers including the commonly used mitochondrial CO1 barcode reveal OTUs that are congruent with a plethora of ‘good species’ recognized by traditional taxonomists (Kress et al., 2015). In beetles, these
are mainly species delimited by the shape of male genitalia (Schmidt et al., 2015; Hendrich et al., 2014). In some insects, including many beetles, the species delimitation is complemented by the study of the endophalus (inner sac). Moreover, it looks like simplicity of the external morphology of the aedeagus and complexity of the endophallus are correlated (Roig-Alsina, 1993; Jaloszynski et al., 2015; Petitpierre & Anichtchenko, 2018; Zhou et al., 2019). Presumably, the endophallus in these and possible other cases is the most, or only (e.g., Danilevski & Kasatkin, 2006; Hayashi & Yoshitomi, 2015) reliable morphological character for delimitation of closely related species. For example, the melyrid beetle species of the genus *Laius* occurring in sympatry exhibit greater differences in body size and sclerites of the endophallus than allopatric species (Yoshitomi, 2014), suggesting that these morphological features maintain species boundaries. In traditionally better-studied taxa like Carabidae, with generally simple external structures of the aedeagus, routine use of the endophallic characters in species diagnoses, even for amber fossils (Schmidt et al., 2016; Schmidt & Michalik, 2017) is becoming a common practice. However, since the various endophallic structures may evolve, also independently, in response to complex interactions between a male and a female or between males through intraspecific competition (e.g., Schmitt & Uhl, 2015; Jaloszynski et al., 2015; Matsumura et al., 2017; Dougherty et al., 2017; Kyogoku & Sota, 2015) they may vary in their value as species-specific markers. Interestingly, Kataev (1996) reported very notable parallel intraspecific aberrations in the endophallic sclerites of some Carabidae.

Complexity of insect genitalia and their use for species delimitation aligns well with the classical evolutionary view of genitalic differences among species acting as isolating mechanisms i.e., the lock and key hypothesis. A closer look at the subject (Eberhard, 1985), however, revealed more diverse factors underlying the evolution of genitalia and led to the reconsideration or even complete rejection of the lock and key hypothesis (Eberhard, 1985; Shapiro & Porter, 1989). Currently, sexually antagonistic coevolution and especially cryptic female choice (Eberhard, 2009) are considered major drivers of morphological evolution in genitalia, though these processes are not so directly associated with speciation. These advancements in evolutionary biology suggest that some structures of the genitalia, just as any other traits, may be more or less variable within and between species and thus perform better or worse as a marker for species delimitation. In this respect, *Oxyporus* is again noteworthy. Its obligate fungivory apparently determines complex mating biology because beetles of both sexes, of the same and different species, are often aggregated within the short-living fruiting bodies of mushrooms. For example, Tokareva et al. (2020) observed large gatherings of *Oxyporus maxillosus* (up to 40 specimens) in the fruiting bodies of *Laetiporus sulphureus* fungus, which they probably used for feeding and mating. After mating, females must move to other fungi to lay eggs as the fungal hosts are so short-lived. We also often observed that several specimens of *Oxyporus* of more than a single species can be found in one, even relatively small fungus. It was as early as in Heeger’s (1853) paper that an observation of *Oxyporus* males subsequently mating with several females has been published. These observations suggest complex intra- and possibly interspecific sexual interactions in this genus, which may be functionally related to morphology of the male genitalia. As noted before (Makranczy, 2012) and can be seen from the survey of hitherto described species, *Oxyporus* (especially s. str.) have a very simple median lobe but complex, eversible endophallus.
All these aspects motivated our paper, which aims to find reliable characters for robust species delimitation in *Oxyporus* in the course of a thorough taxonomic revision of this genus within the limits of the Russian fauna. For species delimitation we explored three character systems: 1) external morphology, including traditionally used characters of body coloration, 2) morphology of the aedeagus and 3) DNA-barcoding. Our approach is inspired by the growing amount of evidence (Pante et al., 2015) that seeking congruence from multiple and alternative lines of evidence is the most robust way to capture the border between closely related species. For the aedeagi, we consistently explore their overall shape (shape of the phallobase, median lobe and parameres) and, as a separate character set, the shape and armature of their endophallus (also called inner sac).

Material and methods

**Specimen collecting and deposition**

This paper is based on specimens from the collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZISP); Federal Scientific Center of the East Asia Terrestrial Biodiversity, Russian Academy of Sciences, Vladivostok (FEB RAS); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (CNC); Museum of Natural History, Prague (MNP); Natural History Museum, London (NHM); Natural History Museum of Denmark, Copenhagen (NHMD), and personal collections of Michael Schülke (cSch) and Kirill V. Makarov (cMk).

Some of the specimens were fresh material recently collected by AT and AS in the Czech Republic and in various regions of Russia. These specimens were collected either by the standard method of sifting leaf-litter with mushrooms, or by a specialized “plastic-bag” method. Each fungal fruiting body with round holes on the hymenophore, typical for *Oxyporus* presence, was picked up in a fast manner by hand covered with two plastic bags, one over another. Then, if *Oxyporus* specimen(s) were present, the pair of bags was everted around the fungus and tied on the top, with the air left inside to let the beetle(s) breathe and prevent early deterioration and destruction of the fungus. A field label for the sample collected was placed between the two plastic bags walls. The samples were processed not later than in three or four hours after being collected.

**Specimen recording, georeferencing, and mapping**

For the type specimens, labels are provided verbatim, separated by backslash; Cyrillic labels are transliterated. For non-type specimens labels are interpreted and translated to English; only in ambiguous cases they are given verbatim. The majority of the examined specimens did not have geographic coordinates on their labels. Using all possible resources we found coordinates for most of the localities and added them in square brackets in the ‘Material examined’ data. We used these coordinates for our distribution maps made with SimpleMappr (Shorthouse, 2010).

**Lectotype designations**

In the interests of the stability of the zoological nomenclature, we have designated lectotypes for species with multiple syntypes that included at least one male. Our respective lectotype and paralectotype labels are added to the specimens.

**Specimen sampling for DNA-barcoding**

To test the morphospecies hypotheses by DNA-barcoding, COI barcodes were assembled for 97 specimens of *Oxyporus*. Of them, 45 specimens were 96% ethanol-preserved
Oxyporus collected by AT and AS in the Czech Republic and in Russia (table 1). Barcodes for other 30 specimens were taken from the recently published paper on Korean Oxyporus (Lee et al., 2020). A single CO1 sequence of O. (O.) maxillosus used by Lee et al. (2020) in their analysis, when checked by us via the BLASTn algorithm, turned out to have 100% similarity with the barcode of Microcara testacea Linnaeus, 1767 (Scirtidae) and thus is not included in our research. Six additional specimens from the CNC were sequenced separately (see below) and uploaded to BOLD Systems (table 1). Finally, barcodes for yet another 17 specimens were taken from online databases, namely BOLD Systems (https://v3.boldsystems.org/index.php/TaxBrowser_Home) and GenBank NCBI (https://www.ncbi.nlm.nih.gov/nucleotide/). The sampling largely covers the morphological diversity of the genus across the entire territory of Russia and adjacent areas. Barcodes for out-group taxa Lordithon fungicola Campbell, 1982 (Tachyporinae), Philonthus tenuicornis Mulsant & Rey, 1853, and Ontholestes murinus Linnaeus, 1758 (Staphylininae) were taken from BOLD Systems.

**DNA extraction, PCR amplification, sequencing, and alignment**

Total DNA was extracted from beetle legs using the Qiagen DNeasy Blood & Tissue Kit with the standard protocol (https://www.qiagen.com/us/resources). Samples were incubated at 56°C in 180 μl of ATL buffer with 20 μl of proteinase K added afterwards for about 24 h. PCR was performed using Evrogen kit for Master Mix (https://evrogen.ru/products/PCR-kits/PCR-kits-polymerasers/): 0.1 μl Taq polymerase in a 25 μl reaction mixture containing 1 μl of each primer, 2 μl dNTPs, 2.5 μl of Taq Buffer and 2 μl of genomic DNA template. The primer pair LCO1490 (5’–GGTCAACAAATCATAAAGATATTGG–3’) and HCO2198 (5’–TAAACTTCAGGGTGA-CAAAAAATCA–3’) was used to amplify a 658 bp fragment of the CO1 gene (Folmer et al., 1994). The thermal cycling program consisted of 35 cycles of 94°C for 30 sec, 42°C for 30 sec and 72°C for 45 sec, followed by a final extension at 72°C for 10 min. Paired forward and reverse reads were assembled and edited in Geneious (v. 9.1). Amplified fragments were sent for sequencing to the “Molecular and Cell Technologies” resource center (St. Petersburg State University) or to Evrogen Inc. (Moscow). Additional specimens were sent to the Biodiversity Institute of Ontario (BIO) (Guelph, Ontario, Canada) for extraction, amplification and sequencing.

Assembled sequences were checked via BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to verify their identity and were aligned with CO1 fragments of Oxyporus (Oxyporus) rufus and O. (O.) maxillosus from NCBI. Sequences were aligned in Geneious 9.1 using MAFFT v. 7.450 (Katoh and Standley, 2013) under the most rigorous L-INS-i strategy (see alignment in supplementary material S3). The sequences were uploaded to Genbank (https://www.ncbi.nlm.nih.gov/genbank/). The accession numbers for all species used in our analysis are given in table 1.

**Microscopy and illustrations**

All photos of beetles were taken using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon D7000 digital SLR camera. Photos of genitalia were taken either using a Leica M205C stereomicroscope equipped with a Canon EFS 6D camera (images stacked with Zerene Stacker 1.04 (Zerene Systems, Richland, WA, USA) or using a Leica M205C stereomicroscope equipped with a Leica DFC495 camera (images stacked with Helicon Focus 6.2.2). Drawings of genitalia structures were made with a Leica DM 2500 microscope equipped with a camera lucida. All illustrations were
| Species                | Locality                          | Museum_specimen_ID | Sequence_ID | Source                                                                 |
|------------------------|-----------------------------------|--------------------|-------------|------------------------------------------------------------------------|
| Philonthus tenuicornis | Germany                           | ZFMK-TIS-2535717   | KU918645    | Rulik et al., 2017                                                     |
| Lordithon fungicola    | Canada                            | MTCOL-0007         | HM432926    | [https://www.ncbi.nlm.nih.gov/nuccore/HM432926.1](https://www.ncbi.nlm.nih.gov/nuccore/HM432926.1) |
| Ontholestes murinus    | Germany                           | BC ZSM COL 02284   | JF889840    | [https://www.ncbi.nlm.nih.gov/nuccore/JF889840.1](https://www.ncbi.nlm.nih.gov/nuccore/JF889840.1) |
| Oxyporus (Oxyporus) basicornis | Russia: Primorsky Territory, Posiet peninsula | ZISP INS_COL_0005310 | MW082052    | original                                                              |
| Oxyporus (Oxyporus) basicornis | Russia: Primorsky Territory, Posiet peninsula | ZISP INS_COL_0005311 | MW082053    | original                                                              |
| Oxyporus (Oxyporus) basicornis | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs | ZISP INS_COL_0005312 | MW082054    | original                                                              |
| Oxyporus (Oxyporus) basicornis | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs | ZISP INS_COL_0005313 | MW082055    | original                                                              |
| Oxyporus (Oxyporus) basicornis | Russia: Primorsky Territory, Gornotaezhnoe | ZISP INS_COL_0005314 | MW082056    | original                                                              |
| Oxyporus (Oxyporus) basicornis | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs | ZISP INS_COL_0005315 | MW082057    | original                                                              |
| Oxyporus (Oxyporus) basicornis | Russia: Republic of Buryatia, Priibaikalsky District, Selenga river valley, Diky Byk cape | ZISP INS_COL_0005316 | MW082058    | original                                                              |
| Species               | Locality                                   | Museum_specimen_ID          | Sequence_ID | Source         |
|----------------------|--------------------------------------------|-----------------------------|-------------|----------------|
| *Oxyporus* (Oxyporus) basicornis | Russia: Primorsky Territory, Gornotaeznoe | ZISP INS.COL.0005317        | MW082059    | original       |
| *Oxyporus* (Oxyporus) basicornis | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs | ZISP INS.COL.0005318        | MW082060    | original       |
| *Oxyporus* (Oxyporus) basicornis | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs | ZISP INS.COL.0005319        | MW082061    | original       |
| *Oxyporus* (Oxyporus) germanus | Russia: Primorsky Territory, South of Anisimovka village  | ZISP INS.COL.0005304        | MW082046    | original       |
| *Oxyporus* (Oxyporus) germanus | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs | ZISP INS.COL.0005305        | MW082047    | original       |
| *Oxyporus* (Oxyporus) germanus | Russia: Primorsky Territory, South of Anisimovka village | ZISP INS.COL.0005306        | MW082048    | original       |
| *Oxyporus* (Oxyporus) germanus | Korea, Gangwon, Jeongseon                   | -                           | MT180875    | Lee et al., 2020 |
| *Oxyporus* (Oxyporus) germanus | Korea, Gangwon, Pyeongchang                | -                           | MT180876    | Lee et al., 2020 |
| *Oxyporus* (Oxyporus) germanus | Korea, Gangwon, Pyeongchang                | -                           | MT180877    | Lee et al., 2020 |
| *Oxyporus* (Oxyporus) germanus | Korea, Gangwon, Pyeongchang                | -                           | MT180878    | Lee et al., 2020 |
| *Oxyporus* (Oxyporus) germanus | Korea, Gangwon, Pyeongchang                | -                           | MT180879    | Lee et al., 2020 |
| *Oxyporus* (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang                | -                           | MT180880    | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180881 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180882 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180883 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180884 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180885 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180886 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Pyeongchang | - | MT180887 | Lee et al., 2020 |
| Oxyporus (Oxyporus) japonicus | Korea, Gangwon, Inje | - | MT180889 | Lee et al., 2020 |
| Oxyporus (Oxyporus) mannerheimii | Russia: Leningrad Region, near Tolmachevo | ZISP INS_COL_0005301 | MW082043 | original |
| Oxyporus (Oxyporus) mannerheimii | Russia: Sverdlovsk District, Visimsky nature preserve | ZISP INS_COL_0005302 | MW082044 | original |
| Oxyporus (Oxyporus) mannerheimii | Russia: Primorsky Territory, South of Anisimovka village | ZISP INS_COL_0005303 | MW082045 | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Republic of Altay, Ust-Kanskij Distr., Kuma river | ZISP INS_COL_0005323 | MW082065 | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Khanty-Mansi Autonomous Area, Malaya Sosva natural preserve | ZISP INS_COL_0005324 | MW082066 | original |
| Species                  | Locality                                                                 | Museum_specimen_ID   | Sequence_ID | Source   |
|-------------------------|--------------------------------------------------------------------------|----------------------|-------------|----------|
| Oxyporus (Oxyporus) maxillosus | Russia: Republic of Altay, Chemalskij Distr., South-East of village Edigan | ZISP INS_COL_0005325 | MW082067    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Rep. of Buryatia, Pribaikalsky District, Selenga river valley, Diky Byk cape | ZISP INS_COL_0005326 | MW082068    | original |
| Oxyporus (Oxyporus) maxillosus | Czech Republic: Moravia, ca. 1 km south from Čížov, Podyjí National Park | ZISP INS_COL_0005327 | MW082069    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Khanty-Mansi Autonomous Area, Malaya Sosva natural preserve | ZISP INS_COL_0005328 | MW082070    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Sverdlovsk District, Visimsky nature preserve | ZISP INS_COL_0005329 | MW082071    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Gornotaezhnoe | ZISP INS_COL_0005330 | MW082072    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Gornotaezhnoe | ZISP INS_COL_0005331 | MW082073    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, South of Anisimovka village | ZISP INS_COL_0005332 | MW082074    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Gornotaezhnoe | ZISP INS_COL_0005333 | MW082075    | original |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Gornotaezhnoe | ZISP INS_COL_0005334 | MW082076    | original |
| Species          | Location                                                                 | Database Code          | Image Code |
|------------------|---------------------------------------------------------------------------|------------------------|------------|
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, South of Anisimovka village                   | ZISP INS_COL_000535    | MW082077   |
|                  |                                                                          |                        | original   |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs       | ZISP INS_COL_000536    | MW082078   |
|                  |                                                                          |                        | original   |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Pogranichny area, Pogranichny suburbs       | ZISP INS_COL_000537    | MW082079   |
|                  |                                                                          |                        | original   |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, near Lazo                                    | AJB0001438             | CNCAJB19-172 |
|                  |                                                                          |                        | BOLD:ACR8154 |
| Oxyporus (Oxyporus) maxillosus | Russia: Kunashir Island, Calder of Golovnin Valcon, env. Ozerny post     | AJB0001439             | CNCAJB19-173 |
|                  |                                                                          |                        | BOLD:ACR8154 |
| Oxyporus (Oxyporus) maxillosus | Russia: Kunashir Island, hills S from Stollchaty Cape                    | AJB0001440             | CNCAJB19-174 |
|                  |                                                                          |                        | BOLD:ACR8154 |
| Oxyporus (Oxyporus) maxillosus | Russia: Irkutsk, River Kunerma, 15 km WSW Kunerma                        | AJB0001441             | CNCAJB19-175 |
|                  |                                                                          |                        | BOLD:ACR8154 |
| Oxyporus (Oxyporus) maxillosus | Japan: Honshu, Iwate pref., Kawai, Yoshibezawa                           | CNC1151252             | CNCAJB19-176 |
|                  |                                                                          |                        | BOLD:ACR8154 |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Gornotaeznoe                                | NHMD620703             | MN508942   |
|                  |                                                                          |                        | Tokareva et al., 2020 |
| Oxyporus (Oxyporus) maxillosus | Russia: Primorsky Territory, Gornotaeznoe                                | NHMD620702             | MN508943   |
|                  |                                                                          |                        | Tokareva et al., 2020 |
| Oxyporus (Oxyporus) niger       | Russia: Primorsky Territory, South of Anisimovka village                 | ZISP INS_COL_0005420   | MW082062   |
|                  |                                                                          |                        | original   |
| Oxyporus (Oxyporus) niger       | Russia: Primorsky Territory, South of Anisimovka village                 | ZISP INS_COL_0005421   | MW082063   |
|                  |                                                                          |                        | original   |
| Species               | Locality                                      | Museum_specimen_ID     | Sequence_ID  | Source       |
|----------------------|-----------------------------------------------|------------------------|--------------|--------------|
| *Oxyporus (Oxyporus) niger* | Russia: Sakhalin District, Sakhalin Island, Listvennichnoe river upper stream | ZISP INS_COL_0005322 | MW082064     | original     |
| *Oxyporus (Oxyporus) niger* | Korea, Gangwon, Pyeongchang                   | -                      | MT180890     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) niger* | Korea, Gyeonggi, Paju                          | -                      | MT180891     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) niger* | Korea, Gyeonggi, Paju                          | -                      | MT180892     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) niger* | Korea, Gangwon, Wonju                          | -                      | MT180893     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) niger* | Korea, Gangwon, Pyeongchang                   | -                      | MT180894     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Pyeongchang                   | -                      | MT180895     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Pyeongchang                   | -                      | MT180896     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Pyeongchang                   | -                      | MT180897     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Pyeongchang                   | -                      | MT180898     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Pyeongchang                   | -                      | MT180899     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Yangyang                     | -                      | MT180900     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) parvus* | Korea, Gangwon, Pyeongchang                   | -                      | MT180901     | Lee et al., 2020 |
| *Oxyporus (Oxyporus) procerus* | Russia: Primorsky Territory, Gornotaezhnoe     | NHMD620700             | MN508940     | Tokareva et al., 2020 |
Oxyporus (Oxyporus) procerus  
Russia: Primorsky Territory, Gornotaezhnoe  
NHMD620701 MN508941 Tokareva et al., 2020

