

RESEARCH PAPER

Revision of *Quedius sensu stricto* (Coleoptera: Staphylinidae)

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Abstract. We here present the first integrative revision of the subgenus *Quedius* Stephens, 1829 sensu stricto where taxonomic decisions are based on morphology, genomic phylogeny (published elsewhere) and single locus DNA evidence. The subgenus is restricted to the Holarctic region and includes some of the largest, most robust members of the genus *Quedius*. For species delimitation, a total of 200 COI barcodes covering nearly all species within the subgenus were evaluated through phylogenetic, cluster and network analysis. Taxonomic, distributional and bionomic data, all hitherto published and new are synthesized and an identification key is constructed for all species. All 20 species of *Quedius* s. str. are divided into five species groups based on genomic phylogeny, morphology, distributional patterns and practical considerations. Overall, there was good congruence among various lines of evidence. As exceptions, high COI barcode variability was found within the wingless and patchily distributed *Q. unicolor* Kiesenwetter, 1847 and *Q. sundukovi* Smetana, 2003 (3 and 5 BOLD BINs, respectively) from the *Q. molochinus*-group without corresponding morphological or geographic patterns. On the contrary, in the *Q. pallipes*-group very little divergence in the COI barcode was found between clearly morphologically separated species. From the taxonomically challenging Nearctic *Quedius molochinoides*-group, *Quedius altanai* Hansen & Brunke sp. nov. is described as new species from the central and southern Rockies, rendering *Q. lanei* Hatch, 1957 to be restricted to the eastern foothills of the Cascades, Sierra Nevada and Blue Mountains. In the case of *Q. subunicolor* and *Q. altaicus*, continuous morphological and COI variation firmly established the earlier suspected synonymy *Quedius subunicolor* Korge, 1961 = *Quedius altaicus* Korge, 1962 syn. nov. Other new synonyms established here are: *Quedius pallipes* Lucas, 1849 = *Quedius simplicifrons* Fairmaire, 1861 syn. nov. = *Quedius levasseuri* Coiffait, 1964 syn. nov.; *Quedius hispanicus* Bernhauer, 1898 stat. reinstated = *Quedius cobosi* Coiffait, 1964 syn. nov.; *Quedius fuliginosus* (Gravenhorst, 1802) = *Quedius latus* Hochhuth, 1851 syn. nov. = *Quedius viduus* Sawada, 1965, syn. nov. *Quedius gracilis* Stephens, 1832 syn. rev. is moved from synonymy with *Q. fuliginosus* and placed into synonymy with *Q. curtippennis* Bernhauer, 1908, the younger being the valid name due to prevailing usage in accordance with the ICZN Article 23.9; *Quedius hammianus* Sharp, 1911 syn. revid., *Q. secundus* Last, 1952 syn. revid., and *Q. rufulus* Blümmel, 1898 syn. revid., are moved from synonymy with *Q. simplicifrons* and placed into synonymy with *Q. hispanicus* Bernhauer, 1898; *Quedius sardous* Gridelli, 1924 syn. revid., and *Q. leonhardi* Bernhauer, 1914 syn. revid., are moved from synonymy with *Q. molochinus* (Gravenhorst, 1806) to synonymy with *Q. pallipes*. Human mediated dispersals, most likely through the historical transport of ship ballast, are noted as regular phenomenon for some members of the subgenus. *Quedius fuliginosus*, *Q. curtippennis* and *Q. molochinus*, introduced from the Palearctic to the Nearctic, are the most noticeable examples.

Key words. Coleoptera, Staphylinidae, Quediini, integrative taxonomy, barcoding, species delimitation, phylogeny, network analysis, COI gene, biogeography, human mediated dispersal, Holarctic Region

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:28D55112-98B1-49A5-B382-58B1B068570B>

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Introduction

We revise the rove beetle subgenus *Quedius* Stephens, 1829 sensu stricto, which includes some of the largest, most robust members of the genus *Quedius*. *Quedius* sensu lato is a very large and non-monophyletic taxon found across most of the Northern hemisphere with more than 700 species currently known (SMETANA 1971, 2017; HERMAN 2001; SOLODOVNIKOV 2012; BRUNKE et al. 2016). The current classification of *Quedius* has not yet been updated to accommodate recent phylogenetic results, which have unambiguously demonstrated that the genus is polyphyletic, especially with respect to the species rich subgenera *Raphirus* Stephens, 1829 and *Microsaurus* Dejean, 1833 (SOLODOVNIKOV 2006; BRUNKE et al. 2016, 2019, 2021). On the other hand, the monophyly of the morphologically uniform *Quedius* s. str. has not been challenged in any of these studies, and is in fact firmly confirmed in a large-scale genomic study of the tribe Quediini (BRUNKE et al. 2021). That study includes members of nearly all known species groups of *Quedius* s. str. and recovered them as a monophyletic sister group to a clade comprising *Quetarsius* Smetana, 1996 and the *pluvialis*, *meei*, *bleptikos*, *himalayicus* groups of the *Quedius* lineage (BRUNKE et al. 2021). Another as yet unpublished phylogenomic and biogeographic study by the authors includes almost all members of *Quedius* s. str., and

we use the phylogenetic topology of that study as a guide for the division of *Quedius* s. str. into species groups in this revision (Fig. 1) (A. Hansen et al., in prep.).

All *Quedius* s. str. are active ground-living predators, and are often found in or around moist debris, tussocks and mosses. They are thus often associated with water bodies, such as lakes, rivers, swamps, but also saline coastal habitats (Fig. 2; SMETANA 1971, SOLODOVNIKOV 2012, SALNITSKA & SOLODOVNIKOV 2019; A. Hansen, pers. observ.). They are regularly sifted out from leaf litter or collected by pitfall traps. *Quedius* s. str. is distributed across the Holarctic Region, with the Palearctic species found in Europe, Northern Africa, Middle East and Middle Asian mountains, and across Siberia to the Far East of Russia. The Nearctic species are found in most areas of North America except the southwest, Arctic, and much of the Great Plains and Canadian Prairies of the continent. Several species have been moved around by humans and thus display unnatural distributions. Some species of *Quedius* s. str. are very common in collections, but most representatives of the group are rare. Instead, they are represented by a single or a handful individuals at most.

Although they are relatively well-known, a taxonomic revision of the genus *Quedius* s. str. is needed, mainly to clarify the identity and distributions of the clusters of

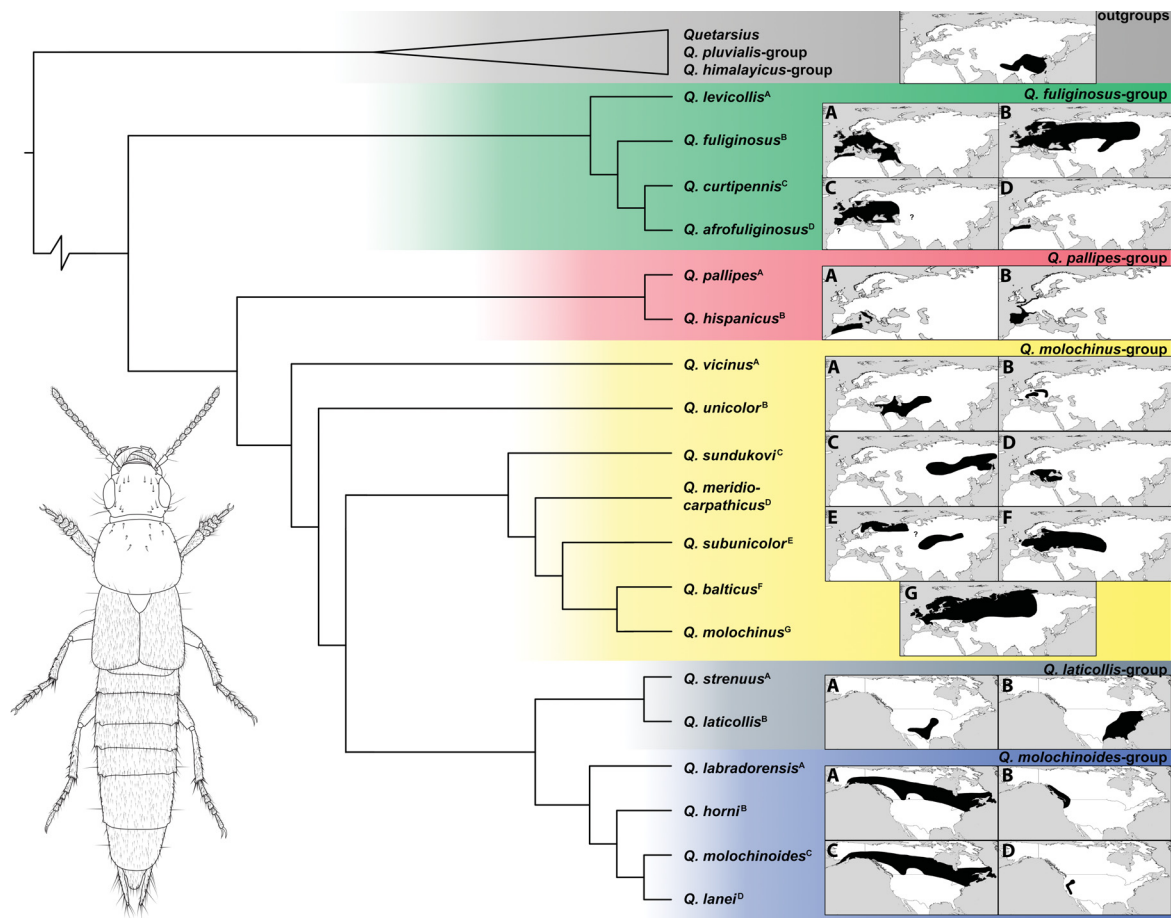


Fig. 1. Phylogenetic tree of *Quedius* s. str. based on preliminary target capture molecular dataset of BRUNKE et al. (2021) and HANSEN et al. (in prep.). Species groups shown in color. *Q. altanai* Hansen & Brunke, sp. nov. of the *Q. molochinoides*-group was not included in the dataset. Habitus sketch is of *Q. fuliginosus* (Gravenhorst, 1802). Lettering denotes species distribution within their respective groups.