Oxyporus (Oxyporus) procerus  
Korea, Gangwon, Pyeongchang  
-  
MT180902 Lee et al., 2020

Oxyporus (Oxyporus) rufus  
Russia: Belgorod Region, Borisovka District, “Belogorye” Nature Preserve  
ZISP INS_COL_0005307 MW082049 original

Oxyporus (Oxyporus) rufus  
Russia: Primorsky Territory, Gornotaezhnoe  
ZISP INS_COL_0005308 MW082050 original

Oxyporus (Oxyporus) rufus  
Russia: Leningrad Region, Peterhof  
ZISP INS_COL_0005309 MW082051 original

Oxyporus (Oxyporus) rufus  
Finland  
ZMUO<FIN>:006011 KJ965221 Pentisaari et al., 2014

Oxyporus (Oxyporus) rufus  
Finland  
ZMUO<FIN>:001322 KJ965277 Pentisaari et al., 2014

Oxyporus (Oxyporus) rufus  
Finland  
ZMUO<FIN>:006012 KJ964395 Pentisaari et al., 2014

Oxyporus (Oxyporus) rufus  
Finland  
ZMUO<FIN>:006011 KJ965221 Pentisaari et al., 2014

Oxyporus (Oxyporus) rufus  
Finland  
ZMUO<FIN>:001322 KJ966577 Pentisaari et al., 2014

Oxyporus (Oxyporus) rufus  
Germany  
ZFMK-TIS-10675 KU906276 Rulik et al., 2017

Oxyporus (Oxyporus) rufus  
Germany  
ZFMK-TIS-8230 KU915441 Rulik et al., 2017

Oxyporus (Pseudoxyporus) dybowskii  
Russia: Republic of Altay, Chemalskij Dist., South-East of village Edigan  
ZISP INS_COL_0005338 MW082080 original

Oxyporus (Pseudoxyporus) dybowskii  
Korea, Gangwon, Pyeongchang  
-  
MT180873 Lee et al., 2020

Oxyporus (Pseudoxyporus) melanocephalus  
Russia: Sakhalin District, Sakhalin Island, Listvennichnoe river upper stream  
ZISP INS_COL_0005339 MW082081 original

Oxyporus (Pseudoxyporus) melanocephalus  
Russia: Primorsky Territory, Gornotaezhnoe  
NHMD620699 MN508938 Tokareva et al., 2020
| Species                        | Locality                                      | Museum_specimen_ID | Sequence_ID  | Source                  |
|-------------------------------|-----------------------------------------------|--------------------|--------------|-------------------------|
| Oxyporus (Pseudoxyporus)      |                                               |                    |              |                         |
| melanocephalus                | Russia: Primorsky Territory,                  | NHMD6209698        | MN508939     | Tokareva et al., 2020   |
|                               | Gornotaezhnoe                                 |                    |              |                         |
| Oxyporus (Pseudoxyporus)      |                                               | -                  | MT180874     | Lee et al., 2020        |
| melanocephalus                | Korea, Gangwon, Pyeongchang                  |                    |              |                         |
| cyanipennis                   | Russia: Primorsky Territory,                  | AJB0001446         | CNCAJB19-186 | BOLD:AEC5738            |
|                               | near Anisimovka village                      |                    |              |                         |
| occipitalis                   | Canada                                        | BIOUG03105-B05     | KM844801     | Hebert et al., 2016     |
|                               |                                               | BIOUG03601-G06     | KM842302     | Hebert et al., 2016     |
|                               | Canada                                        | BIOUG05929-B05     | KM850520     | Hebert et al., 2016     |
|                               | Canada                                        | BIOUG06159-A02     | KM844575     | Hebert et al., 2016     |
|                               | Canada                                        | BIOUG03888-B04     | KM843321     | Hebert et al., 2016     |
|                               | USA                                           | UAM:Ento15598      | KU875723     | Sikes et al., 2017      |
|                               | USA                                           | UAM:Ento15599      | KU875724.1   | Sikes et al., 2017      |
| occipitalis                   | USA                                           | UAM:Ento15599      | KU875724     | Sikes et al., 2017      |
|                               | USA                                           | BIOUG06159-A01     | KM850956     | Hebert et al., 2016     |
| occipitalis                   | USA                                           | BIOUG06159-A02     | KM844575     | Hebert et al., 2016     |
| occipitalis                   | Canada                                        |                    |              |                         |
Endophallus preparation and terminology

For the preparation of the everted endophallus in relatively small beetles such as *Oxyporus*, we developed an osmotic technique based on the suggestions of E.A. Khachikov (Department of Zoology, Southern Federal University, Rostov-on-Don).

To evert a beetle endophallus with our technique, one needs high concentration acetic acid (above 90%), 10% KOH solution, electric hot plate, small ceramic jars as ones used for chemicals, and warm (40–60°C) clean water. The step-by-step procedure is as follows:

1. Place the ethanol-preserved or dry (removed from an insect pin) beetle specimen into a Petri dish with warm water. When the intersegmental membranes become soft enough, detach the tip of the abdomen (terminalia) starting with segment VII or VIII.

2. Place a hot plate set to medium heat under a ventilation hood.

3. Under ventilation, drop 5–15 mL of acetic acid in an empty ceramic jar. The depth of the liquid in the jar should be approximately 8 mm. Place the terminalia inside the jar.

4. Heat the jar on the hot plate but avoid boiling the acetic acid by moving the jar off the plate for five to eight seconds whenever boiling occurs, or adjust the heat. If acid becomes nearly evaporated, remove the jar from the hot plate and pour more acid along the jar wall, distant from the sample. On average, the heating step takes from three to eight minutes. Its duration largely depends on the condition and size of the specimen. To check if the terminalia are ready for the next step, place them in a drop of acetic acid on a slide and try to carefully compress the basal bulb of the aedeagus under a stereomicroscope. Sometimes the endophallus everts at this stage, usually in fresh, ethanol-preserved material. The specimen is ready for the next step if small (often sparkling) air bubbles are observed inside the aedeagus.

5. Remove surrounding tissue from the aedeagus and return to the jar with acetic acid for an additional 15–20 seconds.

6. Transfer the aedeagus to the jar with 10% KOH solution prepared in advance and place on medium heat, under ventilation. Avoid boiling as above. On average, this step takes 6–20 minutes. Its duration depends on the degree of maceration of tissues inside the aedeagus. Sometimes, the endophallus spontaneously everts at this step.

7. Transfer the aedeagus to a Petri dish with warm distilled water. If the inner sac has not everted spontaneously in two minutes, gently press the basal bulb with blunt forceps and then with another pair of blunt forceps, keep pushing the dorsal membrane of the median lobe. The endophallus should evert easily if the osmotic pressure is high enough and the maceration in KOH solution was long enough.

The aedeagus with the everted endophallus should be kept in warm water to dilute all the active chemical agents. Unfortunately, the fully everted endophallus does not stay like that for a long time, and one should take a photo as soon as possible, preferably the same day as it was everted. In most cases the membranous sac shrivels down in glycerin, but can be straightened out again by washing in water and heating in KOH solution for a few minutes. We did not find a better solution than to store aedeagi with the everted endophallus in...
a microvial with glycerin, pinned under the respective specimen.

Our terminology of the endophallic structures is purely descriptive, without any assumptions about possible homology to similar structures observed in other Staphylinidae or beetles in general. It is based on relative positions of the structures and presented in the scheme of the *Oxyporus* s. str. endophallus in fig. 2A–C. Terminology of the main parts of the aedeagus follows Blackwelder (1936).

**Morphological character matrix**

To test the robustness of the DNA barcode-based trees, we conducted a total-evidence analysis with a morphological partition (for details see 2.7) and explored the reliability of particular morphological traits as species-specific characters (for details see 2.8). The set of specimens coded in the morphological matrix is the same as for the DNA extraction, except for sequences provided by Lee et al. (2020) and those downloaded from NCBI. Moreover, there are no specimens included in the matrix without having a barcode. Thus, polymorphic traits which were demonstrated by some DNA-barcoded specimens are included into the matrix as well. The set of characters describing male genitalia is extrapolated to female specimens assuming that if being males, they would had the same characters as males of the same species. All the specimens included into the species tree reconstructions are listed in the table 1 with the museum individual numbers and NCBI accession numbers provided. The morphological matrix includes characters of external morphology (1–9), of which 1–6 were suggested by Nakane and Sawada (1956) for subgenera delimitation; non-endophallic aedeagal characters (10–22); endophallic characters (15–22); and characters of body coloration (23–30), which were traditionally used in species delimitation in *Oxyporus*. The entire list of character is as follows:

1. **Labrum:** (0) divided by membranous median line (Nakane & Sawada, 1956, p. 68); (1) uninterrupted (Hwang & Ahn, 2000; fig. 2, C); (2) fully divided (https://www.zin.ru/animalia/coleoptera/rus/ontmurkm.htm).

2. **Mentum:** (0) with lateral membranous lobes (Nakane & Sawada, 1956; fig. 6); (1) entirely sclerotized (Nakane & Sawada, 1956; fig. 7).

3. **Antenna, length:** (0) distinctly shorter than head (fig. 3A, B); (1) as long as/longer than head (fig. 4B, C).

4. **Antenna, shape:** (0) medial segments wider than long (Hwang & Ahn, 2000; fig. 2, B); (1) medial segments as long as or longer than wide (Hwang & Ahn, 2000; fig. 2A).

5. **Pronotal transverse elevation:** (0) absent (fig. 3D); (1) present (fig. 3B).

6. **Pronotal posterior angles:** (0) indistinct (figs. 3C, D); (1) distinctly elevated (figs 4E, 17B, C).

7. **Mesepisternum-epimeron surface:** (0) smooth; (1) shagreened and thus dull; (2) punctured; (3) hirsute.

8. **Pleural suture of mesopleuron:** (0) well-developed, distinct; (1) faint.

9. **Elytra:** (0) regularly punctured (Makranczy, 2012; fig. 4); (1) punctures around two longitudinal depressions (fig. 3F); (2) punctures in two longitudinal rows (fig. 3D).

10. **Paramere, length:** (0) distinctly shorter than half of median lobe (Nakane & Sawada, 1956; figs 1–7); (1) as long as/longer than half of median lobe (Nakane & Sawada, 1956; figs 1–5).

11. **Basal bulb:** (0) fully sclerotized; (1) partially sclerotized.
Systematic revision of oxyporine rove beetles in Russia

Figure 1 CO1-based molecular phylogeny of Oxyporus from Russia and adjacent lands. BI 50% consensus tree on the left and ML tree on the right. Node numbers correspond to species as shown in the trees and used in the text. Each node is documented with posterior probability (BI tree) or bootstrap support (ML tree).
12. Median lobe, shape: (0) cylindrical (figs 15D, 16B, D); (1) dorsoventrally flattened (figs 13B, 16B).
13. Median lobe, dorsal side: (0) membranous (fig. 9D); (1) sclerotized (fig. 15D).
14. Median lobe, apex: (0) flat (figs 9B, 11D); (1) round (fig. 15D); (2) with single-pointed apex (fig. 15D); (3) with two-pointed apex (fig. 14B); (4) truncate (fig. 16B, D).
15. Endophallus, dorsal distal lobe: (0) absent (Khachikov, 2015; figs 5, 6); (1) transverse, twin-coned, spherical (fig. 13B); (2) narrow, vermiform (fig. 16B, D).
16. Endophallus, dorsal distal lobe subdivision: (0) not subdivided (fig. 16B, D); (1) subdivided by longitudinal line (figs 9A, D, 11A, D, 13B–E); (2) subdivided by transverse line (fig. 15D).
17. Endophallus, direction of apical distal lobe: (0) ventrally curved (figs 14D, 16B, D); (1) dorsally curved (figs 9A, D, 11A, D, 14B, 15D).
18. Endophallus, surface of apical distal lobe: (0) membranous, granulate (figs 14B, D, 16D); (1) sclerotized, not granulate (fig. 13B–E); (2) both types of surface (fig. 16B).

**Figure 2** Everted endophallus of the *Oxyporus* s. str. General scheme based on *O. procerus*. A – lateral view; B – ventral view of apical part; C – dorsal view of basal part.
Figure 3  Oxyporus of Russia. Habitus. A – male and female of O. (O.) maxillosus; B – male and female of O. (O.) niger; C – male and female of O. (O.) mannerheimii; D – male and female of O. (O.) rufus; E – male of O. (O.) aequicollis (new synonym of O. (O.) basicornis); F – female of O. (O.) basicornis; G – female of O. (O.) germanus. Scale bar: 1 mm.
Figure 4 Oxyporus of Russia. Habitus. A – male and female of O. (O.) triangulus; B – male and female of O. (P.) cyanipennis; C – male and female of O. (P.) melanocephalus; D – male and female of O. (O.) procerus; E – male of O. (P.) dybowskii. Scale bar: 1 mm.
Phylogeny of *Oxyporus* from Russia and adjacent lands. Total evidence BI tree with morphological characters plotted under ACCTRAN optimization. Node numbers correspond to species as shown in the tree and used in the text.

FIGURE 5
Figure 6. Ancestral states reconstruction under Mk1 model for three characters of general external morphology: labrum structure (1), mesepisternum-epimeron surface (7), and pleural suture of mesopleuron (8). Pie charts represent the likelihood indices for each node. Character numbers as in section 2.6 of the paper.
**Figure 7** Ancestral states reconstruction under Mk1 model for three characters of endophallus morphology: dorsal distal lobe (15), lower spicula of the apical sclerites (20), ligament sclerite of the apical sclerites (22). Pie charts represent the likelihood indices for each node. Character numbers as in section 2.6 of the paper.
19. Endophallic apical sclerites, dorsal and ventral spicula: (0) not connected with each other along length (figs 11B, 14B); (1) at least partially connected with each other along length (figs 9D, 14D).

20. Endophallic apical sclerites, lower spicula: (0) widened at apex, lamellate (figs 9D, 14D); (1) gradually tapering towards apex (fig. 14D).

21. Endophallic apical sclerites, additional spicula: (0) present (figs 9B, 11B); (1) absent (figs 14B, 15B).

22. Endophallic apical sclerites, ligament sclerite: (0) indistinct (figs 9B, D, 14D); (1) well sclerotized (figs 11D, 14B).

23. Head, color: (0) dark brown to black (fig. 3A–G); (1) yellowish or reddish to dark red (fig. 4D); (2) bicolored (fig. 4B).

24. Pronotum, color: (0) dark brown to black (figs 3A–C, E–G, 4A); (1) reddish to dark red (figs. 3D, 4B–E); (2) bicolored (http://v3.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxid=517910).

25. Elytra, color: (0) evenly colored (fig. 4B, C); (1) bicolored (figs 3A, D–G, 4B, C); (2) tricolored (fig. 4E).

26. Elytra, black and yellow color pattern: (0) absent (fig. 4B, C); (1) black with yellow spot forming trapezoidal pattern, elytral suture black (fig. 3A); (2) black with yellow spot forming trapezoidal pattern, elytral suture yellow (https://www.zin.ru/animalia/coleoptera/rus/oxymaxms.htm); (3) black with yellow spot forming T-shape pattern, elytral suture with wide black line (fig. 1); (4) yellow with black spots on lateral sides of elytra, elytral suture with wide black line (fig. 3E–G).

27. Abdomen coloration, tergite and sternite vi: (0) dark brown to black (figs 3A–C, 4A, C, D); (1) pale yellow to dark red (fig. 4B).

28. Abdomen coloration, tergite and sternite v: (0) dark brown to black (figs 3A–C, 4A, C, D); (1) pale yellow to dark red (fig. 4B).

29. Abdomen coloration, tergite and sternite vii: (0) dark brown to black (figs 3A–C, 4A, C, D); (1) pale yellow to dark red (fig. 4B); (2) with black median areas (figs 3D, 4E).

30. Abdomen coloration, paratergites: (0) same color with tergites and sternites (figs 3A–D, 4A–E); (1) black abdomen with paratergites of abdominal segments iii-v yellow (fig. 3E, F); (2) black abdomen with paratergites of abdominal segments iii-vi yellow (fig. 3G).

The morphological matrix is available as supplementary material S1.

**BI and ML analyses, genetic distances**

Taxonomic hypotheses of species were tested with three types of analysis: Bayesian Inference (BI) and Maximum Likelihood (ML) analyses of the molecular barcodes only and then the total evidence BI analysis of the barcode data combined with the morphological partition (see section 2.7). For all types of analysis the same set of specimens was used (table 1), and for the combined BI analysis a morphological partition for 30 characters (supplementary material S1) was added to the same set of specimens. BI analyses (Ronquist et al., 2011) were performed in MrBayes on XSEDE (3.2.7a), CIPRES Science Gateway (Miller et al., 2010). Four runs with four chains each were running simultaneously for 10 million generations with 0.1 temperature setting; burn-in was set at 25%. We applied the most complex General-Time-Reversible (GTR) with gamma-distributed substitution rates and invariable sites (GTR+I+G) model to the CO1 partition, as recommended by Arenas (2015) and Abadi et al. (2019), and the only available Mk model with a gamma distribution (Lewis, 2001) for morphological partition. Partitions of CO1 (574 bp) and
morphological characters (30) were concatenated in Sequence Matrix 1.7.8 (Vaidya et al., 2011). Chains were sampled every 1000 generations and the respective trees were written to a tree file. After the analyses, the stdout files were checked to ensure that the average standard deviation of split frequencies was below 0.01 in each case. Fifty-percent majority-rule consensus trees and posterior probabilities of clades were calculated using the trees sampled. The ML analysis (Stamatakis, 2016) was launched in RAxML-HPC BlackBox (8.2.12), CIPRES Science Gateway with an auto-generated number of bootstrap iterations and a subsequent thorough ML search, using GTR+I+G model as well. Nodes with bootstrap supports lower than 85 were collapsed. The resulting CO1-based BI and ML trees with posterior probabilities (left phylogram) and bootstrap supports (right phylogram), respectively, are provided in fig. 1. To illustrate apomorphies that characterize each species clade, we performed acttran character optimization in Winclada (Nixon, 2002), based on the total-evidence BI tree as an input. The matrix of genetic distances was calculated using the Kimura 2-parameter (K2P) model of base substitution with MEGA X (Kumar et al., 2018) (supplementary material S2).

**Results**

**Morphology of the endophallus of Oxyporus**

Based on the pool of specimens available from our study region, we observed significant diversity of endophallic structures among species of Oxyporus and a strong difference between its two subgenera. While potentially homologous structures could be identified in the membranous endophallic lobes between the subgenera, the apical sclerites were remarkably difficult to homologize. This was especially true for Pseudoxyporus where the diverse endophallic structures were difficult to homologize even within the subgenus. Within the subgenus Oxyporus, on the contrary, they are more homogenous and thus more comparable. The general scheme of the Oxyporus s. str. endophallus is given in fig. 2 to aid with standardized comparisons between species. In the absence of any comparative study of the endophallic structures across Coleoptera or Staphylinidae, we did not attempt to tie our scheme here to any of a few works of this kind devoted to particular groups of Staphylinidae (Khachikov, 2006, 2015; Jałoszyński et al., 2015; Zhou et al., 2019). They all demonstrate very different types of endophallic structures which would require a comprehensive comparative morphological study across the family to establish homologies. Without such a study, we use as simple and as descriptive terms as possible, naming endophallic membranous lobes and sclerites according to their collocation (fig. 2). We also

Ancestral character state reconstruction analysis and parsimony-based character evaluation

Ancestral character state reconstruction was performed by ML with the Mkv model of morphological evolution (Lewis, 2001) in BayesTraits v2, MultiState (Pagel et al., 2004) using the total evidence BI tree as input. The “Generate BayesTraits Input” function in TreeGraph2 (Stöver et al., 2010) was used to speed up the calculations of character states likelihoods for each node of the respective Bayes tree, and reconstructed states were obtained for each character (figs 6–8; supplementary material S4–S24). Additionally, the parsimonious characteristics (ci, ri, rc) for each character were calculated on the tree topology from the BI total evidence analysis with PAUP 4.0 (Swofford, 2003). They are presented in table 2.
Ancestral states reconstruction under Mk1 model for three characters of coloration: black-and-yellow color pattern on elytra (26), abdominal tergites and sternites III-V coloration (28), and abdominal paratergites coloration (30). Pie charts represent the likelihood indices for each node. Character numbers as in section 2.6 of the paper.
observed that the endophallus is very uniform within a species, even across broad distributional ranges. This was especially remarkable for the Transpalaearctic species *O.* (*O.*) mannerheimii, *O.* (*O.*) maxillosus and *O.* (*O.*) rufus.

**Species delimitation**

Phylogenetic analysis of CO1 barcode regions using BI and ML, as well as the total-evidence BI analysis of the CO1 and morphology combined, for all species of *Oxyporus* hitherto recorded for the fauna of Russia (except *O. triangulus*) revealed highly congruent trees. The molecular only and total-evidence BI analyses resulted in identical topology with insignificant differences in posterior probabilities of several clades. Support values of the BI molecular only tree

| Character | CI | RI |
|-----------|----|----|
| 1 (labrum) | 1 | 1 |
| 2 (mentum) | 1 | 1 |
| 3 (antenna, length) | 1 | 1 |
| 4 (antenna, shape) | 1 | 1 |
| 6 (pronotal posterior angles) | 1 | 1 |
| 7 (mesepisternum-epimeron surface) | 1 | 1 |
| 8 (pleural suture of mesopleuron) | 1 | 1 |
| 10 (paramere, length) | 1 | 1 |
| 11 (basal bulb) | 1 | 1 |
| 12 (median lobe, shape) | 1 | 1 |
| 13 (median lobe, dorsal side) | 1 | 1 |
| 15 (endophallus, dorsal distal lobe) | 1 | 1 |
| 16 (endophallus, dorsal distal lobe subdivision) | 1 | 1 |
| 19 (endophallus apical sclerites, dorsal and ventral spicula) | 1 | 1 |
| 20 (endophallus apical sclerites, lower spicula) | 1 | 1 |
| 22 (endophallus apical sclerites, ligament sclerite) | 1 | 1 |
| 5 (pronotal transverse elevation) | 0.5 | 0.977 |
| 14 (median lobe, apex) | 0.75 | 0.971 |
| 17 (endophallus, direction of apical distal lobe) | 0.5 | 0.96 |
| 18 (endophallus, surface of apical distal lobe) | 0.333 | 0.957 |
| 21 (endophallus apical sclerites, additional spicula) | 0.5 | 0.95 |
| 29 (abdomen coloration, tergite and sternite VI) | 0.667 | 0.917 |
| 23 (head, color) | 0.5 | 0.909 |
| 24 (pronotum, color) | 0.4 | 0.893 |
| 25 (elytra, ground color) | 0.5 | 0.833 |
| 30 (abdomen coloration, pleurites) | 0.4 | 0.813 |
| 26 (elytra, black and yellow color pattern) | 0.25 | 0.789 |
| 27 (abdomen coloration, tergites and sternites I-III) | 0.167 | 0.722 |
| 28 (abdomen coloration, tergites and sternites III-V) | 0.143 | 0.684 |
| 9 (elytra) | 0.2 | 0.333 |
are provided in the discussion below. The molecular only and total-evidence BI trees show better resolution than the ML and reveal all clades representing species, with high support. The ML tree recovered the same species clades except for \( O. (O.) \) \text{germanus} (node 5) and \( O. (O.) \) \text{maxillosus} (node 10). The molecular only BI and ML trees are shown on the left and right of fig. 1, respectively. The total-evidence BI tree is given in fig. 5 with morphological characters plotted under fast optimization (ACCTRAN). Major nodes representing species in our revision are numbered from 1 to 10.

Within the subgenus \textit{Pseudoxyporus}, both BI and ML recover three clades corresponding to species as they are currently recognized: \( O. (P.) \) \text{melanocephalus}, \( O. (P.) \) \text{dybowskii}, and \( O. (P.) \) \text{occipitalis}. The KaP genetic distance between sequences of different species from the same subgenus varies from 0.12 to 0.17, whilst between species from different subgenera it varies from 0.16 to 0.22 (supplementary material S1).

Node 1 confirms the conspecificity of \( O. (P.) \) \text{melanocephalus} specimens (BI: 1.00; ML: 100; zero genetic distance) from the Russian Primorsky Territory and South Korea. This node is defined by a single apomorphy: truncate apex of median lobe (14–4) and four homoplasies: pronotal transverse elevation (5–1), membranous and granulate surface of apical distal lobe of endophallus sac (18–0), and dark brown to black abdominal tergites and sternites III–IV (27–0).

Node 2 supports the conspecificity of \( O. (P.) \) \text{dybowskii} specimens from the Russian Altay and South Korea (BI: 1.00; ML: 100; genetic distance: 0.03) and is corroborated by two synapomorphies: distinctly elevated pronotal posterior angles (6–1), and tricolored elytra (25–2).

Node 3 unites specimens of \( O. (P.) \) \text{occipitalis} (BI: 1.00; ML: 93; genetic distance variation: 0.00 to 0.01) from Canada and the USA, and is defined by three homoplasies: bicolored head (23–2) and pronotum (24–2), and yellow trapezoid elytral pattern with black spot and yellow elytral suture (26–2).

Together with \( O. (P.) \) \text{cyanipennis}, all four \textit{Pseudoxyporus} species are well recognized morphologically and none of them called for further testing of species limits. Their sequences and morphological characters were included in the analysis, mainly to test subgenus-specific characters. Both BI and ML trees here reinforce their current concepts presented in detail in the Taxonomy section.

Within the subgenus \textit{Oxyporus} s. str. our analysis reveal seven clades, which we interpret as species as following:

Node 4 unites \( O. (O.) \) \text{mannerheimii} from the European part of Russia, Siberia and the Russian Far East (BI: 1.00; ML: 100; zero genetic distance). This species is defined by two homoplasious characters: shagreened mesepisternum-epimeron surface (7–1) and evenly colored elytra (25–0).

Node 5 demonstrates the conspecificity of specimens, previously identified as \( O. (O.) \) \text{germanus}, \( O. (O.) \) \text{aequicollis}, and \( O. (O.) \) \text{basicornis} from the Russian Far East and South Korea (BI: 0.97; ML: not recovered; genetic distance variation: 0.00 to 0.03). The node is supported by three homoplasies: elytral punctures in two longitudinal rows (9–2), elytra yellow with black spots on lateral sides, elytral suture with wide black line (26–4), and black abdomen with yellow paratergites III–VI (30–2). All included specimens of this clade are unequivocally united by the uniform structure of the endophallus, which is identical to that of the male lectotype specimen of \( O. (O.) \) \text{germanus} and unique in e.g. lamellate lower spiculae of apical sclerites (20–0) together with the apical lobe pointed dorsad (17–1). Therefore, this clade supports our species concept of \( O. (O.) \) \text{germanus} in this treatment.

Node 6 confirms the conspecificity of \( O. (O.) \) \text{rufus} from Finland, Germany, European
part of Russia, Siberia, and the Russian Far East (BI: 1.00; ML: 1.00; genetic distance variation: 0.00 to 0.01). This node is supported by one synapomorphy: dark brown to black head (23–1) and five homoplasies: dorsally curved apical distal lobe of endophallus sac (17–0), reddish to dark red pronotum (24–1), pale yellow to dark red abdominal tergites and sternites III-IV (27–1) and V (28–1), and bicolored tergites and sternites VII-IX (29–2).

Node 7 unites sequences of beetles, identified as *O. (O.) germanus*, *O. (O.) aequicollis*, and *O. (O.) basicornis*, together with sequences of *O. (O.) parvus*, a recently described species from South Korea (BI: 1.00; ML: 99; genetic distance variation: 0.00 to 0.03). The clade is supported by two homoplasies: elytra yellow with black spots on lateral sides, elytral suture with wide black line (26–4) and black abdomen with yellow paratergites III-V (30–1).

Despite previously defined, significant distinctions in coloration between these ‘species’, all specimens share the same set of aedeagal characters. According to the structure of the endophallic apical sclerites of the type specimen of *O. (O.) basicornis*, clade 7 represents a single species, which corresponds to the revised concept of *O. basicornis*.

Node 8 unites specimens of *O. (O.) procerus* from the Russian Far East and South Korea (BI: 1.00; ML: 1.00; genetic distance variation: 0.00 to 0.01). This node is defined by three homoplasies: apex of aedeagal median lobe two-pointed (14–3), additional spicula in apical sclerites of endophallus (21–1), and reddish to dark red pronotum (24–1).

Node 9 unites sequences of *O. (O.) niger* from the Russian Far East and South Korea (BI: 1.00; ML: 0.70; genetic distance variation: 0.00 to 0.02).

Node 10 demonstrates the conspecificity of specimens that morphologically match descriptions of *O. (O.) maxillosus* and three species described from Japan: *O. (O.) aokii*, *O. (O.) basiventris*, and *O. (O.) japonicus*. The clade includes specimens from the Czech Republic, Russia (Sverdlovsk Province, Republic of Altai, Irkutsk Province, Republic of Buryatia, Primorsky Territory, and Sakhalin Province), South Korea and Japan (BI: 0.96; ML: not recovered; genetic distance variation: 0.00 to 0.03). Apart from similar CO1 sequences, members of this clade share the same structure of the endophallic apical sclerites. Another supportive synapomorphy is bicolored elytra (25–1). The color of abdomen which was the main diagnostic character for *O. (O.) aokii*, *O. (O.) basiventris*, and *O. (O.) japonicus* widely varies and did not allow for recognition of distinct taxa.

**Morphological characters: ancestral state reconstruction and diagnostic value for species delimitation**

To test the diagnostic value of morphological characters at the species level, an Ancestral States Reconstruction (ASR) with Maximum Likelihood, Mk1 model, was performed for all characters. Reconstructed ancestral states are shown in figs 6, 7, and 8 for several characters that were the most illustrative for each of three categories: general external morphology, genital morphology and body coloration. Reconstructed ancestral states for all other characters were added as supplementary material S4-S24. Parsimony-based indices (ci, ri, rc) for all 30 characters optimized on the total-evidence tree are shown in table 2. According to the ci, ri, and rc indices, as well as the likelihood distribution for character states ancestral to each species, all explored characters can be arranged into four groups with respect to their performance as species-specific (table 2):

1. Characters with the highest parsimony indices (ri: 1; ci: 1) include traits that separate the two subgenera (1–4, 8, 10–13, 15, 16) and determine single species,
namely *O. (P.) dybowski*ii (6) and *O. (O.) rufus* (19). These characters are not discussed further in this section. Characters 7, 20 and 22 were shown to be species-specific and also characterized by the highest parsimony indices and ASR likelihoods not lower than 0.99 for the most probable character state of each species. Particularly, character 7 (mesepisternum-mesepimeral surface, fig. 6) can be used to reliably delimit *O. (O.) mannerheimii* from *O. (O.) rufus*, which can be otherwise difficult in case of melanistic *O. (O.) rufus*. Character 20 (form of the lower spicula of endophallus apex, fig. 7) and character 22 (ligament sclerite of endophallus apex, fig. 7) were stable and allow for unequivocal species recognition within the subgenus *Oxyporus* once an endophallus is everted.

2. Characters 5, 14, 17, 18, 21 (supplementary material S7, S14, S17, S19, respectively) concerned the general or aedeagal morphology and also had relatively high parsimony indices (ri: 0.95–0.98; ci: 0.33–0.75). These characters were species specific and did not display interspecific polymorphism, which was supported by high ASR likelihoods for most probable states of each species (not lower than 0.99), and thus can be reliably used in identification.

3. Characters 23–25 (ri: 0.83–0.90; ci: 0.50–0.66) describe coloration of head, pronotum and ground color of elytra, respectively. They did not expose polymorphism for species and ASR likelihoods for most probable states of each species (not lower than 0.99), and thus can be used these characters with caution for identification. For instance, we observed strongly darkened specimens of *O. (O.) rufus* from Kazakhstan initially identified as *O. (O.) mannerheimii*. Only the mesepisternum-mesepimeral surface (character 7) together with the structure of pronotum (character 5) helped to identify these females as *O. (O.) rufus*, which was also supported by the presence of darker zones forming *Oxyporus rufus*-like color pattern on elytra which were visible under a strong light. Use of these characters in case of teneral, non fully-colored adults of species with usually dark body coloration can also lead to misidentification.