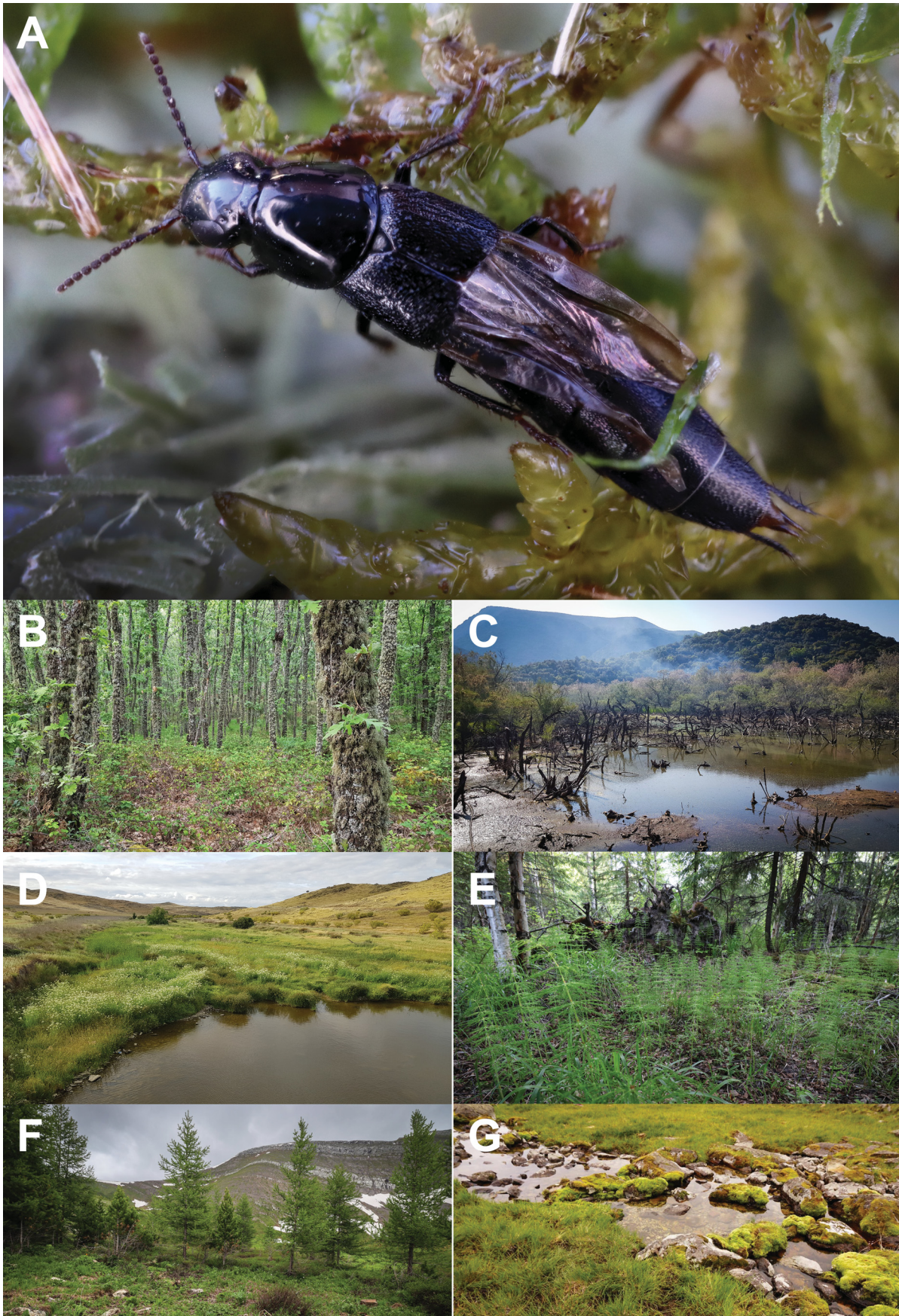


Fig. 2. Habitats of *Quedius* s. str. A – *Q. fuliginosus* (Gravenhorst, 1802) in mossy habitat in a forest on Zealand, Denmark; B – Oak forest habitat of *Q. levicollis* Brullé, 1832 found in litter in Extremadura, Spain; C – Saline lake habitat of *Q. meridiocarpaticus* Smetana, 1958 found in bank litter on Peloponese, Greece; D – River bank habitat of *Q. hispanicus* Bernhauer, 1898 found in flood debris in Extremadura, Spain; E – Wet mixed forest habitat of *Q. fuliginosus* found in litter in Southern Ural, Russia; F – Alpine near tree line habitat of *Q. subunicolor* Korge, 1961 found under stones at 1700 m in Altai Mountains, Russia; G – Alpine mossy creek habitat of *Q. unicolor* Kiesenwetter, 1847 found in moss in Italian Alps (Photo: A. Zanetti).

similar species that have been frequently confused in the past. In the emerging phylogenetic framework of Quediini, *Quedius* s. str. stands out as a well-defined group with a high potential to serve as a model to address various questions about Holarctic ecology and biogeography. For example, they display a clear Nearctic-Palaearctic split, as well as species varying in habitat specificity. We here summarize available data for *Quedius* s. str., including taxonomy, geographical distributions and bionomics. A major focus is to clarify the limits and distributions of several species that historically have been mixed due to their very similar external appearance, which led to a wealth of uncertainty regarding the distribution and their exact characteristics. For that reason, this revision is based on quantitative methods as much as possible, such as species delimitation with cytochrome oxidase I (COI) barcodes and network analysis. The main body of the revision includes morphological diagnoses, mapped distributions, bionomic profiles, as well as an identification key for all species. Immature stages have been outside the scope of this revision, but when available, references to such are mentioned, and future studies will hopefully shed more light on this neglected part of the life cycle. It is the ambition of the current study that it will help to improve further studies of the genus *Quedius* as well as rove beetles in general.

Taxonomic history

The genus *Quedius* was erected for seven valid species and 32 unavailable names. The authorship of the genus has been disputed, as CURTIS (1829) and STEPHENS (1829) both named *Quedius* in the same year, and there has been found no evidence of the exact dates of publication of these two authors. According to the ICZN, STEPHENS (1829) is the author of *Quedius* because TOTTENHAM (1949), the first revisor, gave him preference over CURTIS (1829). This is summarized in SMETANA (1995: 56), as the same problem has persisted for *Philonthus* Stephens, 1829. Furthermore, STEPHENS (1829) attributed the genus to Leach without mentioning a reference. As there is no evidence that Leach formally described and validated the genus, STEPHENS (1829) has become the formal author. Also, the type species of *Quedius* Stephens, 1829 has been cited as '*Staphylinus tristis* Gravenhorst, 1802' but as this is not an available name for the relevant taxon, this problem was discussed in NEWTON (1995) with subsequent action by the ICZN, which designated *Staphylinus levicollis* Brullé, 1832 as the type species of *Quedius* in the Opinion 1851 (ICZN 1996).

The classification of *Quedius* was in flux for a long time, while a few subgenera were proposed. The composition and status of these subgenera were shifting between genus and subgenus rank. For example, both *Raphirus* Stephens, 1829 and *Microsaurus* Dejean, 1833, currently the biggest subgenera of *Quedius*, were originally proposed as genera. MULSANT & REY (1876) were the first to use the broad concept of *Quedius*, which included *Microsaurus* and others as subgenera. They assigned species from what we currently understand as the subgenus *Quedius* s. str. to *Microsaurus*. A modern definition of *Quedius* s. str. and

other subgenera starts with the revision of *Quedius* by GRIDELLI (1924) who recognized members of *Quedius* s. str. by the entire labrum, a character which is still one of the main diagnostic characters of the subgenus. The first species placed currently in *Quedius* s. str. were described by GRAVENHORST (1802, 1806) in *Staphylinus* Linnaeus, 1758 prior to the fixation of the genus by Stephens. These included *Q. fuliginosus* (Gravenhorst, 1802), *Q. molochinus* (Gravenhorst 1806) and the North American species *Q. laticollis* (Gravenhorst, 1802). Even after *Quedius* was formally named, a few species now placed in *Quedius* s. str. were still being described in *Staphylinus*, for example, *Q. levicollis* (Brullé, 1832) and *Q. vicinus* (Ménétriés, 1832). Years later, species like *Q. unicolor* Kiesenwetter, 1847, *Q. pallipes* Lucas, 1849, *Q. hispanicus* Bernhauer, 1898 and *Q. curtippennis* Bernhauer, 1908, were described in *Quedius*.

During the mid 1900s, several additional species were discovered when local faunas throughout Europe were investigated more thoroughly. In this period several countries or geographic regions in Europe were subjected to their first proper taxonomic revisions, keys or ecological reviews that included *Quedius* s. str. These include the publications of TOTTENHAM (1949); HANSEN (1952); SMETANA (1958, 1960b, 1962); COIFFAIT (1961, 1964); PALM (1963); LOHSE (1964); HORION (1965) and BORDONI (1976). This led to the discovery of additional rare species, or species from areas not yet fully explored, including *Q. balticus* Korge, 1960, *Q. meridiocarpaticus* Smetana, 1958, and *Q. subunicolor* Korge, 1961. In fact, the taxonomic publications of Horst Korge should be highlighted in this context since some of them were specifically focussed on species of *Quedius* s. str. in the Western Palearctic (KORGE 1960a,b, 1961, 1962a,b). This period was concluded by COIFFAIT (1978), who made the first attempt to summarize the whole quediine fauna of the Western Palearctic.

Although the first species of *Quedius* s. str. from North America, *Q. laticollis*, was described as early as in GRAVENHORST (1802), the new world fauna was not thoroughly explored until much later. Currently the genus has been reviewed three times in North America. First by HORN (1878), later by CASEY (1915) and most recently by SMETANA (1971a), with supplements in SMETANA (1971b, 1973, 1976, 1978, 1981 and 1990). Apart from that, some species were added by HATCH (1957), who revised the beetle fauna of the Pacific Northwest in North America.

After the monographs of SMETANA (1971) and COIFFAIT (1978) there has been no attempt to synthesize the knowledge of the subgenus *Quedius* s. str. for either the entire Nearctic or Palaearctic. There were only more or less inclusive new data on *Quedius* s. str. published for these regions in LOTT & ANDERSON (2011), SOLODOVNIKOV (2012) and SALNITSKA & SOLODOVNIKOV (2018a, 2019), including the description of two additional species, *Q. afrofuliginosus* Gusarov, 1991 and *Q. sundukovi* Smetana, 2003. This study is the first comprehensive revision of *Quedius* sensu stricto, with the Palearctic and Nearctic faunas of this lineage considered in their integrity.

Material and methods

Material. This study is based on 2543 specimens (Table S1) that are deposited in the following collections:

AFC	Atlantic Forestry Centre, Natural Resources Canada, Canadian Forest Service, Fredericton, New Brunswick, Canada (R.P. Webster);	SMNH	Royal Saskatchewan Museum, Regina, Saskatchewan, Canada (C. Sheffield);
AMNH	American Museum of Natural History, New York, New York, USA (L. Herman);	SNMC	Slovenské Národné Muzeum, Bratislava, Slovakia (V. Jánký);
CAS	California Academy of Sciences, San Francisco, California, USA (C. Grinter);	STFX	St. Francis Xavier University, Antigonish, Nova Scotia (R. Lauff);
CBU	Cape Breton University, Sydney, Nova Scotia (D.B. McCorquodale);	TAMU	Texas A & M University, College Station, Texas, USA (J. Oswald);
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (J. Fetzner);	UAM	University of Alaska Museum, Entomology Collection, Fairbanks, Alaska, USA (D. Sikes);
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ontario, Canada (A. Smetana & A. Brunke);	UASM	University of Alberta, E.H. Strickland Entomological Museum, Edmonton, Alberta, Canada (F. Sperling);
CUIC	Cornell University, Ithaca, New York, USA (C. Moreau);	UBC	University of British Columbia, Spencer Museum, Vancouver, British Columbia, Canada (K. Needham);
cAnl	Personal collection of S. Anlaş, İzmir, Turkey;	UNHC	University of New Hampshire, Durham, New Hampshire, USA (D. Chandler);
cBor	Personal collection of A. Bordoni, Firenze, Italy;	USNM	Smithsonian Institute, National Museum of Natural History, Washington D.C., U.S.A. (D. Furth & F. Shockley);
cCha	Personal collection of C. Chantel, Quebec City, Quebec, Canada;	UWBM	University of Washington, Burke Museum, Seattle, Washington, USA (R. Crawford);
cCor	Personal collection of J. F. Cornell, Boone, North Carolina, USA;	ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (B. Korotyaev & M. Salnitska);
cHoLa	Personal collection of R. R. Hooper and H. Lambert, Sillery, Quebec, Canada;	ZMHB	Museum für Naturkunde, Berlin, Germany (J. Frisch & M. Uhlig);
cJen	Personal collection of J. Jenkins Shaw, London, UK;	ZMMU	Zoological Museum of Moscow State University (A. Gusakov);
cKur	Personal collection of S. A. Kurbatov, Moscow, Russia;	ZMUO	Zoologiska Muset, Universitets Oulu, Oulu, Finland (M. Mutanen).
cNel	Personal collection of G. H. Nelson, Kansas City, Missouri, USA;		
cMaj	Personal collection of C. C. Majka, Halifax, Canada;		
cMil	Personal collection of W. V. Miller, Ramsey, New Jersey, USA;		
cSch	Personal collection of M. Schülke, property of ZMHB;		
cSha	Personal collection of A. Shavrin, Daugavpils, Latvia;		
cSme	Personal collection of A. Smetana, property of National Museum of Nature and Science Tsukuba, Japan;		
cWeb	Personal collection of D. Webster, Kentville, Nova Scotia, Canada;		
DEBU	University of Guelph, Guelph, Ontario, Canada (S. Paiero, S. Marshall);		
DBUM	University of Montreal, Collection Entomologique Ouellet-Robert, Montreal, Quebec, Canada (C. Favret);		
FMNH	Field Museum of Natural History, Illinois, USA (M. Thayer, A. Newton, S. Ware & M. Tucatel);		
INHS	Illinois Natural History Survey, Champaign, Illinois, USA (T. McElrath);		
ISU	Iowa State University, Ames, Iowa, USA (G. Courtney);		
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (C. Maier);		
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain (M. Alonso-Zarazaga);		
MNHN	Muséum National d'Histoire Naturelle, Paris, France (O. Montreuil);		
MUNC	Memorial University of Newfoundland, St. John's, Newfoundland (D. Larson);		
MZH	Finnish Museum of Natural History, Helsinki, Finland (S. Tarasov, J. Mattila, and P. Malinen);		
MZLU	Lund Museum of Zoology, Lund, Sweden (C. Fägerström);		
NHMD	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Denmark (A. Solodovnikov);		
NMEG	Naturkundemuseum, Erfurt, Germany (M. Hartmann);		
NMPC	National Museum, Prague, Czech Republic (J. Hájek);		
NMW	Naturhistorisches Museum Wien, Vienna, Austria (H. Schillhammer);		
NSMC	Nova Scotia Museum, Halifax, Nova Scotia, Canada (C. Majka);		
NSNR	Nova Scotia Department of Natural Resources, Shubenacadie, Nova Scotia, Canada (J. Ogden);		
OSU	Ohio State University, C.A. Triplehorn Insect Collection, Columbus, Ohio, USA (L. Musetti);		
SDEI	Senckenberg Deutsches Entomologisches Institut, Münchenberg, Germany (S. Blank);		

We attempted to study type material as far as possible except cases where it was not necessary because of clear taxonomy. In some cases, we were unable to study type specimens themselves but we received their informative images instead. For the type specimens we examined, labels are transcribed fully, which is indicated by denoting label information by quotation marks (“”) where each particular label start and end is denoted by a slash (/). For the non-type material label data, when unambiguously interpreted, is recorded as follows, independent of the actual wording on labels or their order: **COUNTRY:** **STATE:** Locality, Latitude, Longitude, Elevation, Collecting method, Habitat notes, Date, Collector, (number of specimens and their sex, Collection). Square brackets [] are used for our interpretation of ambiguous label data and for georeferencing labels without coordinates (e.g. finding geographic coordinates for toponyms via Google Maps or similar tools).

Distribution maps were constructed in Simplemapp (SHORTHOUSE 2010) using coordinates either available on labels or found for given localities using Google Maps searches. For the North American species, we use the ecoregion defined through the COMMISSION FOR ENVIRONMENTAL COOPERATION (1997) for discussion and detailed definition of distribution.

Morphological study. Specimens were examined using a Leica MZ APO Stereoscope. Aedeagi were dissected after the detached terminalia (aedeagus, abdominal segments IX and X) were removed and cleared in a 10 % KOH (Potassium hydroxide) aqueous solution for 30 to 90 minutes at room temperature depending on the degree of sclerotization. Dissected aedeagi were either mounted directly on the card of the specimen or put in glycerin filled microvial pinned with their respective specimen. Measurements were performed on 10 specimens (5 males and 5 females) from each species if available using ocular

micrometer on the Leica MZ APO Stereoscope. For long series, specimens for measurements were chosen based on the visual examination of the whole series to include the entire body size range. All measurements are given in millimeters (mm) or ratios. The following measurements have been taken:

HL	head length (along midline from the anterior clypeal margin to the occipital constriction);
HW	head width (maximal, including eyes);
EyL	eye length (in dorsal view);
TL	temple length (in dorsal view);
PL	pronotum length (along midline);
PW	pronotum width (maximal);
EL	elytral length (maximal, from shoulders to the distalmost point of the posterior margin of elytra);
EW	elytral width (maximal);
Esut	elytral sutural length (along suture, from tip of scutellum to sutural angle).

Forebody length (HL+PL+EL) is used in addition to the total body length due to the contractile abdomen of Staphylinidae making total body length difficult to measure accurately.

Photographs were taken using a Canon 5D Mark III with the Canon MP-E 65mm 1-5x Macro Lens fitted. Stacking was performed with the StackShot 3X Macro Rail with 20 to 25 photos stacked using the PMA function in Zerene Stacker. Post-processing of images in Adobe Photoshop CC included adding a scale bar and removing dust using the Healing Brush Tool. Head and habitus illustrations were drawn in Adobe Illustrator using reference images. Aedeagus drawings were made free hand with the camera lucida attached to the dissecting scope and inked digitally using Adobe Illustrator software.

Molecular data. We target the barcode fragment of the mitochondrial cytochrome oxidase I gene (COI) as it is the most commonly used marker in species delimitation studies in animals including several rove beetles studies (HENDRICH et al. 2015, KLIMASZEWSKI et al. 2019, BRUNKE et al. 2020, HU et al. 2020). There is thus a large pool of COI barcode sequences available in databases such as Barcode of Life Datasystems v4 (BOLD) (<http://www.boldsystems.org>) and GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). A further advantage is that COI, like other mitochondrial genes, has a high abundance in especially muscle tissue, which increases the success rate in older museum specimens for sequencing. This makes it possible to target older specimens that may be critical for resolving species boundaries questions. Genomic DNA was extracted from a single leg of each target specimen. Both pinned museum and alcohol preserved specimens were used. DNA extraction, PCR amplification and bi-directional sequencing of the COI barcode fragment were performed by The Canadian Centre for DNA Barcoding (CCDB) (Guelph, Ontario, Canada). All newly generated sequences were uploaded to BOLD and were assigned BINs (Barcode Index Numbers, RATNASINGHAM & HEBERT (2013)) if they were longer than 500bp and contained less than 1% ambiguous bases. Using the BOLD workbench, we performed a sequence cluster analysis with the refined single-linkage algorithm

of RATNASINGHAM & HEBERT (2013) to identify potential Operational Taxonomic Units (OTUs). Novel sequences were made public in BOLD under the following process IDs (QUEDA126-18, QUEDA127-18, QUEDA128-18, QUEDA129-18, QUEDA130-18, QUEDA131-18, QUEDA132-18, QUEDA133-18, QUEDA134-18, QUEDA135-18, QUEDA137-18, QUEDB073-19, QUEDB078-19, QUEDB080-19, QUEDB082-19, QUEDB086-19, QUEDB087-19, QUEDB089-19, QUEDB090-19, QUEDC001-19, QUEDC003-19, QUEDC005-19, QUEDC006-19, QUEDC007-19, QUEDC008-19, QUEDC009-19, QUEDC011-19, QUEDC012-19, QUEDC013-19, QUEDC014-19, QUEDC015-19, QUEDC016-19, QUEDC017-19, QUEDC018-19, QUEDC019-19, QUEDC021-19, QUEDC022-19, QUEDC023-19, QUEDC024-19, QUEDC025-19, QUEDC026-19, QUEDC027-19, QUEDC029-19, QUEDC030-19, QUEDC031-19, QUEDC033-19, QUEDC034-19, QUEDC036-19, QUEDC037-19, QUEDC038-19, QUEDC039-19, QUEDC040-19, QUEDC042-19, QUEDC043-19, QUEDC044-19, QUEDC045-19, QUEDC046-19, QUEDC047-19, QUEDC051-19, QUEDC052-19, QUEDC053-19, QUEDC054-19, QUEDC056-19, QUEDC057-19, QUEDC060-19, QUEDC061-19).

Sequence alignment, phylogenetic and network analysis. All new and previously published sequences were imported to Geneious Prime v.2019.2.3 and aligned using the MAFFT Multiple Alignment v.1.4.0 plugin based on MAFFT (KATO et al. 2002). Using the Species Delimiter plugin (MASTERS et al. 2011) in Geneious we calculated the average pairwise intraspecific tree distance within species clusters and the interspecific distance to nearest neighbor. The complete alignment was exported, partitioned by codon and submitted to PartitionFinder2 (LANFEAR et al. 2017) run on the CIPRES Science Gateway v3.3 (phylo.org). A search for the best substitution models was selected under the Bayesian Information Criterion using the following settings: models choice = all, branch lengths = unlinked, and search choice = greedy. Two separate phylogenetic analyses were conducted using the best partition and substitution model found by PartitionFinder2: a Maximum Likelihood (ML) analysis using IQ-Tree v.1.6.10 (NGUYEN et al. 2015) and a Bayesian analysis (BI) using MrBayes v.3.2.7a (RONQUIST et al. 2012). Both analyses were run on CIPRES. The ML analysis in IQ-Tree was set up with default settings except: Ultrafast Bootstrap (UFB) was run for 1000 iterations (-bb 1000), then re-run with up to 10,000 iterations (-nm 10,000) with a SH-aLRT test (-sh_test true) and run for 1000 iterations (-alrt 1000). The BI analysis consisted of two runs of four chains each, with default settings except that different rates of evolution were allowed in different partitions (ratepr = variable). Convergence was examined manually by checking the Potential Scale Reduction Factor (PSRF) in Tracer v1.7.1 (RAMBAUT et al. 2018). For each analysis we considered posterior probability values (PP) ≥ 0.90 , SH-aLRT ≥ 80 , and UFB ≥ 95 to indicate clade support, respectively.

Table 1. List of DNA barcode sequences generated and used for this study. Sequences excluded from analysis as potential contaminations (*) or because of bad sequence quality (**) are marked in column with sequence length (bp).

Specimen ID	Process ID	Species	bp	BIN	Novel	Locality
CNCAJB19-103	QUEDC003-19	<i>afrofuliginosus</i>	658	BOLD:AEC2087	novel	France: Corse
CNCAJB19-156	QUEDC056-19	<i>altanai</i>	408*	BOLD:AEC1928	novel	Arizona: Apache Co.
CNCAJB19-157	QUEDC057-19	<i>altanai</i>	408		novel	Colorado: Red Mt. Pass
CNCAJB19-114	QUEDC014-19	<i>altaicus</i>	408	BOLD:AEC1928	novel	Russia: Lake Baikal
CNCAJB19-161	QUEDC061-19	<i>altaicus</i>	658	BOLD:AEC1928	novel	Russia: Altai
CNCAJB19-101	QUEDC001-19	<i>altaicus</i>	408	BOLD:AEC1928	novel	Russia: Altai
ZMUO.000630	COLFA400-12	<i>balticus</i>	658	BOLD:ABW4895		Finland: Oulu
CNCAJB19-136	QUEDC036-19	<i>curtipennis</i>	308		novel	Spain: Pyrenees
JX626086	GBCL63837-19	<i>curtipennis</i>	404**			Portugal: Azores
BIOUG12664-D05	SSROA3162-14	<i>curtipennis</i>	514	BOLD:AAZ0388		Ontaria: Toronto
CNCAJB19-134	QUEDC034-19	<i>curtipennis</i>	308		novel	Faroe Islands
BIOUG26579-E07	POBGD124-15	<i>curtipennis</i>	475	BOLD:AAZ0388		Quebec: Montreal
JX626108	GBCL64397-19	<i>curtipennis</i>	454	BOLD:AAZ0388		Portugal: Azores
JX626087	GBCL63818-19	<i>curtipennis</i>	454	BOLD:AAZ0388		Portugal: Azores
JX626088	GBCL63819-19	<i>curtipennis</i>	454	BOLD:AAZ0388		Portugal: Azores
JX626085	GBCL63839-19	<i>curtipennis</i>	454	BOLD:AAZ0388		Portugal: Azores
JX626084	GBCL63838-19	<i>curtipennis</i>	454	BOLD:AAZ0388		Portugal: Azores
BIOUG08060-F10	RBINA5440-13	<i>curtipennis</i>	568	BOLD:AAZ0388		Ontario: Rouge NP
BFB_Col_FK_12681	FBCOO996-13	<i>curtipennis</i>	658	BOLD:AAZ0388		Germany: Saxony
BIOUG26579-E04	POBGD121-15	<i>curtipennis</i>	577	BOLD:AAZ0388		Quebec: Montreal
BIOUG26579-E05	POBGD122-15	<i>curtipennis</i>	604	BOLD:AAZ0388		Quebec: Montreal
ZFMK-TIS-2510049	GCOL7444-16	<i>curtipennis</i>	658	BOLD:AAZ0388		Germany: Thuringia
BIOUG24151-G08	RRSSC6593-15	<i>curtipennis</i>	658	BOLD:AAZ0388		Ontario: Toronto
	GBCOU8183-14	<i>curtipennis</i>	634			Germany: North Rhine
BIOUG26579-E06	POBGD123-15	<i>curtipennis</i>	613	BOLD:AAZ0388		Quebec: Montreal
CNCAJB19-133	QUEDC033-19	<i>curtipennis</i>	658	BOLD:AAZ0388	novel	Portugal: Madeira
11239-H08	GENHP124-11	<i>curtipennis</i>	658	BOLD:AAZ0388		France: Normandy
ZMUO.002352	COLFC167-12	<i>curtipennis</i>	658	BOLD:AAZ0388		Finland: Aland Islands
BIOUG31142-B04	SMTPR9693-16	<i>curtipennis</i>	632	BOLD:AAZ0388		British Columbia: Cranbrook
ZMUO.000544	COLFA504-12	<i>fuliginosus</i>	308**			Finland: Oulo
BIOUG13329-B05	SSBRB5288-14	<i>fuliginosus</i>	353	BOLD:ACB0188		Nova Scotia: Cape Breton
BOLD-0DBQRGZN4	MOBIL1557-16	<i>fuliginosus</i>	615	BOLD:ACB0188		Nova Scotia: Halifax
	GBMIX1219-15	<i>fuliginosus</i>	621			Germany: Bavaria
	COLFH421-15	<i>fuliginosus</i>	636			Finland: ?
ZMUO.003949	COLFD054-12	<i>fuliginosus</i>	634	BOLD:ACB0188		Finland: Karelia
ZMUO.006785	COLFE990-13	<i>fuliginosus</i>	658	BOLD:ACB0188		Finland: Lapland
	GBCOU7368-14	<i>fuliginosus</i>	658			Germany: North Rhine
ZFMK-TIS-2522255	GCOL9778-16	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: Saxony
ZFMK-TIS-2501187	GCOL5175-16	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: Thuringia
	GBCOU8272-14	<i>fuliginosus</i>	658			Germany: North Rhine
	GBCOU7339-14	<i>fuliginosus</i>	658			Germany: North Rhine
ZFMK-TIS-2515386	GCOL8475-16	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: North Rhine
BFB_ZSM_COLA_1636	FBCOJ591-12	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: Bavaria
ZFMK-TIS-2504002	GCOL5541-16	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: Thuringia
ZMUO.006686	COLFF891-13	<i>fuliginosus</i>	658	BOLD:ACB0188		Finland: Aland Islands
GBOL 2211	GBCOU402-13	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: ?
ZFMK-TIS-2515251	GCOL8414-16	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: North Rhine
ZFMK-TIS-2521995	GCOL9688-16	<i>fuliginosus</i>	658	BOLD:ACB0188		Germany: Hesse
	CNCCJ3096-14	<i>horni</i>	658			British Columbia: ?