4. Characters 9, 26–28, 30 demonstrated interspecific polymorphism and the lowest indices of parsimony criteria (ri: 0.33–0.81; ci: 0.20–0.40). In case of elytra punctation (9), the interspecific polymorphism was shown in *O. (O.) basicornis*, *O. (O.) germanus*, *O. (O.) maxillosus*, and *O. (O.) niger* even on the limited dataset of sequenced specimens (fig. 8; Supplements 9, 23). The ASR likelihoods for most probable states at *O. (O.) basicornis*, *O. (O.) germanus*, *O. (O.) maxillosus*, and *O. (O.) niger* nodes were lower than 0.95, in particular 0.92, 0.93, 0.90, and 0.80, respectively. This character was previously used for delimitation of *O. (O.) germanus* and *O. (O.) aequicollis* (Kirshenblatt, 1938; Shabalin, 2012). The character for the elytral color pattern (26) also showed interspecific polymorphism for *O. (O.) maxillosus*. Although ASR likelihoods of the character state 26.3 remained high (0.99) due to the prevalence of the most common coloration type among sampled specimens (fig. 8), the demonstrated polymorphism as well as low parsimony
indices (RI: 0.79; CI: 0.25) should prevent from using this character to delimit species related to *O. (O) maxillosus*, contrary to the earlier practice (Nakane and Sawada, 1956). The same applies to characters 27–28 (coloration of abdominal segments III-IV, supplementary material S23 and V, fig. 8, respectively). The character describing abdominal pleurite coloration (30) reveals polymorphism in *O. (O) basicornis* and *O. (O) germanus*, with the ASR likelihoods 0.93 and 0.90 for the states 30.1 and 30.2 of these species, respectively. Despite indications to the contrary (Shabalin, 2012), our analysis showed low utility of this character set for species delimitation.

Although ASR likelihoods for the most probable states for each species (not lower than 0.97) and parsimony indices (RI: 0.92; CI: 0.67) for the character 29 (abdomen coloration, tergite and sternite VI) were relatively high, due to the presence of only two specimens forming a single cluster with alternative coloration on the tree (supplementary material S24), we do not recommend to use this character for species delimitation. In the much wider dry material sample we observed specimens with a brightly colored sixth abdominal segment but possessing a maxillosus-type endophallus (fig. 13D). Intermediately colored specimens showed no geographically structured pattern and were found in the West and East Palearctic (see Discussion for details).

**Discussion**

Our data showed that all CO1-based clades that could be considered as separate species because of molecular distance are supported by morphological characters that indicate a hiatus between them. This supports the validity of a single locus approach for DNA-based species delimitation, at least for the barcoding CO1 fragment for Palaeartic *Oxyporus*. In the course of checking traditional and novel morphological characters against the molecular results, we revealed seven new morphological traits (7, 14, 17–22) that can be reliably used for species delimitation in *Oxyporus*. Most of them are endophallic characters that are the most reliable for species diagnostics in *Oxyporus*. For some species, e.g., *O. germanus* and *O. basicornis*, the endophallic characters are the only diagnostic traits that we could observe, especially if the degree of impression on pronotum is variable. This confirmed the earlier warnings of Makranczy (2012) against using only body coloration patterns, which were unfortunately broadly used to describe species of *Oxyporus*. Among these body coloration characters, partial utility for species diagnostics was shown for three characters (23, 24, 25), namely the coloration of the head, the pronotum and the ground color of the elytra.

Data integration helped to resolve taxonomic problems, such as discrimination of the morphologically nearly identical species *O. (O) basicornis* and *O. (O) germanus*. In their case, nothing but the CO1 barcode and the endophallic structures can tell that these otherwise identical-looking species are not even sister to each other. In this respect, the congruence of CO1 and endophallus for the delimitation of *Oxyporus* species is remarkable. It is also clear how misleading external characters hitherto used for species delimitation were. In particular, *O. (O) basicornis* and *O. (O) germanus* have the same pattern of variability of coloration, as each can have specimens with three or four yellow abdominal paratergites. Also, the pattern of elytral punctation used in species diagnostics, as well as body length and proportions of various body parts, cannot be unequivocally used for species diagnosis due to their high variability within and among the species. Within a single...

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species body length can vary by up to 5 mm and the head width can be greater or less than the pronotal width. Moreover, we did not find any geographically structured pattern for these polymorphic traits, except coloration of the abdomen of western and eastern specimens of *O. (O.) maxillosus*. In that species, specimens with an entirely brightly colored (pale) abdomen seem to be more frequent in Europe east to the Urals, while those with an entirely dark abdomen mostly occur in the Russian Far East and adjacent territories.

Given such variability of external characters, the rather uniform shape of aedeagus is poorly informative for species diagnostics in clusters of closely related species. Especially in *Oxyporus* s. str., contrary to many other staphylinids and beetles in general, the shape of the aedeagus is not diagnostic. In the case of *O. (O.) basicornis* and *O. (O.) germanus*, it is in fact identical. That makes the difficult procedure of everting the endophallus a desired or even a mandatory step for separating some species of *Oxyporus* from each other, unless CO1 barcoding is performed. Our study demonstrates that in these cases, CO1 barcoding is a rather straightforward shortcut to identification when DNA-grade or recently collected dry pinned material is available.

The remarkable congruence of the species delimited by CO1 barcodes and endophallic structures, especially for otherwise extremely similar *Oxyporus* species stresses the need to explore the biological role of the endophallic structures. There must be something that promotes diversification of these structures among species. As far as known for some species of *Oxyporus* (Tokareva et al., 2020), multiple males and females of the same and several species can encounter each other in the same large and short-living fungal caps during the mating season. Such aggregations provoke complex intra- and interspecific sexual interactions. Given the above reviewed complexity of the evolutionary phenomena that drive morphological diversification of insect genitalia, Oxyporinae might be a suitable model group for the investigation of sexual competition, female choice and the “lock and key” hypothesis, especially with respect to the endophallus. It is noteworthy that the female genitalia in *Oxyporus* remain unexplored. With the approximately 120 species of *Oxyporus* known globally, much taxonomic work remains to be done. Unfortunately, even recent descriptions of new species rarely include photos of the aedeagus and almost never include at least some figures of the endophallus, not to mention one that is properly, fully everted. Until very recently, very few *Oxyporus* species have been barcoded. The only publication that both extensively used barcoding and provided illustrations of the endophallus for a new species is Lee et al. (2020). It is a very progressive and useful study of the Korean fauna which, unfortunately, was performed with coloration-based taxonomy of *Oxyporus* in Japan because the authors did not check all their Korean species on their possible conspecifity with Japanese conegers (for details see below). To progress with the taxonomic study of *Oxyporus*, we suggest endophallus eversion and DNA barcoding as a routine techniques of species delimitation in this genus. We here demonstrate the utility of such an approach in the following revision of the Russian fauna of this genus. Another important taxonomic problem concerns a significant difference observed between the subgenus *Pseudoxyporus* and the nominative subgenus *Oxyporus*, which were originally considered as genera before Campbell (1969) down-ranked them to subgeneric status. Makranczy (2012) argued that this down-ranking was not justified due to the numerous morphological and bionomical traits indicating a notable distance between *Oxyporus* and *Pseudoxyporus*. Makranczy’s conclusion that these taxa represent separate
genera is supported by the large genetic distance between *Oxyporus* and *Pseudoxyporus* (0.16–0.22) and the significant difference between their endophallus types found in our work. However, a problem is that the genus *Pseudoxyporus* was originally erected on the too small, geographically and taxonomically, subsample of Oxyporinae (Nakane & Sawada, 1956). To make the final decision on this taxonomic issue, the world fauna, and especially species which share some characters of both subgenera, such as *Oxyporus smithi* Bernhauer, 1910, must be assessed.

**Taxonomic revision of *Oxyporus* of Russia**

**Genus Oxyporus Fabricius, 1775**

*Oxyporus*: Fabricius, 1775: 267. Type species by subsequent designation: *Staphylinus rufus* Linnaeus, 1758 (Latreille, 1810: 427).

**Diagnosis.** Antennae filiform or clavate, inserted at side of head near anterior margin of eyes; mandibles prominent, sickle-shaped; apical labial palpomere large, transverse, strongly securiform; procoxae large, conical, prominent, protrochantin broadly exposed; middle coxae widely separated; posterior coxae transverse; tarsi 5–5–5; abdomen with six visible sternae and two pairs of paratergites per segment. In Russia, the genus includes 10 species which cannot be confused with any other genus of rove beetles.

**Note.** Soon after Nakane and Sawada (1956) described the genus *Pseudoxyporus* for a number of Japanese species formerly in *Oxyporus*, Campbell (1969), in his revision of the New World Oxyporinae, downgraded *Pseudoxyporus* to subgeneric rank. Since then, both concepts persist in literature, in parallel use. For practical reasons (see the last paragraph of the Discussion) here we use the genus *Oxyporus* in a broad sense, i.e., with *Oxyporus* s. str. and *Pseudoxyporus* as subgenera.

**Key to the *Oxyporus* species of Russia**

1. Elytra metallic blue with reddish-yellow humeri; body red, with some parts of head and abdomen black. Scutellum with faint punctuation. Aedeagus: endophallus with dorsal distal lobe subdivided by transverse line (figs 4B, 15C, D) .................................................. *O. cyanipennis*

- Elytra of different coloration. Scutellum without punctuation, smooth (fig. 3A–G). Aedeagus: dorsal distal lobe of endophallus not divided by transverse line............................................................. 2

2. Pronotum red, or reddish-yellow, never black (figs 3D, 4B–E)....................................... 3

- Pronotum black (figs 3A–C, E–G, 4A). ........................................................................... 6

3. Head reddish or amber-yellow, of the same color as pronotum and elytra; abdomen black. Body on average larger (body length can reach 16 mm; the largest species in the Russian fauna). Aedeagus: median lobe with two-pointed apex, apical distal lobe of endophallus of same width along its entire length (figs 4D, 14A, B)......................... *O. procerus*

- Head black; elytra bicolored. Body on average smaller (body length at most 14 mm)............................................................... 4

4. Antennae relatively short, at most as long as head capsule; middle antennomeres transverse, wider than long; antennomeres with longitudinal asetose middle part forming bold line along antenna (figs 3A–G, 4A, D). Aedeagus: endophallus with one ventral, one pair of lateral and one pair of dorsal lobes; apical distal lobe of endophallus curved dorsad (fig. 14C, D)......................................................... *O. rufus*

- Antennae relatively long, distinctly longer than head capsule; middle antennomeres longer than wide (figs 4B, C, E) ......................................................... 5
5. Mesoventrite, abdomen and legs entirely black; elytra apically black; maxillary and labial palps black. Aedeagus: dorsal lobe of endophallus narrow, vermiform, covered with transverse rows of denticles (figs 4C, 16C, D).................................

.................................. O. (P.) melanocephalus.

Mesoventrite black; abdomen orange-red with black apex only; legs yellow; elytra with largely yellow humeri and sutural angles; maxillary and labial palps yellow. Aedeagus: dorsal lobe of endophallus without rows of denticles (figs 4E, 16A, B).........................O. (P.) dybowskii

**Figure 9** Schemes and photos of everted endophallus of *O. (O.) basicornis* (A, B) and *O. (O.) germanus* (C, D). Acronyms: adsp – additional spiculae; ddl – dorsal distal lobe; dsp – dorsal spiculae; lgsc – ligament sclerite; ltl – lateral lobe; vl – ventral lobe; vsp – ventral spiculae. Scale bar: 0.1 mm.
6. Elytra always entirely black .......................... 7
- Elytra always bicolored .............................. 8
7. Pronotum with transverse impression. Mesepisterna and mesepimera chagreened, not punctured. Aedeagus: apical distal lobe of endophallus forms a sclerotized, narrow, weakly curved hook (figs 3B, 11C, D) ...... .................................................. O. niger
- Pronotum without transverse impression, smooth. Mesepisterna and meseptomera not chagreened but punctured. Aedeagus: apical distal lobe of endophallus membranous (figs 3C, 11A, B) ........................................... O. mannerheimii
8. Pronotum smooth. Paratergites of the abdominal segments II and IV (first and second visible) yellow in contrast to black tergites (fig. 3E–G) ..................... 9
- Pronotum with transverse impression. Paratergites of the abdominal segments II and IV (first and second visible) always of the same colour as their tergites (yellow or black) ................................. 10
9. Aedeagus: apical sclerites of endophallus widened at apex, forming lamellate triangle (fig. 9C, D) ....................... O. germanus
- Aedeagus: apical sclerites of endophallus include a number of paired, arched spicules which form a distinctly sclerotised frame around the secondary gonopore (fig. 9A, B) .................. O. basicornis
10. Elytra at sutural area with distinct black triangle in basal half of elytral length. Aedeagus: median lobe with two-pointed apex, apical distal lobe of endophallus with a spicule inside (figs 4A, 14A, B) ...................... O. triangulus
- Elytra at sutural area yellow or with black, narrow, non-triangular stripe. Aedeagus: median lobe with rounded apex; apical distal lobe of endophallus forms sclerotized, distinctly curved hook (figs 3A, 13A–E) ...................... O. maxillosus

Subgenus Oxyporus Fabricius, 1775

Diagnosis. Labrum divided by membranous median line. Frons smooth, seldom with weak impressions. Antennae distinctly shorter than head, vestiture absent at central area of lateral surface of each segment, medial segments shorter than wide. Posterior pronotal angles broadly rounded or indistinct. Mentum trapzoid, with membranous flaps on each side. Protarsomeres cylindrical with some scattered strong setae. Aedeagus: parameres acicular, distinctly shorter than half of median lobe; median lobe dorso-ventrally flattened, basal bulb and ventral wall membranous, median orifice opening ventrally (Nakane & Sawada, 1956).

Oxyporus (Oxyporus) basicornis Cameron, 1930
O aequicollis Bernhauer, 1935, syn. nov.
O. parvus Lee et al., 2020, syn. nov. (figs 3E, F, 9A, B)
O. lewisi var. basicornis: Cameron 1930: 184.
O. basicornis: Nakane and Sawada 1956: 67; Shabalin 2012: 413.
O. aequicollis: Bernhauer 1935: 6; Kirschenblatt 1938: 529; Shavrin and Gildenkov 2009: 123
O. parvus: Lee et al., 2020: 685.

Type material examined. Oxyporus basicornis: JAPAN: Lectotype, here designated: ♂, ‘Type\ Japan; Chuzenji; AT 4000; 23.VII.28; J.E.A. Lewis\ O. lewisi; v. basicornis; Type Cam.; M. Cameron Bequest. B.M.1955–147; Oxyporus basicornis Cameron; det. M.-H. Kim 2004\ Oxyporus; basicornis; Cameron; det. M. Schülke 2019’ (NHM).

Oxyporus aequicollis: RUSSIA: Possible holotype? ♂, ‘Baikal\ Sharp Coll.; 1905-313; Oxyporus aequicollis Bernh; M.Bernhauer det.’ (NHM).

Other material examined. RUSSIA: Republic of Buryatia: 2 ♂, Pribaikalsky District, Selenga river valley, Diky Byk cape, 52.1405N 107.1186E,
7.VIII.2019, I. Makhov leg. (ZISP); **Primorsky Territory**: 3 ♂, Gornotaezhnoe, 43.6945N 132.15203E, 2–21.IX.2018, in fungi, A. Tokareva leg. (ZISP); ♂, Suputinsky Nature Preserve, [43.6327N 132.2902E], 3.IX.1969, Kryzhanovskij leg. (ZISP); ♀, Posiet peninsula, 42.6622N 130.7933E, 4.VIII.2019. A. Tokareva leg. (ZISP); 4 ex., Pogranichny area, Pogranichny suburbs 44.4230N 131.3649E, 20.VIII.2019, A. Tokareva leg. (ZISP).

**Diagnosis.** Pronotum smooth or at most with slight impression according to Lee et al. (2020; as *O. parvus*), paratergites of first three or four visible abdominal segments yellow while respective tergites and sternites black. Endophallus: distal lobe bent dorsad, consisting of dorsal, ventral and additional pair of thin bow-like spicules and central sclerite of characteristic shape (fig. 9A, B), all covered with membrane; dorsal and ventral pairs of thin spicules bent ventrad and then sharply dorsad to form notable sclerotized frame supporting walls of secondary gonopore.

**Redescription.** Body length 5.7–10.1 mm (n = 10). Head subovate to round, smooth, brown to black. Pronotum without transverse elevation, smooth, brown to black. Elytra black with yellow pattern. Mesepisterna and epimera with rough punctation, black. Abdominal tergites and sternites black, lateral abdominal sclerites of segments i-iii or iv yellow. Aedeagus: median lobe with round apex; endophallus with twin-coned spherical dorsal lobe covered with medium-sized denticles, pair of spherical lateral lobes, and transverse ventral lobe covered with tiny granulation; apical distal lobe membranous, with tiny granulation, bent dorsad, with four pairs of thin long bow-like sclerites under membrane and one thin ligament sclerite dorsally. Basal sclerotization disjunct, additional spiculae of a peculiar form (figs 3E, F, 9A, B).

**Comparison.** *Oxyporus basicornis* is identical to *O. germanus* in coloration and body proportions. Both species can be distinguished only by CO1 barcode and endophallus structure. In particular, the endophallus of *O. basicornis* has two additional spiculae and the additional central sclerite missing in *O. germanus*. From all other species of *Oxyporus* in Russia, *O. basicornis* can be distinguished by the structure of endophallic sclerites and coloration of head, thorax, and elytra.

**Distribution.** *Oxyporus basicornis* is reliably known from Japan (Honshu), South Korea (Lee & Ahn, 2020) and Russia, where it is recorded here for the first time. Russian records come from Primorsky Territory and Buryatia; it is presumably widely distributed in the Russian Far East and East Siberia (fig. 10C).

**Bionomics.** This species can be usually found in large fungal caps together with *O. germanus* and/or *O. rufus*, or alone in *Suillus americanus* (Peck) Snell in the Russian Far East.

**Comments.** *Oxyporus basicornis* was described from Japan as a variety of *O. lewisi* (Cameron, 1930) based on the dark median line on the last six antennomeres and yellow paratergites on the first three (and not four as in *O. lewisi*) abdominal segments. Nakane and Sawada (1956) raised it to the status of a species. In Russia, *O. basicornis* was recorded for the first time in Primorsky Territory, diagnosed only using color (Shabalin, 2012). Our study, however, has revealed that *O. basicornis* overlaps in coloration with *O. germanus*, another species described from Japan, and distributed in the Russian Far east as well (see below). Both species reliably differ from each other only by CO1 barcode and structure of the endophallus. Therefore, it was unclear which species was recorded by Shabalin (2012) under the name *O. basicornis*, while our data here, based on a reexamination of Shabalin’s material as well, are the first reliable records of this species from Russia.

*Oxyporus aequicollis* was described from a single specimen sampled in ‘Irkutsk’ (Bernhauer, 1935) as a species close to *O. mannerheimii*. In fact, the original description of
O. aequicollis is nearly identical to the original description of O. germanus, earlier described from Japan. Kirschenblatt (1938) recorded O. aequicollis from Irkutsk Prov., Republic of Buryatia, Zabaikalsky Terr., and Khabarovsk Terr. and noticed its close affinity to O. germanus. He provided two characters to differentiate O. aequicollis from O. germanus: smaller body size and distinct longitudinal rows of punctuation on elytra. The material available to us which matches the descriptions of O. germanus, O. aequicollis, and O. basicornis shows no hiatus among the specimens in these and other characters as far as external morphology is concerned. At the same time, based on the CO1 barcode and

FIGURE 10  Distributional maps of O. (P.) cyanipennis, O. (P.) melanocephalus, and O. (P.) dybowskii (A); O. (O.) procerus, O. (O.) triangulus, and O. (O.) niger (B); O. (P.) dybowskii O. (O.) basicornis and O. (O.) germanus (C).
structures of the endophallus, this material can be unambiguously divided into two species, one of which includes the type material of *O. germanus*, and another, *O. basicornis*. Because of previous taxonomic confusion, it is also unclear which species was recorded from Russia under the name *O. aequicollis* in Kirschenblatt (1938). Unfortunately, we could not examine the holotype of *O. aequicollis*, which was not found either at the Field Museum or at Vienna Museum of Natural History (A.F. Newton and H. Schillhammer, pers. comm., respectively). It is not even clear if the type is a male or female, and in the latter case, may not be informative for this taxonomic problem. Based on the sample of examined material that includes a female from D. Sharp’s collection in NHM identified by M. Bernhauer as *O. aequicollis* and that maybe in fact a holotype of this species, it is clear that *O. aequicollis* must be a synonym of either *O. germanus* or *O. basicornis*. Since our data shows that reliably identified *O. basicornis* has wider known distribution westwards (found in Buryatia), while reliably identified *O. germanus* is so far restricted to the Far East, we place *O. aequicollis* in synonymy with *O. basicornis*.

*Oxyporus parvus* was described from South Korea (Lee et al., 2020). The authors showed the difference of *O. parvus* from *O. germanus* based on CO1 and provided a scheme of the endophallus of their new species, also mentioning and partly illustrating diagnostic characters of *O. parvus*, namely the presence of the tomentose patches on tergites III and IV in *O. parvus* (on tergite IV in *O. germanus*), brown abdominal tergites III–V in *O. parvus* (III–VI in *O. germanus*) and the presence of a shallow and broad depression on anterior third of pronotum in *O. parvus* (presumably absent in *O. germanus* studied by the authors). Regarding the tomentose patches, our sample of material shows variability of the size, number and location of these patches even within a species, at least in *O. rufus*, *O. germanus*, *O. basicornis*, *O. maxillosus*, *O. procerus*, *O. mannerheimii*, and *O. niger*. The fine scratch-like impression in the anterior third of the pronotum of *O. germanus* appears to be a varying trait as well. Unfortunately, Lee et al. (2020) did not compare *O. parvus* with *O. basicornis*. Inclusion of their molecular data in our analysis, as well as matching the molecular clades with the respective (not sequenced) type material of *O. basicornis* via examination of the endophallus, clearly shows that *O. parvus* is conspecific with *O. basicornis* and thus the former is placed in synonymy with the latter.

*Oxyporus (Oxyporus) germanus* Sharp, 1889 (figs 3G, 9C, D)  
*O. germanus*: Sharp 1889: 409; Shavrin and Gildenkov 2009: 123.

*Type material examined:* JAPAN: Lectotype, here designated. ♂, Type \ Japan.; G. Lewis. \ Sharp Coll.; 190–313 \ Oxyporus; germanus; Type; Sendai Jap.’ (NHM); Paralectotypes: ♂, ‘Japan.; G. Lewis. \ Sharp Coll.; 1905-313 \ Oxyporus; germanus; Sendai; Japan. Lewis’ (NHM); ♀, Japan.; G. Lewis. \ Sharp Coll.; 1905-313 \ Oxyporus; germanus; Sendai; Japan. Lewis’ (NHM).

*Other material examined.* RUSSIA: Primorsky Territory: ♂, Gornotaezhnoe, 43.6945N 132.15203E, 2–21.IX.2019, in fungi, A. Tokareva leg. (ZISP); ♂, Kedrovaya Pad’ Nature Preserve, Kedrovaya river valley, [43.1029N 131.4897E], 25.VIII.1998, O. Kireichuk leg. (ZISP); 2 ex., South of Anisimovka village, 43.154N 132.7893E, 27.VII.2019, A. Tokareva leg. (ZISP); ♂, Vladivostok, Sputnik station, [43.2328N 132.0412E], 13.IX.2009, S. Shabalin leg. (FEB RAS); ♂, Pogranichny area, Pogranichny suburbs 44.4230N 131.3649E, 20.VIII.2019, A. Tokareva leg. (ZISP); Sakhalin Province: 3 ♂, Sakhalin Island, Okha suburbs,
near Medvezhye lake, [53.6139N 142.9568E], 28.viii.1979, in fungi, Okulov leg. (FEB RAS).

**Diagnosis.** Pronotum smooth, paratergites of first three or four visible abdominal segments yellow while respective tergites and sternites black. Endophallus: distal lobe of apical sclerites consisting of ventral pair of spiculae and dorsal pair of complex sclerites flattening and widening in the middle of distal lobe and forming characteristic structure supporting walls of distal lobe (fig. 9C, D).

**Redescription.** Body length 5.2–9.8 mm (n = 10). Head subovate to round, smooth, brown to black. Pronotum without transverse elevation, smooth. Elytra black with yellow pattern. Mesoepisterna and epimera with rough punctuation, black. Abdominal tergites and sternites black, paratergites of segments III-V or III-VI yellow. Aedeagus: median lobe with round apex; endophallus with twinned spherical dorsal lobe covered with medium-sized denticles and transverse, relatively large ventral lobe covered with tiny granulation, pair of spherical lateral lobes, and apical distal lobe membranous, with tiny granulation, bent dorsal; one pair of thin long bow-like ventral spiculae and paired complex additional spiculae in center flattening and widening towards apex under membrane and small obscure ligament sclerite dorsally; basal sclerotization obscure (fig. 3G, 9C, D).

**Comparison.** Oxyporus germanus is identical to *O. basicornis* in coloration and body proportions. Both species can be distinguished only by CO1 barcode and endophallus morphology. In particular, the endophallus of *O. germanus* has paired additional central spiculae flattening and widening towards apex, which are absent in *O. basicornis*. From all other species of *Oxyporus* in Russia *O. basicornis* can be distinguished by the structure of endophallic sclerites and coloration of head, thorax, and elytra.

**Distribution.** *Oxyporus germanus* is reliably known from Honshu, Japan (Sharp, 1889) and Russia (Primorsky Territory, new data) (fig. 10C).

**Bionomics.** This species can be usually found in large fungal caps together with *O. basicornis* and/or *O. rufus*, or alone in *Suillus americanus* (Peck) Snell in the Russian Far East.

**Comments.** *Oxyporus germanus* was described from the Japanese Honshu island (Sharp 1889) and recently recorded from Russia (Shavrin & Gildenkov 2009). Since, based on our data (see above), reliable discrimination of *O. germanus* from *O. basicornis* is impossible without DNA barcoding or study of the endophallus, Shavrin and Gildenkov’s (2009) record needs verification. Here, *O. germanus* is reliably recorded from Russia for the first time.

**Oxyporus (Oxyporus) mannerheimii**
*Gyllenhal, 1827* (figs 3C, 11A, B)
*O. mannerheimii*: Gyllenhal 1827: 495; Kirschenblatt 1938: 531; Shabalin 2012: 413. (Also a number of published more or less precise records from European Russia in the faunistic literature).

**Material examined.** BELARUS: Vitebsk Province: ♂, Korolevo, [53.5988N 27.4470E], VII-VIII.1894, ex coll. Birulya (ZISP); ♀, Korolevo, [53.5988N 27.4470E], VII-VIII.1894, ex coll. Birul’. (ZISP); KAZAKHSTAN: Western Kazakhstan Province: ♂, inflow Tautekeli of river Kara-Koba, [48.936N 85.6630E], 7.VIII.1989, V. Kastcheev leg. (ZISP); ♀, Rakmanovskie Kluchi, Berel’ river, [49.5701N 86.4994E], 11.VIII.1988, V. Kastcheev leg. (ZISP); Aqmola Province: ♂, near Stepnyak, Zhikey lake, [52.8931N 70.5845E], 20.VII.2002, V. Kastcheev leg. (ZISP); MONGOLIA: 2 ♀, Tov
Province, near Batumber, Suzukte clove, s-w Kentay, [48.4122N 106.7590E], 20.VIII.1924, Kozlov leg. (zisp); RUSSIA: Leningrad Province: ♀, [59.59N 31.09E], 18.VI.1902, Borovsky leg. (zisp); ♂, 1.VII.1902, F. Zaytsev leg. (zisp); Pskov Province: ♀, Shchepets, [58.7641N 34.0709E], 16.VI.1901, N. Ivanov leg. (zisp); Sebezhskiy District, near Osyno, [56.1495N 28.6672E], 25.VII.2009, V.N. Prasolov leg. (zisp); Sverdlovsk Province: 4 ex.,

Figure 11 Schemes and photos of everted endophallus of *O. (O.) mannerheimii* (A, B) and *O. (O.) niger* (C, D). Acronyms: adsp – additional spiculae; bsc – basal sclerotization; lgsc – ligament sclerite. Scale bar: 0.1 mm.
Visimsky Nature Reserve [57.4296N 60.0287E], 16.viii.2019, in fungi, N. Ukhova leg. (ZISP); 3 ♀, near Yekaterinburg, Uktus station, [56.7807N 60.6553E], 20.vi.1910, G. Jacobson leg. (ZISP); ♂, Pivovarikha, [52.2803N 104.4665E], 1903, Soldatov leg. (ZISP); Irkutsk Province: ♂, Listvyanka, near Baikal lake, [51.8589N 104.8725E]; 22.vii.1912, Kuligin leg. (ZISP); ♂, 12.vii.1912, Kuligin leg. (ZISP); Kemerovo Province: ♂, near lake Berchikul, [55.6277N 88.3580E], 15–31.vii.1903, (ZISP); Primorsky Territory: 2 ♂, Anisimovka, Litovka mountain, [43.10263N 132.78437E], 26.viii.2019, in fungi, A. Tokareva leg. (ZISP); 3 ♂, Gornotaezhnoe, 43.6945N 132.15203E, 2–21.ix.2018, in fungi, A. Tokareva leg. (ZISP); 2 ♂, Lazo District, Tachingoiz Bay, [43.0214N 134.1298E], 20.vii.1975, V. Kastcheev leg. (ZISP).

Diagnosis. Entirely black, except yellowish tarsi, apical portion of labial palps, and lateral parts of antenna. Pronotum smooth, without transversal ridge or impression; mesepisterna and mesepisterna smooth, shagreened, without punctation. Endophallus: apical distal lobe membranous; spiculae relatively short, additional pair of spiculae slightly flattened, located in apical portion of lobe (fig. 11A, B).

Redescription. Body length 8.5–10.7 mm (n = 10). Head subovate to round, smooth, brown to black. Pronotum without transverse elevation, smooth. Elytra black. Mesepisterna and epimera shagreened, black. Abdomen black. Aedeagus: median lobe with round apex; endophallus with twin-coned spherical dorsal lobe covered with medium-sized denticles and transverse ventral lobe covered with tiny granulation, pair of spherical lateral lobes, and apical distal lobe membranous, with tiny granulation, bent dorsad; it includes one pair of relatively short dorsal and ventral spiculae and paired additional spiculae in center disposed in apical portion of lobe, and ligament sclerite closely connected with dorsal spiculae; basal sclerotization connected only to ligament sclerite (figs 3C, 11A, B).

Comparison. Among all other species of Oxyporus in Russia, O. mannerheimii is most similar in coloration to O. niger, from which it differs by the smooth pronotum and shagreened, not punctured surface of mesepisterna and mesepimera, and by the structure of the endophallus (compare fig. 11A, B and 11C, D).

Distribution. Oxyporus mannerheimii is a Transpalaearctic species and its distribution is confirmed here by matching DNA barcodes of the European and Far Eastern specimens. In Russia, it occurs from Leningrad Region, through Urals and Irkutsk Region to Primorsky and Sakhalin Regions (fig. 12A).

Bionomics. In Leningrad Province, Russia, it was collected from fungal caps of Pleurotus spp.

Comments. This species appears to be phylogenetically remote from other Russian members of the subgenus Oxyporus (K2P-distance 0.09–0.15).

Oxyporus (Oxyporus) maxillosus Fabricius, 1793
(figs 1, 3A, 13A–E)
O. amurensis: Ganglbauer, 1895: 605 (described as a variety of O. maxillosus).
O. angularis: Gebler 1829: 69.
O. aokii: Shavrin and Gildenkov 2009: 123.
O. basiventris: Shabalin 2012: 413.
O. maxillosus: Fabricius 1793; Ryabukhin 1999: 41; Shavrin and Gildenkov 2009: 123; Shabalin 2012: 413; Tokareva et al., 2020: 250. There are also a number of published, more or less precise records from European Russia in the faunistic literature.