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Table 1. Continued.

Specimen ID	Process ID	Species	bp	BIN	Novel	Locality
CNCAJB19-82	QUEDB082-19	<i>horni</i>	658	BOLD:ACM0300	novel	Alaska: Auke Bay
CNCAJB19-152	QUEDC052-19	<i>horni</i>	658	BOLD:ACM0300	novel	Washington: Olympic NP
BIOUG13331-C02	SSBRA3301-14	<i>labradorensis</i>	568	BOLD:ACA7261		Nova Scotia: Cape Breton
	COLNF2039-15	<i>labradorensis</i>	622			Alberta: ?
BIOUG25126-A06	SSBCA5927-15	<i>labradorensis</i>	592	BOLD:ACA7261		British Columbia: Burnt Cabin
BIOUG25126-A07	SSBCA5928-15	<i>labradorensis</i>	592	BOLD:ACA7261		British Columbia: Burnt Cabin
BIOUG25126-B05	SSBCA5938-15	<i>labradorensis</i>	592	BOLD:ACA7261		British Columbia: Burnt Cabin
BIOUG25126-B04	SSBCA5937-15	<i>labradorensis</i>	592	BOLD:ACA7261		British Columbia: Burnt Cabin
BIOUG05929-H07	SSEIB12884-13	<i>labradorensis</i>	585	BOLD:ACA7261		Alberta: Elk Island NP
BIOUG09049-H02	SSPAC11229-13	<i>labradorensis</i>	576	BOLD:ACA7261		Saskatchewan: Prince Albert NP
	COLNF2036-15	<i>labradorensis</i>	658			Alberta: ?
BIOUG09049-H01	SSPAC11228-13	<i>labradorensis</i>	576	BOLD:ACA7261		Saskatchewan: Prince Albert NP
BIOUG05929-H08	SSEIB12885-13	<i>labradorensis</i>	566	BOLD:ACA7261		Alberta: Elk Island NP
BIOUG09049-G12	SSPAC11227-13	<i>labradorensis</i>	508	BOLD:ACA7261		Saskatchewan: Prince Albert NP
	CNCCH935-12	<i>labradorensis</i>	658			Quebec: ?
	CNCCH937-12	<i>labradorensis</i>	658			Quebec: ?
BIOUG05859-B02	SSPAA9896-13	<i>labradorensis</i>	572	BOLD:ACA7261		Saskatchewan: Prince Albert NP
BIOUG05859-B03	SSPAA9897-13	<i>labradorensis</i>	584	BOLD:ACA7261		Saskatchewan: Prince Albert NP
	CNCCJ3092-14	<i>labradorensis</i>	658			Alaska: ?
BIOUG05859-B12	SSPAA9906-13	<i>labradorensis</i>	593	BOLD:ACA7261		Saskatchewan: Prince Albert NP
BIOUG05859-B07	SSPAA9901-13	<i>labradorensis</i>	593	BOLD:ACA7261		Saskatchewan: Prince Albert NP
	CNCCJ3094-14	<i>labradorensis</i>	658			Northwest Territory: ?
	CNCCJ3091-14	<i>labradorensis</i>	658			Ontario: ?
CNCAJB18-140	QUEDA135-18	<i>labradorensis</i>	658	BOLD:ACA7261	novel	Alaska: Delta Junction
	CNCCH934-12	<i>labradorensis</i>	658			Ontario: ?
	CNCCJ3100-14	<i>lanei</i>	658			Nevada: Lake Tahoe
CNCAJB19-154	QUEDC054-19	<i>lanei</i>	408	BOLD:ACM0054	novel	Oregon: Strawberry Lake
CNCAJB19-151	QUEDC051-19	<i>lanei</i>	408	BOLD:ACM0054	novel	California: Lassen NP
CNCAJB19-153	QUEDC053-19	<i>lanei</i>	408	BOLD:ACM0054	novel	Oregon: Gearhart Mt.
CNCAJB19-89	QUEDB089-19	<i>laticollis</i>	658	BOLD:AAN6181	novel	Tennessee: Lake Co.
CNCAJB19-86	QUEDB086-19	<i>laticollis</i>	407		novel	Arkansas: Logan Co.
TDWG-0662	TDWGB526-10	<i>laticollis</i>	655*	BOLD:ABA6318		Massachusetts: Woods Hole
CNCAJB19-90	QUEDB090-19	<i>laticollis</i>	407		novel	Kentucky: Trigg Co.
TDWG-0183	TDWGB068-10	<i>laticollis</i>	658	BOLD:AAN6181		Massachusetts: Woods Hole
TDWG-0661	TDWGB525-10	<i>laticollis</i>	658	BOLD:AAN6181		Massachusetts: Woods Hole
TDWG-0659	TDWGB523-10	<i>laticollis</i>	658	BOLD:AAN6181		Massachusetts: Woods Hole
BIOUG35454-E02	ELPCH702-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
	CNCCJ3090-14	<i>laticollis</i>	658			Mississippi: ?
TDWG-0660	TDWGB524-10	<i>laticollis</i>	658	BOLD:AAN6181		Massachusetts: Woods Hole
TDWG-0184	TDWGB069-10	<i>laticollis</i>	658	BOLD:AAN6181		Massachusetts: Woods Hole
BIOUG34966-A07	ELPCG6266-17	<i>laticollis</i>	593	BOLD:AAN6181		Ontario: South Frontenac
BIOUG35440-C04	ELPCH144-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
BIOUG35454-E03	ELPCH703-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
CNCAJB19-87	QUEDB087-19	<i>laticollis</i>	658	BOLD:AAN6181	novel	Arkansas: Newton Co.
BIOUG35450-B07	ELPCG11068-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
BIOUG35453-H11	ELPCH652-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
BIOUG35459-A02	ELPCH813-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
BIOUG35453-A06	ELPCH478-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: South Frontenac
BIOUG34219-H05	OPPZI012-17	<i>laticollis</i>	658	BOLD:AAN6181		Ontario: Lions Head
CNCAJB19-116	QUEDC016-19	<i>levicollis</i>	658	BOLD:ACB9476	novel	Greece: Karpathos
CNCAJB19-117	QUEDC017-19	<i>levicollis</i>	658	BOLD:ACB9476	novel	Syria: Mashta al Hilu

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Table 1. Continued.

Specimen ID	Process ID	Species	bp	BIN	Novel	Locality
CNCAJB19-118	QUEDC018-19	<i>levicollis</i>	658	BOLD:ACB9476	novel	Iran: Sepidor
CNCAJB19-119	QUEDC019-19	<i>levicollis</i>	658	BOLD:ACB9476	novel	Spain: Extremadura
	GBCOU7999-14	<i>levicollis</i>	658			Germany: North Rhine
	GBEPT963-14	<i>levicollis</i>	658			Hungary: ?
CNCAJB19-115	QUEDC015-19	<i>levicollis</i>	658	BOLD:ACB9476	novel	Morocco: Bad Bessen
BFB_Co1_FK_8906	FBCOG1021-12	<i>levicollis</i>	658	BOLD:ACB9476		Germany: North Rhine
ZMUO.005817	COLFF212-13	<i>levicollis</i>	658	BOLD:ACB9476		Sweden: Öland
	GBCOU8000-14	<i>levicollis</i>	658			Germany: North Rhine
CNCAJB19-122	QUEDC022-19	<i>meridiocarpaticus</i>	658	BOLD:AAZ0388	novel	Greece: Peloponnese
CNCAJB19-121	QUEDC021-19	<i>meridiocarpaticus</i>	658	BOLD:AAZ0388	novel	Italy: Bibione
CNCAJB19-123	QUEDC023-19	<i>meridiocarpaticus</i>	658	BOLD:AAZ0388	novel	Russia: Krasnodar Krai
BIOUG09622-G02	SSJAF8757-13	<i>molochinoides</i>	387			Alberta: Jasper NP
BIOUG09622-E06	SSJAF8737-13	<i>molochinoides</i>	513			Alberta: Jasper NP
CNCAJB19-80	QUEDB080-19	<i>molochinoides</i>	658	BOLD:ACU4505	novel	New Hampshire: Mt. Washington
CNCAJB18-142	QUEDA137-18	<i>molochinoides</i>	658	BOLD:ACU4505	novel	Alaska: Becharof Peninsula
UAM:Ento:29521	UAMIC400-13	<i>molochinoides</i>	558	BOLD:ACU4505		Alaska: Becharof Peninsula
	COLNF2042-15	<i>molochinoides</i>	442			Alberta: ?
BIOUG09622-H04	SSJAF8771-13	<i>molochinoides</i>	523			Alberta: Jasper NP
CNCAJB19-78	QUEDB078-19	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Washington: Stevens Co.
CNCAJB19-73	QUEDB073-19	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	British Columbia: Prince George
BIOUG24582-B02	SSKNA9647-15	<i>molochinoides</i>	592	BOLD:AAQ0037		British Columbia: Kinasken Lake
CNCAJB18-135	QUEDA130-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: South Chilkat
BIOUG09884-E05	INRMA1650-14	<i>molochinoides</i>	407			British Columbia: St. Elias
BIOUG24582-B05	SSKNA9650-15	<i>molochinoides</i>	592	BOLD:AAQ0037		British Columbia: Kinasken Lake
BIOUG24584-A04	SSKNA9782-15	<i>molochinoides</i>	592	BOLD:AAQ0037		British Columbia: Kinasken Lake
BIOUG24584-A08	SSKNA9786-15	<i>molochinoides</i>	583	BOLD:AAQ0037		British Columbia: Kinasken Lake
UAM:Ento:259211	UAMIC2876-15	<i>molochinoides</i>	658	BOLD:AAQ0037		Alaska: Chichagof Island
10PCCOL-1009	BBCCM104-10	<i>molochinoides</i>	658	BOLD:AAQ0037		British Columbia: Mt. Revelstoke
CNCAJB18-133	QUEDA128-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: Hawthorne Peak
CNCAJB18-134	QUEDA129-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: Boulder Creek
CNCAJB18-136	QUEDA131-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: Haines
CNCAJB18-137	QUEDA132-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: Hawthorne Peak
10PCCOL-1008	BBCCM103-10	<i>molochinoides</i>	658	BOLD:AAQ0037		British Columbia: Glacier NP
CNCAJB18-138	QUEDA133-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: Chichagof Island
CNCAJB18-139	QUEDA134-18	<i>molochinoides</i>	658	BOLD:AAQ0037	novel	Alaska: Chichagof Island
BIOUG24583-H04	SSKNA9771-15	<i>molochinoides</i>	511	BOLD:AAQ0037		British Columbia: Kinasken Lake
BIOUG04808-E01	SSWLA2101-13	<i>molochinoides</i>	591	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-D08	SSWLA2096-13	<i>molochinoides</i>	616	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-E05	SSWLA2105-13	<i>molochinoides</i>	615	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-C11	SSWLA2087-13	<i>molochinoides</i>	636	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-E12	SSWLA2112-13	<i>molochinoides</i>	634	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-F03	SSWLA2115-13	<i>molochinoides</i>	616	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04122-H04	SSBAB2954-12	<i>molochinoides</i>	638	BOLD:ACU4504		Alberta: Banff NP
BIOUG04808-B11	SSWLA2075-13	<i>molochinoides</i>	634	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04122-H06	SSBAB2956-12	<i>molochinoides</i>	615	BOLD:ACU4504		Alberta: Banff NP
BIOUG04122-H05	SSBAB2955-12	<i>molochinoides</i>	615	BOLD:ACU4504		Alberta: Banff NP
BIOUG05929-A09	SSWLC3723-13	<i>molochinoides</i>	487	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04122-H07	SSBAB2957-12	<i>molochinoides</i>	615	BOLD:ACU4504		Alberta: Banff NP
BIOUG06159-A08	SSBAE3713-13	<i>molochinoides</i>	634	BOLD:ACU4504		Alberta: Banff NP
BIOUG04808-D09	SSWLA2097-13	<i>molochinoides</i>	629	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-D03	SSWLA2091-13	<i>molochinoides</i>	633	BOLD:ACU4504		Alberta: Waterton NP

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Table 1. Continued.

Specimen ID	Process ID	Species	bp	BIN	Novel	Locality
BIOUG04808-D01	SSWLA2089-13	<i>molochinoides</i>	634	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-C08	SSWLA2084-13	<i>molochinoides</i>	615	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-E09	SSWLA2109-13	<i>molochinoides</i>	554	BOLD:ACU4504		Alberta: Waterton NP
BIOUG05929-A08	SSWLC3722-13	<i>molochinoides</i>	553	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-E06	SSWLA2106-13	<i>molochinoides</i>	611	BOLD:ACU4504		Alberta: Waterton NP
BIOUG05929-C02	SSWLD3828-13	<i>molochinoides</i>	565	BOLD:ACU4504		Alberta: Waterton NP
BIOUG04808-E08	SSWLA2108-13	<i>molochinoides</i>	607	BOLD:ACU4504		Alberta: Waterton NP
CNCAJB18-131	QUEDA126-18	<i>molochinus</i>	610	BOLD:ACK9517	novel	Quebec: Portneuf Co.
CNCAJB19-160	QUEDC060-19	<i>molochinus</i>	658	BOLD:ACK9517	novel	Czech Rep.: Podyji NP
ZFMK-TIS-2500523	GCOL4820-16	<i>molochinus</i>	658	BOLD:ACK9517		Germany: Thuringia
ZFMK-TIS-2500536	GCOL4832-16	<i>molochinus</i>	658	BOLD:ACK9517		Germany: Thuringia
ZFMK-TIS-2527486	GCOL11134-16	<i>molochinus</i>	658	BOLD:ACK9517		Germany: Thuringia
CNCAJB18-132	QUEDA127-18	<i>molochinus</i>	658	BOLD:ACK9517	novel	Quebec: Montmorency
ZFMK-TIS-2527509	GCOL11135-16	<i>molochinus</i>	658	BOLD:ACK9517		Germany: Thuringia
ZFMK-TIS-2512535	GCOL8160-16	<i>molochinus</i>	658	BOLD:ACK9517		Germany: North Rhine
ZFMK-TIS-2512534	GCOL8159-16	<i>molochinus</i>	658	BOLD:ACK9517		Germany: North Rhine
CNCAJB19-137	QUEDC037-19	<i>molochinus</i>	658	BOLD:ACK9517	novel	Czech Rep.: Karlov
ZMUO.005990	COLFF290-13	<i>molochinus</i>	658	BOLD:ACK9517		Finland: Lapland
ZMUO.006695	COLFF900-13	<i>molochinus</i>	658	BOLD:ACK9517		Finland: Åland Islands
CNCAJB19-113	QUEDC013-19	<i>molochinus</i>	408	BOLD:ACK9517	novel	Russia: Transbaikal
CNCAJB19-130	QUEDC030-19	<i>pallipes</i>	658	BOLD:ACR8319	novel	Italy: Calabria
CNCAJB19-129	QUEDC029-19	<i>pallipes</i>	658	BOLD:ACR8319	novel	Italy: Sardinia
CNCAJB19-131	QUEDC031-19	<i>pallipes</i>	408	BOLD:ACR8319	novel	Morocco: Tetouan
JX626110	GBCL64391-19	<i>simplicifrons</i>	454			Portugal: Azores
JX626109	GBCL64390-19	<i>simplicifrons</i>	454			Portugal: Azores
CNCAJB19-126	QUEDC026-19	<i>simplicifrons</i>	408	BOLD:ACR8319	novel	Spain: Tenerife
	GBCOU8670-14	<i>simplicifrons</i>	658			France: Brittany
CNCAJB19-127	QUEDC027-19	<i>simplicifrons</i>	658	BOLD:ACR8319	novel	Spain: Extremadura
CNCAJB19-124	QUEDC024-19	<i>simplicifrons</i>	658	BOLD:ACR8319	novel	Portugal: Madeira
CNCAJB19-125	QUEDC025-19	<i>simplicifrons</i>	658	BOLD:ACR8319	novel	Spain: Andalusia
ZMUO.005986	COLFF286-13	<i>subunicolor</i>	407	BOLD:AEC1928		Finland: Lapland
CNCAJB19-139	QUEDC039-19	<i>sundukovi</i>	408		novel	Russia: Khabarovsk
CNCAJB19-140	QUEDC040-19	<i>sundukovi</i>	408		novel	Russia: Sakhalin Island
CNCAJB19-144	QUEDC044-19	<i>sundukovi</i>	658	BOLD:AEC6428	novel	Russia: Khabarovsk
CNCAJB19-147	QUEDC047-19	<i>sundukovi</i>	658	BOLD:AEC6428	novel	Kazakhstan: Altai
CNCAJB19-138	QUEDC038-19	<i>sundukovi</i>	658	BOLD:AEC3770	novel	Russia: Khabarovsk
CNCAJB19-142	QUEDC042-19	<i>sundukovi</i>	658	BOLD:AEC6429	novel	Russia: Khabarovsk
CNCAJB19-143	QUEDC043-19	<i>sundukovi</i>	658	BOLD:AEC6429	novel	Russia: Khabarovsk
CNCAJB19-145	QUEDC045-19	<i>sundukovi</i>	658	BOLD:AEC5328	novel	Russia: Transbaikal
CNCAJB19-146	QUEDC046-19	<i>sundukovi</i>	658	BOLD:AEC5328	novel	Russia: Transbaikal
CNCAJB19-111	QUEDC011-19	<i>unicolor</i>	408		novel	Slovakia: High Tatras
CNCAJB19-109	QUEDC009-19	<i>unicolor</i>	408		novel	Spain: Picos de Europa
BC ZSM COL 2394	FBCOD1064-11	<i>unicolor</i>	658	BOLD:ABU5684		Austria: Carinthia
CNCAJB19-112	QUEDC012-19	<i>unicolor</i>	658	BOLD:ABU5684	novel	Italy: Trento
CNCAJB19-105	QUEDC005-19	<i>vicinus</i>	658	BOLD:AEC2086	novel	Georgia: Kumisi
CNCAJB19-107	QUEDC007-19	<i>vicinus</i>	658	BOLD:AEC2086	novel	Turkey: Antalya
CNCAJB19-106	QUEDC006-19	<i>vicinus</i>	658	BOLD:AEC1709	novel	Israel: Lower Galilee
CNCAJB19-108	QUEDC008-19	<i>vicinus</i>	658	BOLD:AEC1709	novel	Jordan: Amman

A subset of the alignment containing the specimens of the morphologically very similar *Quedius* species from the *molochinoides*-group (*Q. altanai*, *Q. horni*, *Q. lanei* and *Q. molochinoides*) was subjected to a haplotype network analysis in POPART (LEIGH & BRYANT 2015), where all sequences with more than 5 % of missing data (i.e. sequences with less than 625 bp) were excluded. A Median Joining Network analysis (BANDELT et al. 1999), was performed using default settings. The obtained network was subsequently colored using the species clusters gathered from morphological and genetic analysis.

Species and species group concepts. Species delimitation is a core problem in taxonomy. This is a particular challenge in *Quedius* where morphological characters, including those that are traditionally used for species diagnosis, both vary and are often not easily measurable (e.g., SALNITSKA & SOLODOVNIKOV 2018a,b; HU et al. 2020). As an alternative, a measurable divergence in the genetic barcode (COI) is sometimes used as an alternative proxy for species delimitation. Although a greater than 2% divergence in COI is often considered to correspond to distinct species, there are always higher divergence values and other exceptions as well (LUKHTANOV 2019), e.g. much higher values (up to 15%) were found within single species in a large barcode study of German Coleoptera (HENDRICH et al. 2015). Whether these correspond to cryptic species or large variation is still unknown, but presumably it is a mix, with some species maintaining large intraspecific variation. Various approaches have been proposed to account for these factors, for example, BOLD is using BINs which considers multiple factors including quality control of input data, a 2.2% difference between sequences, and a validation of all OTUs within 4.4% of each other (RATNASINGHAM & HEBERT 2013). Nevertheless, the usage of COI barcodes for species delimitation has been criticised as a stand-alone tool, and it has been suggested that COI barcodes should be used in combination with other characters (e.g. WILL & RUBINOFF 2004, COGNATON 2006, DUPUIS et al. 2012, KONDANDARAMAIAH et al. 2013, SIMONSEN et al. 2019, TOKAREVA et al. 2021, SALNITSKA & SOLODOVNIKOV 2021). Because of the ambiguities associated with species delimitation based on genetic data alone, and the practical utility of the morphologically distinct species at this state of knowledge of *Quedius* s. str., we refrain from using such genetic differences alone to assign species status to molecular clusters. At the current stage of knowledge of *Quedius* s. str. it is important to deal with the taxonomic species which can be distinguished based on morphology alone. Within this framework, we therefore use BINs and OTUs to define genetic clusters that help to evaluate morphological variation and detect morphological characters that show hiatus between these clusters. Only such morphologically diagnosable clusters are given species status; molecular clusters not supported by morphological characters are worth exploring in the future.

For defining species groups, we use monophyletic lineages from our genomic phylogeny of *Quedius* sensu stricto (Fig. 1; A. HANSEN et al., in prep.) where *Quedius*

s. str. was sampled rather densely and well represented. The only exception to this is that *Q. unicolor* and *Q. vicinus* were added to the *Q. molochinus* species group, although they appear as monotypic lineages. This is done for practical reasons as these species are externally very similar to species of the *Q. molochinus*-group and would otherwise only be separable through dissection of males.

Results

Species delimitation: OTUs, BINs and clustering. The COI barcode dataset comprised sequences from a total of 200 specimens (Table 1), of which four were excluded due to insufficient data quality, and one outgroup sequence was included. Among these, 66 are new sequences generated here from both pinned and alcohol preserved specimens. 47 new sequences were full (658 bp) and 19 were partial sequences (407–610 bp). The oldest specimen from which we successfully sequenced a full DNA barcode was collected in 1975; the oldest from which we successfully sequenced a partial DNA barcode was collected in 1973. Nearly all currently recognized species were represented in the dataset by at least one specimen. For *Q. altanai* sp. nov., only a partial sequence (408 bp) was generated. We were unable to get sequence data for *Q. strenuus*, which was represented by old specimens only. Most of the hitherto recognized taxonomic species were supported as monophyletic in both the BI and ML analyses (Figs 3, 4). The exceptions were the *Q. subunicolor* × *Q. altaicus* and *Q. hispanicus* × *Q. pallipes* species pairs. A supported cluster was recovered with unsupported internal relationships between a *Q. subunicolor* specimen from Lapland, Finland, and specimens of *Q. altaicus*: one from Transbaikalia and two from Altai, Russia. Another supported cluster was recovered with unsupported internal relationships between specimens morphologically clearly belonging to *Q. hispanicus* from mainland Spain, Tenerife, Azores, Madeira and France, and specimens belonging to *Q. pallipes* from Morocco and Italy. Most of the currently accepted species were identical to a single OTU or BIN, with the exceptions of *Q. vicinus* (2 OTUs, 2 BINs), *Q. molochinoides* (3 OTUs, 3 BINs), *Q. unicolor* (3 OTUs, 1 BIN) and *Q. sundukovi* (5 OTUs, 4 BINs) (Table 2). Taxonomic species clusters had an intraspecific distance variation ranging from 0.1% to 3.7% (average 1.1%) and an interspecific distance to nearest neighbor of 4.7%–11.0% (8.0%), disregarding a single partial sequence of *Q. altanai* from Red Mt. Pass, Colorado with an interspecific distance of 1.2%.