Material examined. GERMANY: 1 ex., ’Oxyporus Schonherri’ germ Manh’, Mannerheim leg.
CZECH REPUBLIC: Moravia: 1 ex., ca. 1 km south from Čížov, Podyji National Park, 48.865117N 15.872317E, 5–8.vi.2016, in 96% ethanol, A. Solodovnikov, J. Jenkins Shaw, M. Salnitska leg. (NHMD); 2 ♀, Paskov ‘Umeb. Paskau’, [49.718540N, 18.274909E], Reitter leg., (NMP); Smrk, [49.225379N, 15.992735E], in fungi, vi.1934, Hlisińskiowski leg. (NMP); BELARUS: Korolevo, [53.598790N, 27.450460E], VIII–VIII.1994; KAZAKHSTAN: 1 ex., near Dzhambul, [49.236848N, 86.307687E], 10.VIII.1998, V. Kastcheev leg. (ZISP); 1 ex., near Rachmanovskie Kluchi, Berel’ river, [50.408681N, 86.415546E], 11.VIII.1998, V. Kastcheev leg. (ZISP); 1 ex., near Ridder, Marchikha river, [50.385888N, 83.499507E], 14.VIII.1998, V. Kastcheev leg. (ZISP); 1 ex., near Topkain, [49.187551N, 85.420010E], 14.VIII.1998, V. Kastcheev leg. (ZISP); MONGOLIA: Bulgan Aimak: 1 ex, 21 km NE from Selenge-Buren, [49.6684N 104.2016E, 28.VII.1975], Guryeva leg. (ZISP); RUSSIA: Leningrad Province: 1 ex., Krasnoselskiy District, Duderhof Heights Protected Area, [59.697378N, 30.131421E], 02.VII.1993, V. N. Prasolov leg. (ZISP); 1 ex., Lomonosovsky District, Volkovtsy, [59.645009N, 29.827387E], 5–7.IX.2005, A. V. Matveev leg. (ZISP); 1 ex., Priozersky District, Orekhovo, [60.499986N, 30.288594E], 04.VII.1983, O. N. Kabakov leg. (ZISP); 1 ex., Saint Petersburg, Beloostrov village, [60.148329N, 30.017235E], in fungi, 24.VIII.1987, V. N. Prasolov leg. (ZISP); 1 ex., near Siversky, [59.367338N, 30.54738E], 30.VI.1983, O.N. Kabakov leg. (ZISP); Vologda Province: 1 ex., Kirillovsky District, National Park “Russkiy Sever”, near Kochevino village, 59.99167N 38.81111E, in fungi, 15.VIII.2017, N. Kolesova leg. (ZISP); 1 ex., Torkhovichi, [58.8602N 30.3470E], 30.VI.1997, Kabakov leg. (ZISP); 1 ex., Krasnoy Selo, Dudergof, [59.6977N 30.1311E], 2.VII.1993,

FIGURE 12 Distributional maps of O. (O.) rufus and O. (O.) mannerheimii (A); and O. (O.) maxillosus (B). Material examined abbreviated as ME.
Prasolov leg. (ZISP); 1 ex., Orekhovo, [60.4962N 30.2828E], 4.VII.1983, Kabakov leg. (ZISP); 1 ex., Siverskaya, [59.3356N 30.0597E], 30.VI.1993, Kabakov leg. (ZISP); 1 ex., Luga, [58.7443N 29.8299E], 7–14.IX.1921, Kosyakov leg. (ZISP); Kaluga Province: ♀, Kaluga, [54.597038N, 36.309278E], in fungi, VII.1998 (ZISP); 1 ex., SE, between Melikhovo and Yagodnoye, near river Dubenka, 53.5839N 35.6216E, 20–30.V.2010, Alekseev leg. (ZISP); Sverdlovsk Province: 1 ex., Dvurechensk, [56.695402N, 61.12352E], 13.VIII.2006, K. I. Fadeeva leg. (ZISP); 1 ex., Visimsky nature preserve, 57.468964N 60.026137E, on Leccinum

FIGURE 13 Schemes and photos of everted endophallus of O. (O.) maxilosus (A, B) and its color forms described as separate species: O. (O.) aokii (C), O. (O.) basiventris (D), and O. (O.) japonicus (E). Acronyms: bsc – basal sclerotization; lgsc – ligament sclerite. Scale bar: 0.1 mm.
scabrum, 16.VIII.2019, 3 ex. in 96% ethanol, N. L. Ukhova leg. (ZISP); 1 ex., Denezhkin Kamen Nature Reserve, 60.148471N 59.994707E, 21.VII.2017, in 96% ethanol, A. B. Ryvkin leg. (ZISP); Khanty-Mansi Autonomous Area: 1 ex., Malaya Sosva natural preserve, 62.340682N 64.042810E, 16.VIII.2018, A. B. Ryvkin leg. (ZISP); Republic of Altai: 5 ex., Chemalskij Distri., South-East of village Edigan, 51.054633N 86.379133E, in fungi, 27.VI.19, in 96% ethanol, A. Solodovnikov, A. K. Hansen leg. (NHMD); 1 ex., Ust-Kanskij Distri., Kuma river, 51.008567N 84.189917E, in fungi, 4.VII.2019, in 96% ethanol, A. Solodovnikov, A. K. Hansen, M. J. Justesen leg. (NHMD); Altai Territory: 1 ex., Chernovaya village, [52.0242N 84.6866E], 7.VIII.1897, Silantyev leg. (ZISP); Tomsk Province: 1 ex., Tomsk area, Selimuzhki village, [56.617541N 85.353229E], 4.VIII.2008, Emelyanov leg. (ZISP); 1 ex., Selimuzhki, [56.6174N 85.3654E, 4.VIII.2008], Emelyanov leg. (ZISP); Krasnoyarsk Territory: 1 ex., Kemerovo region, Tashtagolskiy area, [52.433627N 88.504214E], 19.VI.1908, Chvorov leg.; 1 ex., near Minusinsk, [53.6798N 91.6801E, 12.X.1933], Kozhanchikov leg. (ZISP); Kemerovo Province: 2 ex., Minusinskii suburbs, [53.707321N, 91.744777E], 12.X.1933, V. Kozhanchikov leg. (ZISP); Republic of Buryatia: 3 ex., Pribaikalsky District, Selenga river valley, Diky Byk cape, 107.11861N, 107.11861E, in fungi, 7.VII.2019, I. Makarov leg. (ZISP); Irkutsk Province: 1 ex., lake Baikal shore, near Listvyanka village, [51.861431N 104.871892E], 21.VII.1912, Kulinig leg. (ZISP); 1 ex., Nizhneduginsk, [54.901233N 98.026987E], 31.VII.1912, Parchevskaya leg. (ZISP); 1 ex., Sinyushina Mountain, [52.2605N 104.1985E], VIII.11812, Lukashev & Merkalev leg. (ZISP); 1 ex., Slyudyanka river, [51.6298N 103.6472E], 10.VII.1914, Rodionoff leg. (ZISP); 1 ex., Irkutsk, garden of Rodionoff’s estate, [52.2761N 104.2766E], 29.VII.1916, Rodionoff leg. (ZISP); 1 ex., near Mikhaelevo, [52.0608N 104.4184E], 24.VII.1912, Pakhomov leg. (ZISP); Zabaykalsky Territory: 1 ex., Chita, near Kaidalovka river, [52.0489N 113.4701E], 7.VII.1912, Valueva leg. (ZISP); Primorsky Territory: 5 ex., Pogranichny area, Pogranichny suburbs, 44.423085N 131.364975E, 18–20.VIII.1919, in fungi, in 96% ethanol, A. Tokareva leg. (ZISP); 6 ex., Arboretum of Gornotaezhnaya Station FEB RAS, 43.6945498N 132.1520375E, 5.X.18, in fungi, in 96% ethanol, A. Tokareva leg. (ZISP); 1 ex., Kaverlovskskiy District, [44.220022N, 135.079615E], in Leccinum sp., 21.VII.1978, L. D. Filatova leg. (FEB RAS); 2 ex., Shkotovskiy rayon, South of Anisimovka village, 43.150428N 132.789302E, 27.VII.1919, in fungi, in 96% ethanol, A. Tokareva leg. (ZISP); 5 ex., Lazovsky Nature Preserve, Tachingouz post, [43.023611N, 134.163899E], in fungi, 16.IX.2009, S. A. Shabaline leg. (FEB RAS); 1 ex., Ussuriysky Nature Preserve ‘Suputinsky zap.’, [43.633455N, 132.289070E], 10.X.1960, O. Kovalev leg. (ZISP); Ussuriysky Nature Preserve ‘Suputinsky zap.’, [43.633455N, 132.289070E], 18.X.1969, leg. O. L. Kryzhanovskiy (ZISP); 95 ex., Pogranichny area, Pogranichny suburbs, 44.423085N 131.364975E, 18–27.VII.1919, in fungi, in 96% ethanol, A. Tokareva leg. (ZISP); 1 ex., Ussuriysky nature preserve, [43.649665N 132.502690E], 14.IX.1969, O. L. Kryzhanovskiy (ZISP); 105 ex., Arboretum of Gornotaezhnaya Station FEB RAS, 43.6945498N 132.1520375E, 2–21.X.18, in fungi, in 96% ethanol, A. Tokareva leg. (ZISP); 1 ex., Vladivostok, Okeanskaya station, [43.224835N 132.009251E], 27.VII.1937, [probably Kirschblatt] leg. (ZISP); 1 ex., Okeanskaya, [43.2349N 132.0082E], 14.IX.1985, Kabakov leg. (ZISP); 1 ex., Yakovlevka, [44.4259N 133.4582E], 17.IX.1926, Dyakonov & Filippov leg. (ZISP); 1 ex., Petrov island, Japan See, [42.863385N, 133.806730E], 26.IX.1934, Dyakonov leg. (ZISP); 1 ex., Petrov island, Japan See, [42.8643N 133.8046E], 26.IX.1934, Dyakonov leg. (ZISP); 1 ex., Lazovsky Nature Preserve, Formozov stream, [43.001667N, 134.086944E], in
Laethiporus sulphureus, 10.VII.2005, Makarov leg. (cMk); 4 ex., Pogranichny area, Pogranichny suburbs, 44.423085N 131.64975E, 19.VIII.19, in fungi, in 96% ethanol, A. Tokareva leg. (zisp); 1 ex., Preobrazheniya Bay (Syukhe), [42.8940N 133.9194E], 15.VII.1975, Mamedova leg. (zisp); 1 ex., same locality but 17.VII.1974, Kashch leg. (zisp); 3 ex., Arboretum of Gornotoaezhnaya Station FEB RAS, 43.6945498N 132.1520375E, 5–21.VIII.18, in fungi, in 96% ethanol, A. Tokareva leg. (zisp); 1 ex., Preobrazheniya Bay (Syukhe), [42.8940N 133.9194E], 15.VII.1975, Mamedova leg. (zisp); 1 ex., same locality but 17.VII.1974, Kashch leg. (zisp); 1 ex., Pogranichny area, Pogranichny suburbs, 44.423085N 131.64975E, 19.VIII.19, in fungi, in 96% ethanol, A. Tokareva leg. (zisp); 1 ex., Preobrazheniya Bay (Syukhe), [42.8940N 133.9194E], 15.VII.1975, Mamedova leg. (zisp); 1 ex., same locality but 17.VII.1974, Kashch leg. (zisp); 3 ex., Arboretum of Gornotoaezhnaya Station FEB RAS, 43.6945498N 132.1520375E, 5–21.VIII.18, in fungi, in 96% ethanol, A. Tokareva leg. (zisp); 1 ex., Shkotovskiy rayon, South of Anisimovka village, 43.150428N 132.789302E, 26–27.VIII.19, in fungi, in 96% ethanol, A. Tokareva leg. (zisp); 1 ex., Amur Province, Ekimchan, [53.068766N, 132.945219E], 30.VII.1979, O. N. Kabakov leg. (zisp); ♂, Amur Province, near Blagoveschensk, [50.333555N, 127.530516E], in fungi, 19.VIII.2001, V. G. Bezborodov leg. (zisp); Khabarovsk Territory: 3 ex., Komsomol’sk-on-Amur, [50.566517N, 137.041066E], in yellow fungi on a Tilia sp. trunk, 23.VIII.1975, V. A. Mutin leg. (zisp); Khabarovsk, Korovskaya street, [48.522460N 135.121764E], 1.IX.1956, Kabakov leg. (zisp); 1 ex., Khreteb Mevachen, [53.887263N, 139.161294E], 30.VII.1957, O. N. Kabakov leg. (zisp); 34 ex., Shkotovskiy area, South of Anisimovka village, 43.150428N 132.789302E, 26–27.VIII.19, in fungi, in 96% ethanol, A. Tokareva leg. (zisp); 1 ex., Amur Province, Chingouz Bay, [42.994822N 134.067961E], 20.VII.1957, V. Kastcheev leg. (zisp); 1 ex., Amur river right shore, Malmyzh, [49.851211N, 136.756478E], 26–27.VIII.1926, Starokodomsky leg. (zisp); 1 ex., Malmyzh, right side of Amur river, [49.8613N 136.7562E], 30.VIII.1926, Starokodomsky leg. (zisp); Sakhalin Province: 1 ex., Yuzhno-Kurilskiy urban district, Kunashir island, Filatova river, [44.209465N 145.972299E], 15.XI.1988, Kabakov leg. (zisp); 1 ex., Yuzhno-Kurilskiy urban district, Kunashir island, Filatova river, [44.193889N, 146.019722E], 03.IX.2009, I. Melnik leg. (zisp); 5 ex., Sakhalin island, near Yuzhno-Sakhalinsk, Rogatka river, [46.966064N, 142.748755E], 31.VIII.2009, K. Makarov, A. Zaytsev leg. (cMak); 1 ex., Sakhalin island, K. Tamanuki leg. (zisp); 1 ex., Kunashir Island, Goryachee Lake, 43.864444N, 145.498056E, 3–5.IX.2015, Yu. Sundukov leg. (zisp); 2 ex., Kunashir Island, Alekhina river middle stream, 43.916944N, 145.545556E, 04.VIII.2011, K. Makarov, A. Zaytsev leg. (cMak); 2 ex., Kunashir Island, Alekhina Cape, [43.925-43.920278N], 145.545556-145.53898E, 02.VIII.2009, K. Makarov, A. Zaytsev leg. (cMak); 2 ex., Kunashir Island, Mendeleevko, [43.963669N, 145.683072E], 07.IX.1997, A. Ryvkin leg. (zisp); 5 ex., Kunashir Island, Mendeleevko, [43.963669N, 145.683072E], 07.IX.1997, B. Korotyaev leg. (zisp); 1 ex., Yuzhno-Kurilskiy urban district, Kunashir island, Zolotaya river, [44.35792N 146.040382E], 24.IX.1981, Kabakov leg. (zisp); 2 ex., Kunashir island, Goryachee lake, 43.864444N, 145.498056E, 3–5.IX.2015, Yu. Sundukov leg. (cMak); ♂, Kunashir island, Goryachee lake, 43.864444N, 145.498056E, 3–5.IX.2015, Yu. Sundukov leg. (cMak); ♂, Kunashir island, Goryachee lake, 43.8725N, 145.484167E, 3–5.IX.2015, Yu. & L. Sundukov leg. (cMak); 4 ex., Kunashir island, Alekhina river middle stream, 43.916944N, 145.548333E, 04.VIII.2011, K. Makarov, A. Zaytsev leg. (cMak); 8 ex., Kunashir island, Saratovskaya river, 43.916944N, 145.548333E, 10–16.VIII.2013, Yu. & L. Sundukov leg. (cMak); JAPAN: Niigata: 3 ex., Tainai river, [38.283333N, 139.733333E], 29–31.VIII.1996, L. Masner leg. (zisp), for J-40 (cnc); 1 ex., Konuma, [37.95930N, 139.335076E], 12.VIII.1944, K. Kurasawa leg. (cnc); Tochigi: 3
Diagnosis. Pronotum black, with transverse elevation followed by impression; mesepimeron and mesepisternum without rough punctation; elytra black and yellow; abdomen at base yellow-brownish and black apex, or entirely black. Endophallus: apical distal lobe modified into sclerotized hook, spiculae forming this hook adjunct to common basal sclerotization (fig. 13A–E).

Among all species of *Oxyporus* in Russia *O. maxillosus* is most similar to *O. niger* from which it clearly differs by the presence of yellow spots on elytra and by shorter and wider bow-like, joined spiculae forming the apical hook of the endophallus.

Redescription. Body length 6.9–13.8 mm (n = 10). Head subovate to round, smooth, brown to black. Pronotum with transversal elevation followed by impression. Elytra black and yellow. Mesoepisterna and epimera with rough punctation, black. Abdomen at base yellow-brownish and black apex, or entirely black. Aedeagus: median lobe with round apex; endophallus with twin-coned spherical dorsal lobe covered with medium-sized denticles and transverse ventral lobe covered with tiny granulation, pair of spherical lateral lobes, and apical distal lobe modified into relatively wide sclerotized hook, bent dorsad; dorsal side of hook formed with relatively big ligament sclerite; spiculae pairs which form hook joined to basal sclerotization (figs 3A, 13A–E).

Comparison. Externally *O. maxillosus* is similar to *O. triangulus* from which it clearly differs by the narrower and differently shaped black band on elytra as well as by the structure of the endophallus, namely the sclerotized apical hook in place of the membranous distal lobe in *O. triangulus*.

Distribution. *Oxyporus maxillosus* is a Transpalaearctic species which in Europe is absent only in Spain, Italy and Sweden. This common species is widespread across Russia, where it is known from Leningrad, Vologda, Arkhangelsk, Murmansk, Kaluga, Sverdlovsk Provinces, Khanty-Mansi Autonomous Area, Republic of Altai, Tomsk Province, Krasnoyarsk Territory, Kemerovo Province, Republic of Buryatia, Irkutsk Province, Republic of Saha, Primorsky and Khabarovsk Territories, and Magadan and Sakhalin Provinces (fig. 12B).

Bionomics. Data on larval stages, life cycle duration and known fungal hosts, as well as a relatively complete account of all earlier published data concerning bionomics of this species, can be found in Tokareva et al. (2020).

Comments. *Oxyporus maxillosus* is a morphologically variable and widespread species with a very large pool of published data of varying quality and reliability. Our data here are sufficient to clarify its identity across the Russian territory, but it still requires a revision as far as the fauna of Japan is concerned. As in Europe, from where it was described (Germany) (Fabricius, 1793), *Oxyporus maxillosus* occurs in Siberia and Far East of Russia as two forms: a nominative form with bicolored abdomen and a form with the entirely black abdomen described by Gebler (1829) as *O. angularis* from Altai Region (Barnaul) and described by Ganglbauer (1895) as *O. maxillosus var. amurensis* from ‘Amur’. Based on the examination of extensive material here, some of which was DNA barcoded and dissected to examine the aedeagus including endophallus, both forms are conspecific and occur sympatrically. Therefore we corroborate their current widely accepted status as synonyms of *O. maxillosus*. We also note that the form with
the entirely black abdomen is much more frequent in the Eastern Palaearctic than the form with the bicolored abdomen. Another conclusion is that there is no sharp border between these two color forms, as sometimes a greater or lesser number of abdominal segments can be dark, or some segments can be transitionally bicolored. Analysis of the CO1 barcodes of a sample of these variously colored specimens from a broad geographic area including the Czech Republic, Russia (from Urals, Buryat and Altaí Republic, Khanty-Mansî Autonomous Area, and Primorsky Territory), Japan, and South Korea revealed 0.03 as a maximum genetic distance among them. Molecular and morphological examination of the material from Japan matching descriptions of *O. basiventris*, *O. aokii*, and *O. japonicus*, all species described from Japan (Jarrige, 1948; Dvořák, 1956; Sharp, 1889, respectively), confirmed our suspicion that they are conspecific with the morphologically variable *O. maxillosus*, and thus all should be synonymized with the latter when the respective type material is examined. For the purposes of this revision, we conclude that the form of *O. maxillosus* with bicolored abdomen was wrongly reported from the Russian Far East as *O. aokii* by Shavrin and Gildenkov (2009) and *O. basiventris* by Shabalin (2012). Although less relevant for our revision, we should note that *O. (O.) kobayashii* Hayashi, 2015 from Japan is highly likely a synonym of *O. maxillosus* as well, judging from the illustrations and characters given in the original description (Hayashi, 2015). Again, to check this hypothesis, a proper investigation including the type material should be done.