Phylogenetic and haplotype network analyses. A single partition under the TVM+I+G model was selected by PartitionFinder2. The BI analysis was run for 30 million generations, with 10% burn-in (3 million generations), whereafter it had reached convergence. All PSRF values were nearing 1.000 and most analysis parameters had effective sampling size (ESS) above 2000. All taxonomic species sampled (Table 1) were recovered in both the BI and ML analyses, which produced nearly the same results

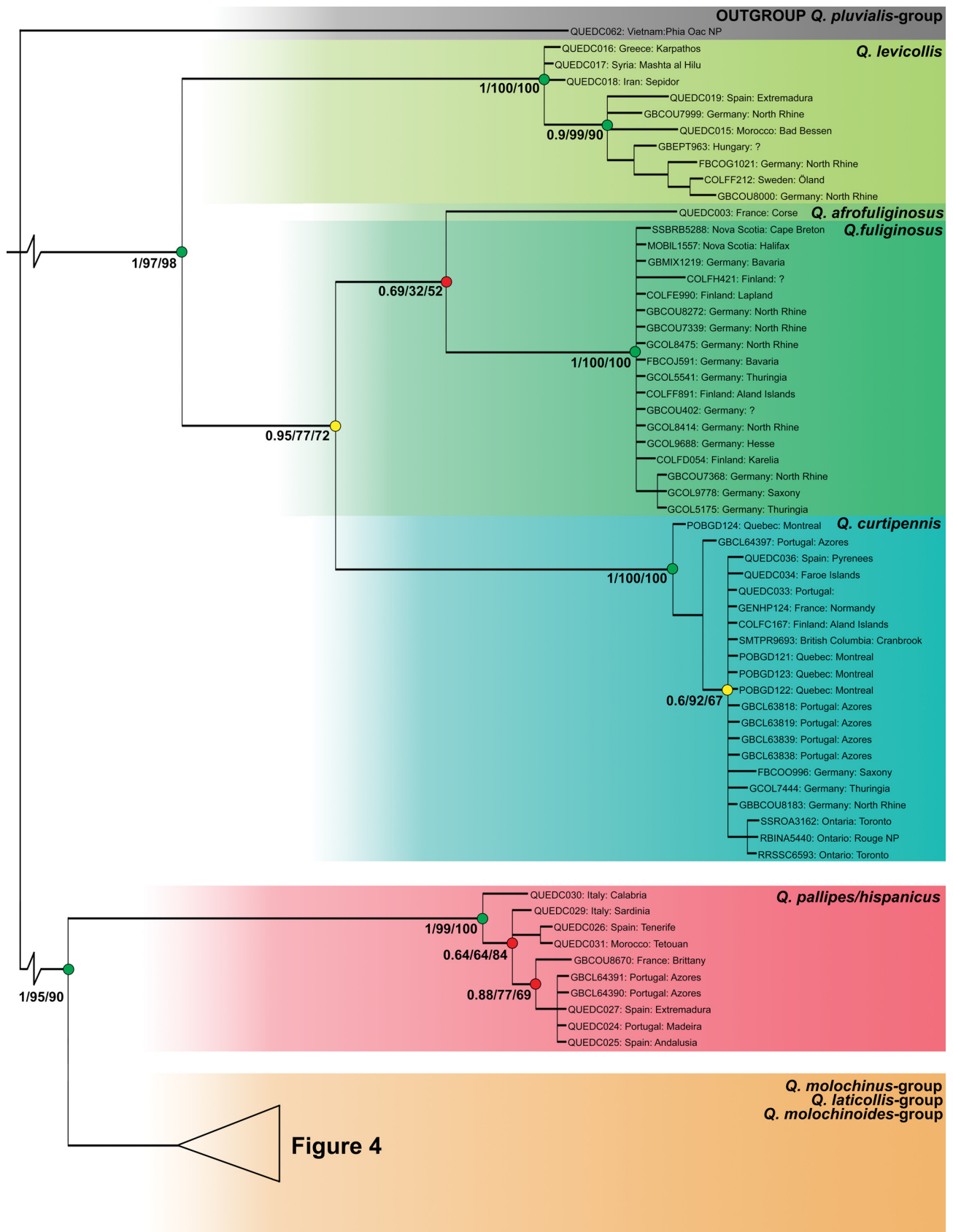


Fig. 3. Phylogeny of *Quedius* s. str. based on Bayesian Inference (BI) and Maximum Likelihood (ML) analyses of COI barcodes (part 1). BI posterior probabilities (PP), ML ultrafast bootstrap support (UFB) and ML SH-aLRT test are shown. Nodes coloured as: green, PP ≥ 0.90 , and either UFB ≥ 95 or SH-aLRT ≥ 80 ; yellow, one of PP ≥ 0.90 , UFB ≥ 95 or SH-aLRT ≥ 80 ; red, PP < 0.90 , UFB < 95 and SH-aLRT < 80 .

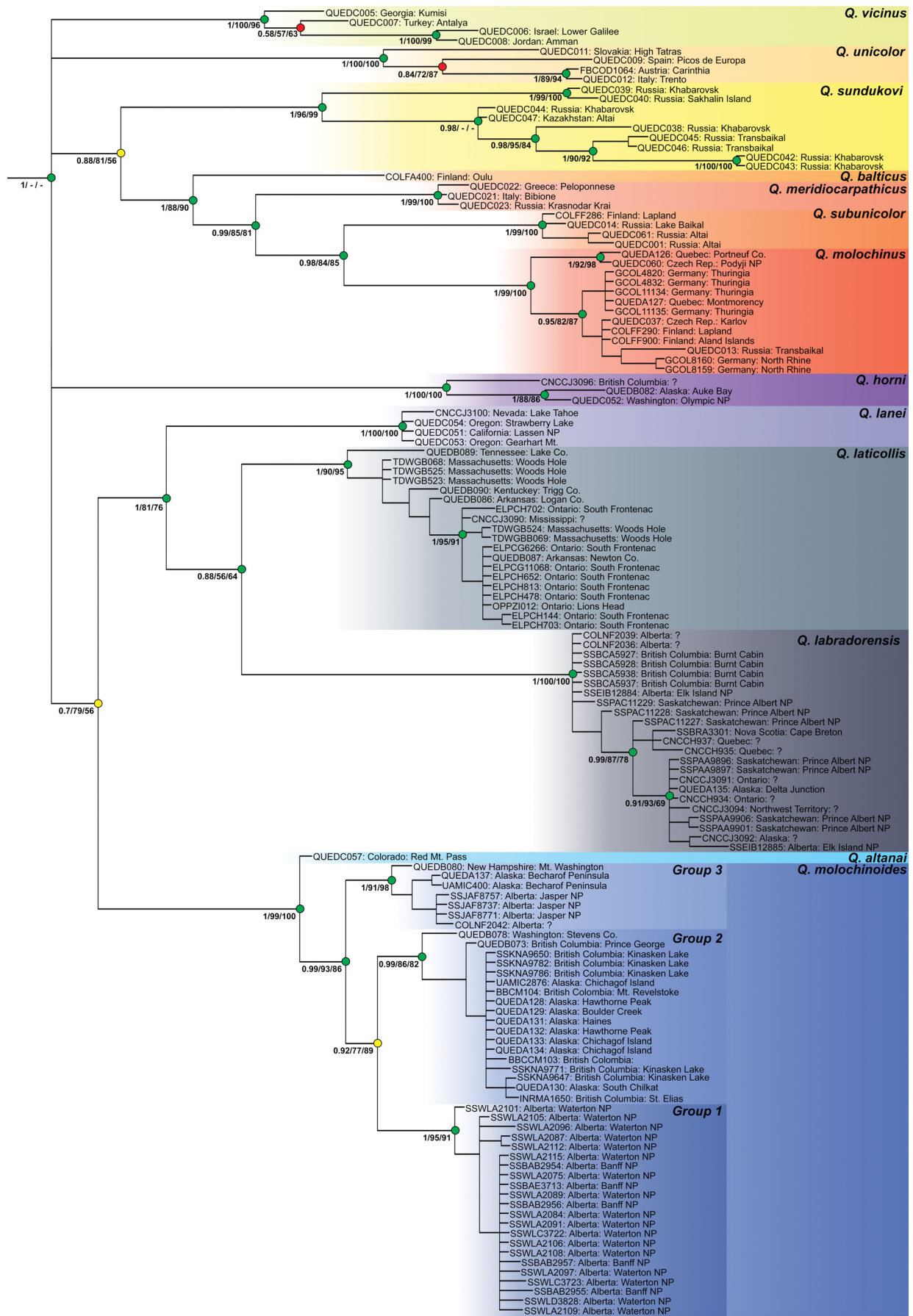


Fig. 4. Phylogeny of *Quedius* s. str. species based on Bayesian Inference (BI) and Maximum Likelihood (ML) COI barcodes (part 2). BI posterior probabilities (PP), ML ultrafast bootstrap support (UFB) and ML SH-aLRT test are shown. Nodes coloured as: green, PP \geq 0.90, and either UFB \geq 95 or SH-aLRT \geq 80; yellow, one of PP \geq 0.90, UFB \geq 95 or SH-aLRT \geq 80; red, PP $<$ 0.90, UFB $<$ 95 and SH-aLRT $<$ 80.

Table 2. Genetic distance between clusters of CO1 barcodes. n = number of specimens barcoded. Number of OTUs found by species delimiter plugin in Geneious. Intraspecific distance within cluster. Interspecific distance is distance to nearest other cluster.

Species	n	No. of OTU	Average IntraD	Closest InterD	BIN(s)
<i>levicollis</i>	10	1	1.5%	9.0%	BOLD:ACB9476
<i>fuliginosus</i>	18	1	0.2%	4.9%	BOLD:ACB0188
<i>afrofuliginosus</i>	1	1	na	4.9%	BOLD:AEC2087
<i>curtipennis</i>	21	1	0.4%	6.6%	BOLD:AAZ0388
<i>pallipes</i> / <i>simplicifrons</i>	10	1	0.5%	11.0%	BOLD:ACR8319
<i>labradorensis</i>	23	1	0.8%	9.8%	BOLD:ACA7261
<i>unicolor</i>	4	3	3.2%	9.8%	BOLD:ABU5684
<i>horni</i>	3	1	2.0%	9.8%	BOLD:ACM0300
<i>vicinus</i>	4	2	2.1%	9.8%	BOLD:AEC2086, BOLD:AEC1709
<i>altanai</i>	1	1	na	1.2%	
<i>lanei</i>	4	1	0.1%	9.8%	BOLD:ACM0054
<i>molochinoides</i>	47	3	1.6%	9.8%	BOLD:ACU4504, BOLD:AAQ0037, BOLD:ACU4505
<i>molochinoides1</i>	22	1	0.6%	2.3%	BOLD:ACU4504
<i>molochinoides2</i>	18	1	0.3%	2.3%	BOLD:AAQ0037
<i>molochinoides3</i>	7	1	0.3%	1.2%	BOLD:ACU4505
<i>laticollis</i>	19	1	0.7%	9.8%	BOLD:AAN6181
<i>sundukovi</i>	9	5	3.7%	9.8%	BOLD:AEC5328, BOLD:AEC6429, BOLD:AEC3770, BOLD:AEC6428
<i>meridio- carpathicus</i>	3	1	0.3%	4.7%	BOLD:AAZ0388
<i>balticus</i>	1	1	na	4.7%	BOLD:ABW4895
<i>altaicus</i>	4	1	0.6%	5.5%	BOLD:AEC1928
<i>/subunicolor</i>					
<i>molochinus</i>	13	1	0.7%	5.5%	BOLD:ACK9517
average			1.1%	8.0%	
minimum			0.1%	4.7%	
maximum			3.7%	11.0%	

(Figs 3, 4) and differed only in a less resolved tree for ML within the *laticollis*-, *molochinus*- and *molochinoides*-groups. Three well supported clades were recovered by both analyses (support values are given in Table 3). The first clade is the *Q. fuliginosus*-group (comprising *Q. afrofuliginosus*, *Q. fuliginosus*, *Q. curtipennis* and *Q. levicollis*) recovered with high support (PP = 1, SH-aLRT = 97.2, UFB = 98) as sister to a well supported clade comprising the remaining members of *Quedius* sensu stricto (PP = 1, SH-aLRT = 94.7, UFB = 90). The latter clade is divided into two well supported clades the *Q. pallipes*-group (comprising *Q. hispanicus* and *Q. pallipes*) was well supported (PP = 1, SH-aLRT = 99.1, UFB = 100), and a clade comprising the remaining species groups (*Q. laticollis*-group, *Q. molochinus*-group and *Q. molochinoides*-group), which is also well supported (PP = 1, SH-aLRT = 97.6, UFB = 96). There was no support for the remaining species group, except *Q. laticollis*-group (only *Q. laticollis* in this study), which was recovered within members of the *Q. molochinoides*-group.

In the *Q. fuliginosus*-group, *Q. levicollis* was strongly supported (PP = 1, SH-aLRT = 99.6, UFB = 100) and

recovered as sister to the other members of the group, which were supported by the BI analysis, but not in the ML analysis (PP = 0.95, SH-aLRT = 77.4, UFB = 72). The single *Q. afrofuliginosus* sequence was recovered together with *Q. fuliginosus* with low support (PP = 0.69, SH-aLRT = 31.5, UFB = 52). *Quedius fuliginosus* and *Q. curtipennis* each formed well supported clades (PP = 1, SH-aLRT = 99.8, UFB = 100; PP = 1, SH-aLRT = 97.8, UFB = 98, respectively).

In the *Q. pallipes*-group specimens morphologically belonging to *Q. hispanicus* and *Q. pallipes* were intermixed in a highly supported clade (PP = 1, SH-aLRT = 99.1, UFB = 100) without clear resolution within the clade.

The remaining species groups formed a well supported clade, but with unresolved internal relationships. The BI analysis supported five clades, each without internal resolution. Three of these clades each comprising only a single species – *Q. vicinus*, *Q. unicolor* and *Q. horni*, respectively – were all well supported (all PP = 1). Two clades: a Nearctic clade comprising *Q. labradorensis*, *Q. molochinoides*, *Q. lanei*, *Q. altanai* and *Q. laticollis*; and a Palearctic clade comprising *Q. sundukovi*, *Q. subunicolor*, *Q. molochinus*, *Q. balticus* and *Q. meridiocarpathicus* – both weakly supported (PP = 0.70; and PP = 0.88, respectively). The ML analysis recovered a well supported clade comprising the species *Q. horni* (SH-aLRT = 99.7, UFB = 100) as sister to the remaining two clades. These two clades were: a Nearctic clade comprising *Q. labradorensis*, *Q. molochinoides*, *Q. lanei*, *Q. altanai* and *Q. laticollis*; and a Palearctic clade comprising *Q. vicinus*, *Q. unicolor*, *Q. sundukovi*, *Q. subunicolor*, *Q. molochinus*, *Q. balticus* and *Q. meridiocarpathicus* – both weakly supported (SH-aLRT = 78.8, UFB = 56; SH-aLRT = 83.5, UFB = 37, respectively).

The ML analysis recovered three clades within the Palearctic lineage without fully resolved relationships. Among them, *Q. vicinus* and *Q. unicolor* are well supported as monophyletic species clades (SH-aLRT = 100, UFB = 96; and SH-aLRT = 99.9, UFB = 100, respectively), while the remaining species grouped together in a weakly supported clade (SH-aLRT = 81.1, UFB = 56) similar to the results of the BI analysis. The internal relationships within this clade were supported in the BI analysis, but not in the ML analysis where *Q. sundukovi* is sister to a grade of the remaining *molochinus*-group species (P = 0.88, SH-aLRT = 81.1, UFB = 56), *Q. balticus* (P = 0.99, SH-aLRT = 87.6, UFB = 90), *Q. meridiocarpathicus* (P = 0.98, SH-aLRT = 85.4, UFB = 81), and then *Q. subunicolor* sister to *Q. molochinus* (P = 0.98, SH-aLRT = 83.8, UFB = 85).

All the taxonomic species in the Palearctic clade – *Q. sundukovi*, *Q. subunicolor*, *Q. meridiocarpathicus* and *Q. molochinus* – were monophyletic and highly supported in both analyses (PP = 1, SH-aLRT = 96, UFB = 99; PP = 1, SH-aLRT = 99.2, UFB = 100; PP = 1, SH-aLRT = 99.4, UFB = 100; PP = 1, SH-aLRT = 98.8, UFB = 100, respectively). The taxonomic cluster of *Q. subunicolor* contained specimens from Scandinavia, Altai, and the Transbaikalia region of Russia. Specimens from Sca-

Table 3. Clade support values of the COI species tree, only values of PP ≥ 0.90 , SH-aLRT ≥ 80 , and UFB ≥ 95 indicated.

Species groups and species	PP	SH-aLRT	UFB	Support
<i>Q. fuliginosus</i> -group	1	97.2	98	High
<i>Q. levicollis</i>	1	100	100	High
<i>Q. fuliginosus</i> , <i>Q. curtipennis</i> and <i>Q. afrofuliginosus</i>	0.95	77.4	72	Low
<i>Q. fuliginosus</i>	1	99.8	100	High
<i>Q. curtipennis</i> and <i>Q. afrofuliginosus</i>	0.69	31.5	52	No
<i>Q. curtipennis</i>	1	97.8	98	High
<i>Q. afrofuliginosus</i>	na	na	na	na
<i>Q. pallipes</i> -, <i>Q. molochinus</i> -, <i>Q. molochinoides</i> - and <i>Q. laticollis</i> -groups	1	94.7	90	High
<i>Q. pallipes</i> -group	1	99.1	100	High
<i>Q. molochinus</i> -, <i>Q. molochinoides</i> - and <i>Q. laticollis</i> -groups	1	97.6	96	High
Palaearctic members				
<i>Q. vicinus</i>	1	100	96	High
<i>Q. unicolor</i>	1	100	100	High
<i>Q. sundukovi</i> , <i>Q. balticus</i> , <i>Q. meridiocarpaticus</i> , <i>Q. subunicolor</i> and <i>Q. molochinus</i>	0.88	81	56	Low
<i>Q. sundukovi</i>	1	96	99	High
<i>Q. balticus</i> , <i>Q. meridiocarpaticus</i> , <i>Q. subunicolor</i> and <i>Q. molochinus</i>	1	88	90	High
<i>Q. balticus</i>	na	na	na	na
<i>Q. meridiocarpaticus</i> , <i>Q. subunicolor</i> and <i>Q. molochinus</i>	0.99	85	81	High
<i>Q. meridiocarpaticus</i>	1	99	100	High
<i>Q. subunicolor</i> and <i>Q. molochinus</i>	0.98	884	85	High
<i>Q. subunicolor</i>	1	99	100	High
<i>Q. molochinus</i>	1	99	100	High
Nearctic members				
<i>Q. horni</i>	1	100	100	High
<i>Q. lanei</i> , <i>Q. laticollis</i> , <i>Q. labradorensis</i> , <i>Q. altanai</i> and <i>Q. molochinoides</i>	0.7	79	56	Low
<i>Q. lanei</i> , <i>Q. laticollis</i> and <i>Q. labradorensis</i>	1	81	76	High
<i>Q. lanei</i>	1	100	100	High
<i>Q. laticollis</i> and <i>Q. labradorensis</i>	0.88	56	64	High
<i>Q. laticollis</i>	1	90	95	High
<i>Q. labradorensis</i>	1	100	100	High
<i>Q. altanai</i> and <i>Q. molochinoides</i>	1	99	100	High
<i>Q. altanai</i>	na	na	na	na
<i>Q. molochinoides</i>	0.99	93	86	High
<i>Q. molochinoides</i> -gr 3	1	91	98	High
<i>Q. molochinoides</i> -gr 2	0.99	86	82	High
<i>Q. molochinoides</i> -gr 1	1	95	91	High

ndinavia and Altai were previously recognized as two separate species – *Q. subunicolor* and *Q. altaicus*.

Within the weakly supported Nearctic clade (PP = 0.70, SH-aLRT = 78.8, UFB = 56) two subclades were recovered. One with high support comprising *Q. molochinoides* and *Q. altanai* (PP = 1, SH-aLRT = 99.4, UFB = 100), and one with weak support comprising *Q. lanei* as sister to *Q. labradorensis* and *Q. laticollis* (PP = 0.93, SH-aLRT = 81.2, UFB = 76). The sister group relationship of *Q. labradorensis* and *Q. laticollis* received weak support (PP = 0.88, SH-aLRT = 56.3, UFB = 64). All the taxonomic species in the Nearctic clade – *Q. lanei*, *Q. laticollis*, *Q. labradorensis*, and *Q. molochinoides* (PP = 1, SH-aLRT = 100, UFB = 100; PP = 0.99, SH-aLRT = 90, UFB = 95; PP = 1, SH-aLRT = 100, UFB = 100; PP = 0.99, SH-aLRT = 92.5, UFB = 86) – were monophyletic and highly supported in both analysis, except for *Q. altanai*, which was only represented by a single sequence, and thus without support. *Q. molochinoides* was further clustered in three distinct subgroups each with high support – *Q. molochinoides*-group 1, -group 2, and -group 3 (PP = 1, SH-aLRT = 95.3, UFB = 99; PP = 0.98, SH-aLRT = 86.1, UFB = 92; PP = 0.99, SH-aLRT = 91.5, UFB = 86, respectively).

The haplotype network analysis of the morphologically rather uniform *Q. molochinoides*-group (*Q. molochinoides*, *Q. lanei*, *Q. horni* and *Q. altanai*) showed clear gaps between the known taxonomic species (Fig. 5). After filtering, the network was represented by a total of 44 sequences most belonging to *Q. molochinoides*, only three of *Q. horni* and one of *Q. lanei*. The current taxonomic species were separated as follows: 28 SNPs between *Q. molochinoides* and the single sequence of *Q. lanei* and 22 SNPs between *Q. molochinoides* and *Q. horni*. The three subgroups of *Q. molochinoides* found in both the BI and ML analyses were recovered in the network analysis with four distinct SNPs between each subgroup. Within each of these subgroups most sequences were separated by a single SNP, except for a few sequences, which were separated by two or three SNPs.

Species groups. The species groups outlined in this paper are based on a combination of molecular and morphological data combined with biological and geographical considerations. As the COI gene is not very reliable at resolving the phylogenetic backbone species group relationship, we instead rely on data from two upcoming papers (BRUNKE et al. 2021; A. HANSEN et al., in prep.), that use target capture of 1229 orthologous loci to resolve the phylogeny of *Quedius* s. str. is presented in Fig. 1 and is used as a genetic backbone to base our decisions on. Based on these data, the *fuliginosus*-group, *pallipes*-group, *molochinoides*-group and *laticollis*-group are well resolved and have morphological characters easily defining them. On the other hand, the *molochinus*-group is paraphyletic and was resolved as three distinct groups, namely the monotypic *Q. vicinus* and *Q. unicolor*, as well as the rest of the *Q. molochinus*-group. Here we have instead used morphological and distributional data to group species according to practical purposes, so that the species groups are as easy to distinguish morphologically within each biogeographic region as possible.