**Oxyporus (Oxyporus) niger** Sharp, 1889
(figs 3C, nA, B)

*Oxyporus niger* Sharp, 1889: 407; Kirschenblatt, 1938: 53; Shavrin and Gildenkov, 2009: 123; Shabalin, 2012: 414.

Type material examined. JAPAN: Lectotype, here designated: ♂, Oxyporus niger; Type D.S.; Japan. Lewis. Type Japan.; G. Lewis. Sharp Coll.; 1905-313’ (NHM); Paratypes: ♀, ‘O. niger. Japan.; G. Lewis.; 1910-320. Oya; 1.6.81’ (NHM); ♂, Japan.; G. Lewis. Sharp Coll.; 1905-313’ (NHM).

Other material examined. RUSSIA: Republic of Komi: ♂, middle flow of Maly Patok river, [64.3124N 59.0669E], 5.VII.1995, A.A. Medvedev leg. (MSh); Primorsky Territory: 2 ex., Anisimovka, Litovka mountain, 43.10263N 132.78437E, 26.VII.2019, in fungi, A. Tokareva leg. (ZISP); Lazovsky Nature Preserve, Korpat’ cordon, [43.2547N 134.1331E], 13–18.VII.2005, K. Makarov leg. (ZISP); Sakhalin Province: 4 ex., Kunashir Island, valley of Asin stream, S from Tretyakovo village, [43.9842N 145.6258E], 2.VII.2009, K. Makarov & A. Zaytsev leg. (MSh); 2 ex., Kunashir Island, Filatova river, [44.2100N 145.9727E], 15.VIII.1981, Kabakov leg. (MSh); ♀, Kunashir Island, Stolbchaty Cape, [44.0055N 145.7013E], 23.IX.2009, Mel’nik leg. (MSh); ♂, Kunashir Island, Tretjakovo env valley of Valentiny Stream, [43.9884N 145.6514E], 14.IX.2009, Mel’nik leg. (MSh); 2 ♀, Kunashir Island, hills S from Stolbchaty Cape, [44.0055N 145.7013E], 9.VII.2009, K. Makarov & A. Zaytsev leg. (MSh); 2 ♀, Kunashir Island, Stolbchaty Cape, [44.0055N 145.7013E], 9.VII.2009, K. Makarov & A. Zaytsev leg. (MSh); 2 ex., Kunashir Island, middle flow of river Zolotaya, 44.3622N 146.0283E, 24.VII.2013, K. Makarov leg. (KMk); 2 ex., Kunashir Island, near Alyokhina river, 43.9169N 145.5483E, 4.VII.2011, K. Makarov & A. Zaytsev leg. (KMk); JAPAN: Nagano prefecture: 2 ♂, Matsumoto, Kamikochi, [36.5986N 138.1897E], 23–24.VI.1939, E. Suenson leg. (MSh); Tochigi prefecture: ♀, Yumoto, Nikko, [36.6938N 139.8158E], 29.VI.1982, S. Naomi leg. (CNC).

Diagnosis. Body black, except pale brown tarsi, apical parts of labial palps and lateral parts of antennae. Pronotum with transverse ridge followed by impression; mesepimera and mesepisterna with scattered small
punctuation. Aedeagus: median lobe apically flat; endophallus: apical distal lobe modified into relatively narrow sclerotized hook, spiculae forming this hook adjunct to common basal sclerotization (fig. 11A, B).

**Redescription.** Body length 9.1–12.9 mm (n = 10). Head subovate to round, smooth, brown to black. Pronotum with transverse elevation followed by impression. Elytra black. Mesoepisterna and epimera with scattered punctuation, black; abdomen black. Aedeagus: median lobe with round apex; endophallus with twin-coned spherical dorsal lobe covered with medium-sized denticles and transverse ventral lobe with tiny granulation, pair of spherical lateral lobes, and apical distal lobe modified into relatively narrow sclerotized hook, bent dorsad; dorsal side of hook formed by relatively big long ligament sclerite; pairs of spiculae forming hook adjunct to prolonged common basal sclerotization (figs 3C, 11A, B).

**Comparison.** Among all other species of *Oxyporus* in Russia, *O. niger* is most similar to *O. maxillosus* from which it clearly differs by the lack of yellow spots on the elytra as well as by the distinctly longer and narrower hook-forming spiculae of the endophallus. *Oxyporus niger* is somewhat similar to *O. mannerheimii* in coloration but differs from the latter by the smooth pronotum without transverse ridge or impression, by the scattered and small punctuation of the mesopleurites, not to mention the different structure of endophallus.

**Distribution.** *Oxyporus niger* is known from the islands Kyushu (Sharp, 1889), Hokkaido, Honshu, and Shikoku (Nakane & Sawada, 1956) in Japan; from South Korea (Hwang & Ahn, 2000) and Russia. In Russia, it is currently known from the Komi Republic, Primorsky Territory and Sakhalin island (Kirschenblatt, 1938; Shavrin & Gildenkov, 2009; Shabalin, 2012 and our data) (fig. 10B).

**Bionomics.** This species was frequently found in *Pleurotus* sp. in the Russian Far East.

*Oxyporus (Oxyporus) procerus* Kraatz, 1879 (figs 4D, 14A, B)

*Oxyporus procerus*: Kraatz, 1879: 122; Kirschenblatt, 1938: 530; Shavrin and Gildenkov, 2009: 123; Shabalin, 2012: 414; Tokareva et al. 2020: 255.

**Material examined.** RUSSIA: Primorsky Territory: 2 ♀, Gornotaezhnoe, 43.6945N 132.15203E, 2–21.ix.2018, A. Tokareva leg. (ZISP); 3 ex., Vladivostok, Sputnik station, [43.2328N 132.0412E], 13.IX.2009, S. Shabalin leg. (FEB RAS); 4 ex., Ussuriysky District, [43.7889N 132.0276E], 10.VII.1976, Meshcheryakov leg. (FEB RAS); Primorsky Territory, Amgu, [45.8314N 137.6602E], 3.VII.2005, S. Surmach leg. (FEB RAS); 2 ex., Ussuriysky Nature Preserve, [43.6814N 132.5102E], 9.VII.1976, Makarkin leg. (FEB RAS); ♂, Shkotovsky District, upper flow of Zimukhe river, [43.3457N 132.6199E], 8.VI.1968, Krivolutskaya leg. (ZISP); 1 ex., Suputinsky Reserve, [43.6330N 132.2930E], 3.IX.1969, Kryzhanovskij leg. (ZISP); 1 ex., “Kedrovaya Pad” Nature Reserve, [43.1037N 131.4914E], 30.VIII.1980, Kireichuk leg. (ZISP); 1 ex., Tigrovaya, Suifun, near river Ussuri, [46.5621N 134.0073E], 20.IX.1926, Mayevsky leg. (ZISP); 1 ex., Preobrazhenskaya Bay (Syaukhe), [42.8940N 133.9194E], 5.VIII.1974, Pervakov leg. (ZISP); Khabarovsk Territory: 2 ♀, Sikhote-Alin mountains, near Amur, [48.8721N 137.4390E], 1910, Efremov leg. (ZISP); 1 ex., Zvenjevoj station, [46.7331N 134.3445E], 18–20.V.1958, Kabakov leg. (ZISP); 1 ex., Komsomolsk-on-Amur, Ilinsky Park, [50.5697N 137.0395E], 12.IX.1976, in *Pleurotus* sp., Mutinleg. (FEB RAS); 1 ♂, Bikin District, near Bira river, [47.1412N 134.2360E], 24.VI.1958, Kabakov leg. (ZISP).

**Diagnosis.** Rather large species with reddish or amber-yellowish forebody and black
abdomen. Aedeagus: median lobe apically two-pointed; endophallus: distal apical lobe membranous, slightly bent antero-dorsad, of equal width at base and apically; pair of dorsal and ventral spiculae connected by common weak basal sclerotization; ligament sclerite distinct (fig. 14A, B).

**Redescription.** Body length 11.1–16 mm (n = 11). Head subovate to round, smooth, brownish yellow to amber. Pronotum with slight transverse elevation. Elytra amber. Mesoepisterna and epimera with punctation, black; abdomen black. Aedeagus: median lobe apically two-pointed; endophallus with twin-coned

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**FIGURE 14** Schemes and photos of everted endophallus of *O. (O.) procerus* (A, B) and *O. (O.) rufus* (C, D). Acronyms: adsp – additional spiculae; ddl – dorsal distal lobe; dsp – dorsal spiculae; lgsc – ligament sclerite; ltl – lateral lobe; vl – ventral lobe; vsp – ventral spiculae. Scale bar: 0.1 mm.
spherical dorsal lobe covered with medium-sized denticles and two slightly transverse ventral lobes covered with tiny granulation, pair of spherical lateral lobes, and membranous apical distal lobe with pair of ventral and pair of dorsal thin spiculae, adjunct to common basal sclerotization and slightly tapering towards apex, and ligament sclerite (figs 4D, 14A, B).

Comparison. Among all species of Oxyporus in Russia, *O. procerus* is easy to distinguish by the large size and unique coloration.

Distribution. *Oxyporus procerus* is known from Primorsky Territory in the Russian Far East (Kirschenblatt, 1938; Shavrin & Gildenkov, 2009; Shabalin, 2012; Tokareva et al., 2020 and our data) and was recorded from China (Heilongjiang Prov.) by Aleksandrov (1934) (fig. 10B).

Bionomics. Data on larval stages, life cycle duration and known fungal hosts for this species can be found in Tokareva et al. (2020).

Comments. According to the structure of apical endophallic sclerites, *O. triangulus* is the closest relative of *O. procerus* in the Russian fauna, albeit both species look very different externally. Unfortunately, no CO1 sequences of *O. triangulus* are currently available.

**Oxyporus (Oxyporus) rufus** Linneus, 1758  
(figs 3D, 14C, D)

*Oxyporus rufus*: Linnaeus, 1758: 422; Kirschenblatt, 1938: 530; Shavrin and Gildenkov, 2009: 123 (as *O. rufus osawai*); Shabalin, 2012: 414. There are also a number of published, more or less precise records from European Russia in the faunistic literature.

Material examined. FINLAND: 1 ex., Rajala, Saima-Kanal, [61.0732N 28.3020E], 3.VII.1910, Adelung leg. (ZISP); 1 ex., Rajala, Saima-Kanal, [61.0732N 28.3020E] 14.VII.1907, Adelung leg. (ZISP); LITHUANIA: ♀, Vilnius, [54.7566N 25.4329E], VIII.1960, Kryzhanovskij leg. (ZISP); CZECH REPUBLIC:♂, Tachlovice, [49.9890N 14.2358E], 1944, (CNC); BULGARIA: ♀, Harmanli, [41.9285N 25.9224E], 9.VI.1974, O. Morek leg. (CNC); UKRAINE: Poltava Province: 1 ex., Yaresky, [49.8483N 33.9226E], 7.VII.1925, Fabri leg. (ZISP); Zhytomir Province: 1 ex., Zhytomir, [50.2816N 28.6790E], 16.VI.1897, Birulya leg. (ZISP); Khmel'nitskaya Province: 1 ex., Kam'yane'ts'-Podil's'kijy, [48.6709N 26.5788E] 1907, Yakubovsky leg. (ZISP); AZERBAIJAN: Astara Province: ♀, Astara, near Talysy river, [38.4927N 48.8596E], 19.VI.1932, Znoyko leg. (ZISP); GEORGIA: Tbilisi Province: 1 ex., Bakuriani, [41.7502N 43.5464E], 19.VI.1910, L. Mlokosewitsch leg. (ZISP); 3 ex., near Lagodekhi, [41.8463N 46.2786E], 24.IX.1968, in lamellate fungus, Kryzhanovskij leg. (ZISP); KAZAKHSTAN: 1 ex., Katon-Karagay Nature Preserve, near Bukhtarma river, [49.1736N 85.5791E], 15.VII.1989, Kastcheev leg. (ZISP); RUSSIA: Crimea Republic: 1 ex., Kuybyshev, [44.6286N 35.8633E], 27.V.1921, Kyzeritsky leg. (ZISP); Kaliningrad Province: 1 ex., near Chernyakhovsk, [54.6150N 21.8517E], 24.IX.1968, Lebedyazhe, [59.9554N 29.4305E] 2.VIII.1899, L. Bianchi leg. (ZISP); 1 ex., Peterhof District, Lebyazhye, [59.8948N 131.3649E], 4.VIII.2018, A. Tokareva leg. (ZISP); Leningrad Province: 1 ex., Saint Petersburg, Kamenny Island, [59.9785N 30.2898E], Yakobson leg. (ZISP); ♀, 59.59N 31.09E, (ZISP); ♀, Peterhof District, Olgino, [59.9941N 30.1291E], VII.1898, Tschitscherin leg. (ZISP); ♂, Luga District, railway to Warsaw, [58.7142N 24.6286E].
29.8115E], 25.VII.1905, Chekini leg. (ZISP);
Tver Province: 1 ex., Bologoye, [54.5154N 37.1242E], 15.VII.1898,
Bezval leg. (ZISP);
Tula Province: 1 ex., Aleksin, [53.9212N 39.5226E], 2.VI.1990,
Semenov leg. (ZISP);
Moscow Province: 1 ex., Boblovo, [56.3824N 37.0132E], 10.VI.1904,
Smirnov leg. (ZISP);
Yaroslavl Province: 1 ex., Belkino, [57.4550N, 39.7507E], 11–18.VI.1896,
Kokuev leg. (ZISP);
Voronezh Province: ♀, 30 km South from Ostrogozhsk, [50.6382N 39.1343E], 18.VII.2000, in fungi, Zurikov leg. (ZISP);
Lipetsk Province: ♀, “Galichya Gora” Natural Reserve, Morozova Gora area, [52.6011N 38.9262E], 6.VII.1995, oak forest, in Xerocomus sp., Zurikov leg. (ZISP);
Belgorod Province: 3 ♀, Borisovskaya District, “Belogorey” Nature Reserve, 50.6145N 35.9694E, 18.VII.2019, A. Tokareva leg. (ZISP); 1 ex., Novooskolsky District, [50.8191N 37.781576E], 9.VI.1897, Lindholm leg. (ZISP); 1 ex., Volgograd Province: [48.6594N 45.1542E], 9.VII.1990, Grebennikov leg. (ZISP);
Krasnodar Territory: ♀, Samara, [53.2942N 50.2117E], ex coll. Faust, (ZISP); 1 ex., near Bezymyanka river, [52.8523N 103.5001E], 12.VI.1909, Plyushchinskaya leg. (ZISP);
Republic of Chuvashia: 2 ♀, Ilyinka, [56.1807N 46.8262E], 25.VII.1928, “Zoological expedition” leg. (ZISP); 2 ex., Ilyinka, [56.1807N 46.8262E], 25.VII.1928, “Zoological expedition” leg. (ZISP);
Republic of Adygea: 7 ex., Guzeripl, road to cordon, [43.9996N 40.1294E], 15–16.VII.1971, in fungi, Pototskaya leg. (CNC);
Perm Territory: ♀, Kishert’ District, Preditalsky forest, [57.2317N 57.8849E], 6.VII.1961, Ponomareva leg. (ZISP);
Republic of Bashkortostan: 1 ex., Irgizly, [52.9632N 57.0292E], 6–7.VII.1999, Yakobson & Schmidt leg. (ZISP); 1 ex., Primorsky Territory: 2 ♀, Barabash-Levada, near Komissarovka river, [46.8000N 143.0702E], 25.VII.1978, in lamellate fungi, Filatova leg. (FEB RAS); 2 ex., Khasansky District, near Ryazanovka, [42.7995N 131.2404E], 13.VII.1979, Plutenko leg. (FEB RAS); 3 ex., Gornotaezhnoe, 43.6945N 132.15203E, 2–21.IX.2018, in fungi, A. Tokareva leg. (ZISP); ♀, Vladivostok, 43.2328N 130.0412E, 16.IX.2014, Leley leg. (FEB RAS); Pogranichny District, Pogranichny suburbs, 5 ex., 44.4230N 131.3649E, 20.VIII.2019, A. Tokareva leg. (ZISP).

Diagnosis. Pronotum reddish-yellow, smooth; pleurites and ventrite of mesothorax black; legs reddish with black coxae; elytra black with two reddish-yellow spots at base; abdomen reddish with black apex. Endophallus: apical distal lobe membranose, bent ventrad, dorsal and additional pairs of spicules form a cylinder broadening into weakly sclerotized oval supporting walls of the distal lobe (fig. 14C, D).

Redescription. Body length 6.5–11.5 mm (n = 10). Head subovate to round, smooth, black. Pronotum without transverse elevation, smooth. Elytra black with two reddish-yellow spots at base. Mesoepisterna and epimera with punctuation, black. Abdomen reddish with black apex. Aedeagus: median lobe apically rounded; endophallus: with twin-coned...
spherical dorsal lobe covered with medium-sized denticles and two slightly transverse ventral lobes covered with tiny granulation, pair of relatively big spherical lateral lobes, and membranous apical distal lobe bent ventrad, with pair of ventral spiculae tapering towards apex and pairs of dorsal and additional spiculae forming a complex, broadening into weakly sclerotized oval supporting walls of the distal lobe (figs 3D, 14C, D).

**Comparison.** Among all other species of *Oxyporus* in Russia, *O. rufus* is easy to distinguish by its stable and distinct coloration. In case of color aberration, this species is easily distinguished by the apical distal lobe of endophallus, which is curved ventrad and has central sclerites widening towards apex.

**Distribution.** *Oxyporus rufus* is a widespread Transpalaearctic species (Herman, 2001). In Russia, it is known from its European part, Siberia (numerous records) and Far East localities (Kirschner, 1938; Shavrin & Gildenkov, 2009; Shabalin, 2012) (fig. 12A).

**Bionomics.** A relatively complete account of all earlier published data concerning bionomics of this species can be found in Tokareva et al. (2020).

**Comments.** *Oxyporus rufus* is here confirmed as a single, widespread species based on the examination of DNA barcodes from a large sample of specimens.

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**Oxyporus (Oxyporus) triangulus** Sharp, 1889
(figs 4A, 15A, B)

*Oxyporus triangulus:* Sharp, 1889: 407; Shabalin, 2012: 415.

**Type material examined.** JAPAN: *Lectotype, here designated:* ♀, ‘Oxyporus triangulum; Type D.S.; Oyama 24.5.1880 Lewis\ Type\ Japan. G. Lewis\ Sharp Coll.; 1905-313’ (NHM);

*Paralectotypes:* 1 ♂, 1 ♀, ‘Oxyporus triangulum; var. D.S.; Nikko. Japan. Lewis\ Japan. G. Lewis \ Sharp Coll.; 1905-313’ (NHM); ♀, ‘Oxyporus triangulum; var. D.S.; Oyama 24.5.1880 Lewis\ Japan. G. Lewis\ Sharp Coll.; 1905-313’ (NHM).

**Other material examined.** RUSSIA:

Sakhalin Province: ♀, Kunashir Island, Tretjakovo, [43.9891N 145.6419E], 1.VII.1973, on fungi, I. Kerzhner leg. (ZISP); ♀, Kunashir Island, stream Zolotoy, [44.1725N 145.9470E], 22 IX.1981, I. Kabakov leg. (ZISP); ♀, Kunashir Island, Tretjakovo, [43.9891N 145.6419E], 1.VII.1971, Dolin leg. (ZISP); ♀, Kunashir Island, Stolbchaty Cape, [44.0055N 145.7013E], 23 IX.2009, Melnik leg. (KMK); ♀, Kunashir Island, Stolbchaty Cape, [44.0055N 145.7013E], 3.VII.2013, Yu. & L. Sundukovs leg. (KMK); ♀, Kunashir Island, Tretjakovo, [43.9891N 145.6419E], 1.VII.1957, Kabakov leg. (ZISP); ♀, Kunashir Island, Zolotaya river, [44.3571N 146.0403E], 23.VII.1988, Kabakov leg. (ZISP).

**Diagnosis.** Pronotum black, with transverse elevation followed by impression; mesepimera and mesepisterna with coarse punctation; elytra black and yellow with wide triangle longitudinal black band in the middle. Aedeagus: median lobe with apically two-pointed; endophallus: apical distal lobe membranous, slightly bent antero-dorsad, slightly widened at secondary gonopore; pair of dorsal and ventral spiculae connected by common weak basal sclerotization; ligament sclerite distinct (fig. 15A, B).

**Redescription.** Body length 8–13.4 mm (n = 13). Head subovate to round, smooth, dark brown to black. Pronotum with transverse elevation, black. Elytron with dense punctation across disk, black and yellow with wide triangular black band across in the middle (not reaching humerus). Mesoepisterna and epimera with punctation, black. Abdomen black. Male genitalia: median lobe apically two-pointed; inner aedeagal sac with twinned spherical dorsal lobe covered with medium-sized denticles and slightly transverse ventral lobe covered with tiny granulation, pair of spherical lateral lobes, and
membranous apical distal lobe with pair of ventral and pair of dorsal thin spiculae, adjunct to common basal sclerotization and widening towards apex, and ligament sclerite (figs 4A, 15A, B).

Comparison. Among Russian Oxyporus, O. triangulus is most similar to O. maxillosus, from which it differs in the wider triangular black band on elytra and in the structure of the apical sclerites of the endophallus (e.g., the absence of the strongly sclerotized apical hook).

Distribution. Oxyporus triangulus is known from the islands of Kyushu (Sharp, 1889),

FIGURE 15  Schemes and photos of everted endophallus of O. (O.) triangulus (A, B) and O. (P.) cyanipennis (C, D). Acronyms: ddl – dorsal distal lobe; dsp – dorsal spiculae; lgsc – ligament sclerite; vsp – ventral spiculae. Scale bar: 0.1 mm.
Hokkaido, Honshu, and Shikoku (Nakane and Sawada, 1956) in Japan, South Korea (Hwang and Ahn, 2000) and Primorsky Territory in Russia (Shabalin, 2012 and our data) (fig. 10B).

**Bionomics.** Currently unknown.

**Comments.** *Oxyporus triangulus*, described from Japan, was only recently recorded for Russia (Shabalin, 2012). Examination of the endophallus of the Japanese and Russian specimens confirmed their conspecificity and thus corroborated Shabalin’s record. Unfortunately, none of the available dried specimens of this species produced barcode sequences.

**Subgenus Pseudoxyporus Nakane & Sawada, 1956**

**Diagnosis.** Labrum without median line. Frons with median fovea or suboblong foveoid impression, and with such depressions on sides; antennae slender, as long as or longer than head, pubescent, medial antennomeres longer than width. Mentum trapezoid, evenly sclerotised, without membranous flaps on each side. Posterior pronotal angles usually with protuberances. Protarsomeres dorso-ventrally flattened, feebly dilated with fine and dense pubescence on ventral side of basal tarsomeres. Aedeagus: parameres about as long as median lobe, or at least half of its length; median lobe cylindrical, as strongly sclerotized as basal bulb, ventral wall sclerotized, median orifice opened apically (Nakane & Sawada, 1956).

**Oxyporus (Pseudoxyporus) cyanipennis Kirshenblat, 1938**

(figs 4B, 15C, D)

*O. cyanipennis:* Kirshenblat, 1938: 528; Shabalin, 2012: 415; Makranczy 2012: 115.

**Type material examined.** RUSSIA: Holotype: ♂, ‘(gold colored paper disk)\ Between Upper Pyankovka and Kebezen [in Russian]\ Oxyporus; cyanipennis, sp.n.; Kirschenblatt det.\ Holotyper; Oxyporus; cyanipennis Kirsch.; ver. Makranczy, 2005\ Pseudoxyyporus; cyanipennis Kirschenblatt; det. Makranczy, 2005’ (ZISP).

**Other material examined.** RUSSIA: Primorsky Territory: 9, Anisimovka, Litovka mountain, [43.10263N 132.78437E], 3.V.1975, A.V. Plutenko leg. (FEB RAS); ♂, Suputinsky, [43.6327N 132.2902E], 20. VI.1961, Kabakov leg. (ZISP).

**Diagnosis.** Head bicolored, scutellum with faint punctures, elytra metallic blue with dense rough punctuation. Ventral lobe of endophallus transversely divided.

**Redescription.** Body length: 7.5–8.4 mm (n = 3). Head round to subovate, smooth, black and red. Pronotum smooth, without distinct protuberances on posterior angles. Scutellum with several faint punctures. Elytra with irregular rough punctuation, metallic blue with red-yellow humeri. Mesepisterna and epimera smooth, red. Abdominal segments i–vi pale yellow to dark red, sometimes with black areas on tergite and sternite vi, segments vii–ix dark brown to black. Aedeagus: median aedeagal lobe with oval aperture with membrane at dorsal side of basal bulb and with acute apex; endophallus: with single dorsal circular lobe with fine granulation and twin-coned ventral lobe subdivided by transverse line covered with medium-sized denticles; apical distal lobe ventrally curved and consisting of three solid sclerites forming two shells and apical hood, apical membranous shell with massive distinct sclerite inside protruding from hood (figs 4B, 15C, D).

**Comparison.** This species is easy to distinguish from any other *Oxyporus* in Russia due to its spectacular coloration alone.

**Distribution.** *Oxyporus cyanipennis* is known from Russia: Primorsky Territory.
(Kirschenblatt, 1938; Shabalin, 2012) and Japan (Shibata, 1997) (fig. 10A).

**Bionomics.** Unknown.

**Comments.** This rare and remarkable species, described from Russia, was later revised by Makranczy (2012), where the photo of habitus, detailed description, and figures of endophallus inside the median lobe were presented for the first time. Even though at the moment it is very easy to distinguish this species based on the coloration alone, here we report the structure of its fully everted endophallus and CO1 sequence for the first time.

**Oxyporus (Pseudoxyporus) dybowskii Solsky, 1871**

(figs 4E, 16A, B, 17)

*O. dybowskii:* Solsky, 1871: 242; Kirschenblatt, 1938: 529; Shabalin, 2012: 415; Makranczy 2012: 116

**Type material examined.** RUSSIA: Lectotype: ♂, ‘Irkutsk-Ussol; Dybw. 9-o Uo. Oxyporus; Dybowskii mihi Solsky’s collection [in Russian]. Oxyporus; dybowskii; Kirschenblatt det. Zoological Institute; Russian Academy; of Sciences; St. Petersburg; Lectotypus; Oxyporus; dybowskii Solsky; des. Makranczy, 2012 Oxyporus (Pseudoxyp.); dybowskii Solsky; det. Makranczy, 2012’ (ZISP).

*Other material examined.** RUSSIA: Republic of Altai: 4 ex., Chemalsky District, South-East of village Edigan, 51.0546N 86.3791E, 27.VII.2019, A. Solodovnikov & A. Hansen leg. NHMD; Primorsky Territory: ♂, Suputinsky, [43.6327N 132.2902E], 23.VI.1961, Kabakov leg. ZISP; ♀, Kavalersky District, Lipovy stream, [44.3010N 134.9825E], 20.VII.1978, Filatova leg. (FEB RAS); ♂, Anisimovka, [43.10263N 132.78437E], 10.VII.1978, Filatova leg. (FEB RAS), Sakhalin Province: ♀, Sakhalin Island, Listvennichnoe river upper stream, 46.8683N 142.7648E, 29.V.2019, K.V. Makarov leg (cMk).

**Diagnosis.** Pronotum red, with conspicuous protuberances on posterior angles, elytra tricolored with reddish-yellow markings on humeri and pale yellow posterior edges. Aedeagus: median lobe with two-pointed apex; endophallus small, with vermiform ventral lobe and four sclerotised shells not surrounded with membrane as apical sclerites.

**Redescription.** Body length: 6.1–8.5 mm (n = 4). Antennae piceous to light brown, longer than head, narrow; antennal segments reverse semi-triangular. Head round to subovate or slightly rectangular, smooth, black; frons with two longitudinal depressions behind antennae. Pronotum red, with distinct protuberances on posterior angles and thus slightly trapezoid. Scutellum smooth. Elytra black with reddish-yellow point on humeri and pale yellow posterior edge. Mesoepisterna and epimera smooth, black. Abdominal segments III-VI reddish to dark red, sometimes with black areas on middle line of each tergite and almost fully black tergite VI, segments VII-IX dark brown to black. Aedeagus: median lobe with two-pointed apex; endophallus: rather small, with single ventral circular lobe with tiny granulation and vermiform dorsal lobe without granulation; apical distal lobe ventrally curved and consists of four solid sclerites forming two pairs of shells, ventral pair bigger than dorsal, each sclerite of this pair apically curved (figs 4E, 16A, B, 17).

**Comparison.** *Oxyporus (P.) dybowskii* is close in coloration to *O. (O.) rufus*, but can be easily distinguished by the elevated posterior angles of pronotum (figs. 17).

**Bionomics.** Unknown.

**Distribution.** *Oxyporus (P.) dybowskii* is known only from Russia, from Irkutsk Province (Solsky, 1871), Primorsky Territory (Shabalin 2012; material here) and Altaisky Territory (new data). This first record from
Altay significantly broadens the known distribution of this species (fig. 10A).

Comments. This rare species, described from Russia, was revised by Makranczy (2012), who provided a photo of the habitus, detailed description, and the figures of endophallus inside the median lobe for the first time. Even though at the moment this is a very easy to distinguish species based on coloration alone, here we report the structure of its fully everted endophallus for the first time because of its high potential for species diagnostics. Based on the description of external morphology, habitus photo and drawing of the aedeagus
of *O.(P.) pulchellus* in its original description (Huang et al., 2006), we suspect that this species, described from two specimens from the Mt. Changbai from Jilin Province of China, may be conspecific with *O.(P.) dybowskii*.

*Oxyporus (Pseudoxyporus) melanocephalus* Kirschenblatt, 1938
(figs 4C, 16C, D)

*O. melanocephalus*: Kirschenblatt, 1938: 529, 534; Makranczy, 2012: 122; Shavrin and Gildenkov, 2009: 123; Shabalin, 2012: 415; Tokareva et al., 2020: 257.

*Type material examined.* RUSSIA: Holotype: ♂, ‘[gold colored paper disk]\ Sedanka 31.V.; Приморск. обл. 0,15; Римский-Корсак [Sedanka 31.V. Primorskaya Province 0,15]\ Oxyporus; melanocephalus, sp.n.; Kirschenblatt det.\ Zoological Institute; Russian Academy; of Sciences; St. Petersburg\ Holotypus; Oxyporus; melanocephalus Kir.; ver. Makranczy, 2012\ Oxyporus (Pseudoxyp.); melanocephalus Kirsch.; det. Makranczy, 2012’ (ZISP).

*Other material examined.* RUSSIA: Kamchatka Territory: 4 ex., upper flow of Listvennichnaya river, 52.3316N 158.3076E, 29.V.2019, K. Makarov leg. (KMk); Primorsky Territory: ♂, Suputinsky, [43.6327N 132.2902E], 12.VI.1960, Kabakov leg. (ZISP); ♂, middle course of Dalnaya river, [46.2741N 135.6691E], 31.VIII.1985, Kabakov leg. (ZISP); ♂, Gornotaezhnoe, 43.6945N 132.15203E, 2–21.IX.2018, in fungi, A. Tokareva leg. (ZISP); ♂, Kedrovaia Pad’ Nature Preserve, Kedrovaia river valley, [43.1029N 131.4897E], 16.VI.1983, Kireichuk leg. (ZISP).

*Diagnosis.* Head black and pronotum and elytra piceous red. Aedeagus with oval aperture with membrane at dorsal side of basal bulb; endophallus with relatively big vermiform ventral lobe and apical sclerite surrounded with membrane.

*Redescription.* Body length: 8.1–12.8 mm (*n = 3*). Antennae black, longer than head, narrow; antennal segments distinctly widened apicad. Head round to subovate or slightly rectangular, smooth, black; frons with two longitudinal depressions behind.

**Figure 17** *O.* (*P.*) *dybowskii* on a mushroom in Altay mountains where it was collected. Photo by Aslak Kappel Hansen.
antennae. Pronotum brick-red, with transverse elevation. Scutellum smooth. Elytra brick-red. Mesoepisterna and epimera smooth, black. Abdomen black. Aedeagus: median lobe truncate; endophallus: with vermiform dorsal lobe with granulation in rows, wide transverse ventral lobe with fine granulation, and pair of spherical lateral lobes; apical distal lobe divided by the membranous fold, bent ventrad and twin-coned, consisting of small membranous granulated spherical lobe dorsally and protruding granulated membranous lobes with r sclerite adjunct to inner proximal edges, lobes apically connected by membranous hood (figs 4C, 16C, D).

Comparison. This species is easy to distinguish from any other Oxyporus in Russia due to its spectacular coloration alone, i.e., a combination of black head and abdomen and reddish pronotum and elytra.

Bionomics. Data on larval stages, life cycle duration and known fungal hosts, including a relatively complete account of all earlier published bionomic information about this species can be found in Tokareva et al. (2020).

Distribution. This species is known only from Russia: Primorsky Territory (Kirschenblatt, 1938; Shabalin, 2012) and Sakhalin Province (new data) (10A).

Comments. This species was described from Russia and is more common than other Russian Pseudoxyyporus. It was revised by Makrancy (2012), who provided a habitus photo, a detailed description, and the first figures of its endophallus. Even though at the moment this is a very easy to distinguish species based on the coloration alone, here we report the structure of its endophallus in detail.

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Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.14267558

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