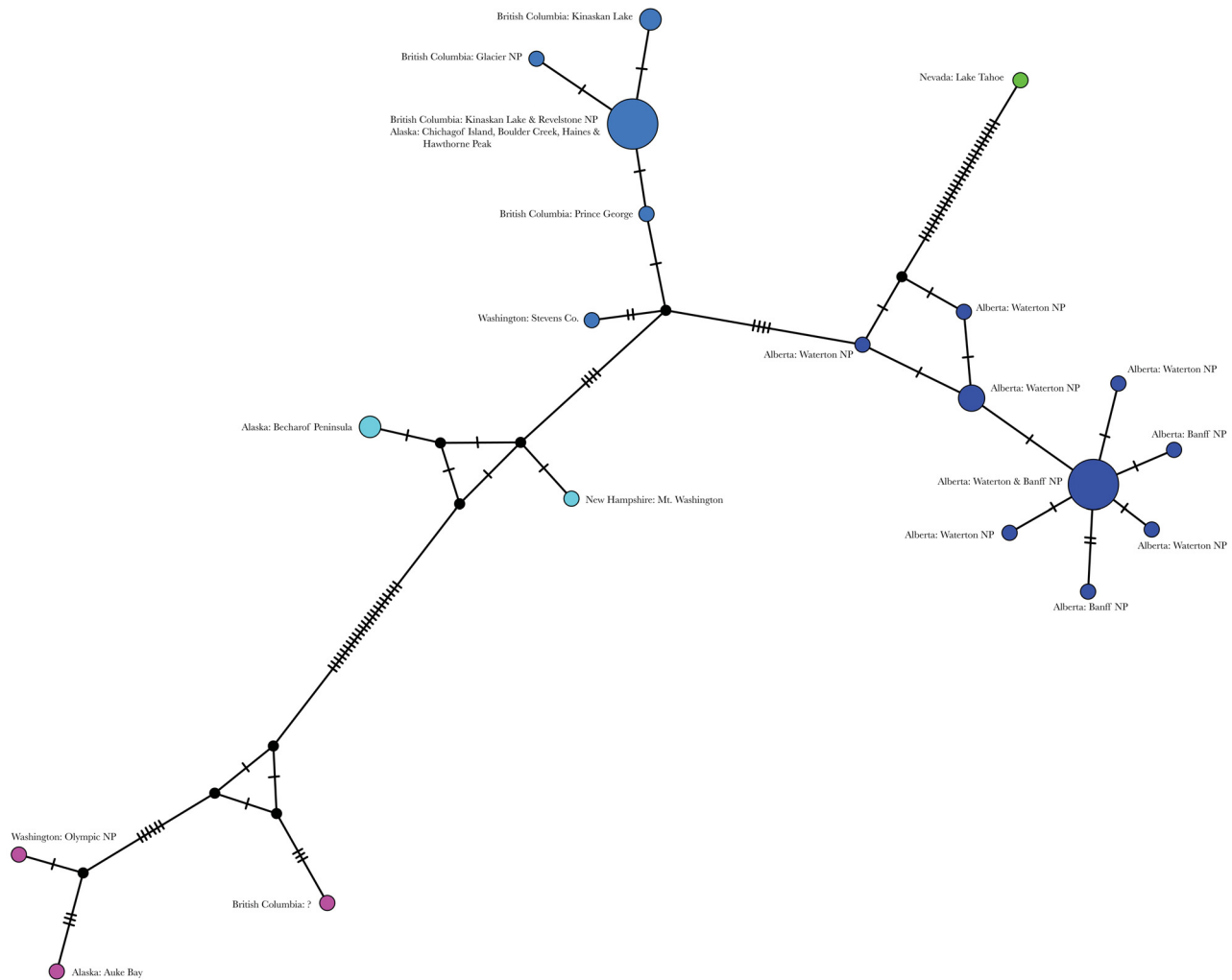


Fig. 5. Network analysis of *Quedius molochinoides*-group: *Quedius horni* Hatch, 1957 (purple), *Q. lanei* Hatch, 1957 (green), *Q. molochinoides*-group 1 (dark blue), *Q. molochinoides*-group 2 (light blue), and *Q. molochinoides*-group 3 (teal).

Taxonomy

Genus *Quedius* Stephens, 1829

Subgenus *Quedius* Stephens, 1829

Type species. *Staphylinus levicollis* Brullé, 1832 by subsequent designation in Opinion 1851 (ICZN 1996: 215).

Diagnosis. Generally large and robust species; pronotum with deflexed hypomera; head with large eyes, fully developed infraorbital ridges and entire (not bilobed or apically notched) labrum; tarsi of forelegs rather wide in both sexes; mesoscutellum with two basal carinae; abdomen almost parallel sided, not notably tapering apicad; aedeagus with sharply pointed median lobe, internal sac well developed and often having heavily sclerotized structures, with longitudinal rows of sensory peg setae on paramere apically.

Quedius fuliginosus-group

Diagnosis. Head with 4 or 6 interocular punctures between anterior frontal punctures. Generally largest species within the subgenus with entire body dark; only rarely elytra reddish. Temporal puncture situated at posterior margin of eye. Paramere does not extend over median lobe apex, peg

setae arranged in single rows; median lobe without large teeth on parameral side, at most with small teeth or sub-apical notch; internal sac without large c-shaped sclerite. Generally widespread species, common in the Palearctic region, found in diverse ground-based debris in both forest and open landscapes. Only *Quedius afrofuliginosus* is rare, possibly an artefact of both misidentifications and poor sampling in parts of its range.

Quedius afrofuliginosus Gusarov, 1991

(Figs 1, 3, 6E, 7A, 11A, 18)

Quedius afrofuliginosus Gusarov, 1991: 9 [Type locality: Algeria]

Type material. HOLOTYPE: "Algerie, Raffray / [black circle] / c. A. Yakovleva [in Russian] / Holotypus *Quedius afrofuliginosus* V. Gusarov 1990 [red label] / Zoological Institute St. Petersburg INS_COL_0002505" (♂ ZIN). PARATYPES: same as holotype, except "Allotypus *Quedius afrofuliginosus* V. Gusarov 1990 [red label] / Zoological Institute St. Petersburg INS_COL_0002506" (1 ♀ ZIN); same as holotype, except "Paratypus *Quedius afrofuliginosus* V. Gusarov 1990 [red label] / Zoological Institute St. Petersburg INS_COL_0002507-000250710" (3 ♂♂ 1 ♀ ZIN).

Additional material examined. FRANCE: CORSE: Col de Bravella, [41.83, 9.26], 490m, 25.VII.1994, leg. Zerche (1 ♂ SDEI). ITALY: SARDINIA: Aritzo, Mte. Gennargentu, [39.94, 9.17], leg. C. Krüger (2 ♂♂ NMW); Ottana, [40.23, 9.04], 11.X.1974 (1 ♀ cBor); MOROCCO: Ain Leuh, [33.28, -5.33], 17.V.1925, leg. M. Escalera (1 ♀ MNCN). SPAIN:

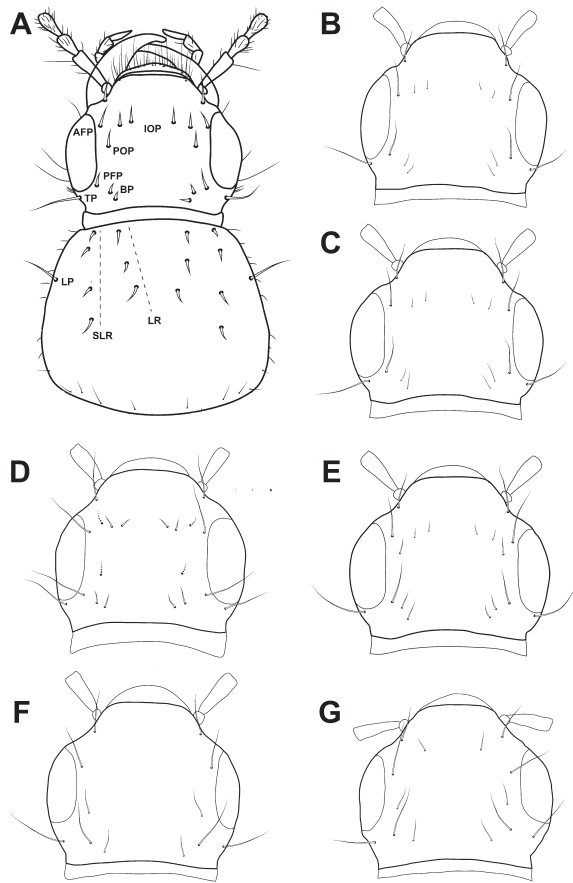


Fig. 6. Head and pronotal chaetotaxy of *Quedius* s. str. A – general scheme; B – *Q. curtipennis* Bernhauer, 1908, C – *Q. fuliginosus* (Gravenhorst, 1802); D – *Q. levicollis* Brullé, 1832; E – *Q. afrofuliginosus* Gusarov, 1991; F – *Q. molochinus*- and *Q. laticollis*-groups; G – *Q. molochinoides*-group. Abbreviations as follows: anterior frontal puncture (AFP); basal punctures (BP); interocular punctures (IOP); lateral puncture (LP); lateral row (LR); posterior frontal puncture (PFP); parocular punctures (POP); sublateral row (SLR).

Cadiz, Laguna de la Janda, [36.24,-5.84], 30.V.1966, leg. Besuchet (1♂ NMPC).

Redescription. Measurements ♂♂ (n = 6): HW = 1.78–1.89 (1.84); HL = 1.54–1.58 (1.56); HL/HW 0.82–0.89 (0.85); PW = 2.24–2.44 (2.36); PL = 2.11–2.22 (2.16); PL/PW 0.89–0.96 (0.92); EW = 2.33–2.68 (2.59); EL = 2.40–2.51 (2.47); EL/EW 0.90–1.03 (0.95); EL/PL 1.10–1.19 (1.14); PW/HW 1.44–1.57 (1.51); forebody length 6.10–6.29 (6.19). ♀♀ (n = 3): HW = 1.84–1.89 (1.87); HL = 1.56–1.62 (1.59); HL/HW 0.84–0.86 (0.85); PW = 2.38–2.40 (2.39); PL = 2.04–2.24 (2.17); PL/PW 0.86–0.94 (0.91); EW = 2.69–2.73 (2.72); EL = 2.36–2.58 (2.48); EL/EW 0.88–0.94 (0.91); EL/PL 1.06–1.26 (1.15); PW/HW 1.47–1.53 (1.50); forebody length 6.18–6.36 (6.24).

Large species; body black (Fig. 7A).

Head black, distinctly transverse, with microsculpture of head transverse waves, four punctures between anterior frontal punctures, one additional unique puncture on either side posterior of these (Fig. 6E), eyes very large (EyL/TL = 3.17–3.91 (3.68)) and clearly protruding; antennae and palpi pale reddish, all antennomeres elongate.

Thorax: pronotum black, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row, two punctures in sublateral row with posteriormost puncture reaching level of middle puncture of dorsal row; scutellum smooth and glabrous; elytra black, uniformly pubescent, quadrate or slightly wider than long, slightly longer than pronotum; legs dark brown with inner face of tibia darkened and tarsi paler.

Abdomen black, tergites uniformly punctured, slightly iridescent.

Male. Aedeagus (Fig. 11A): paramere broad, rather parallel-sided, reaching apex of median lobe, with sensory peg setae forming two single rows along parameral lateral margins for 2/3 of their length; median lobe on parameral side with clear apical protrusion and two subapical small teeth, the latter positioned near end of peg setae rows of paramere; internal sac with four distal elongate medial sclerites.

Differential diagnosis. *Quedius afrofuliginosus* can be distinguished from all other *Quedius* s. str. by the unique head chaetotaxy, with a puncture on either side posterior of the anterior frontal puncture (Fig. 6E). Within the *fuliginosus*-group it is additionally distinguished from *Q. fuliginosus* by the pale antennae, from *Q. levicollis* by the impunctate and glabrous scutellum, and from *Q. curtipennis* by wider head (HW/HL = 0.74 vs 0.85) and aedeagal median lobe with apical protrusion.

Bionomics. Nothing is known about the biology of *Q. afrofuliginosus*. Based on collecting sites it is most likely occurring in forested areas of medium elevation (450 to 1400 m).

Distribution. *Quedius afrofuliginosus* was originally described from an unknown locality in Algeria. The new material studied in this paper brought to light additional specimens from Tunisia and Morocco in Northern Africa, as well as the first records of this species from the Mediterranean region in southern Spain and on the southern European islands of Corse and Sardinia (Fig. 18).

Quedius curtipennis Bernhauer, 1908

(Figs 1, 3, 6B, 7B, 11C, 12, 18)

Quedius curtipennis Bernhauer, 1908e: 335 [Type locality: Faroe; Romania; Buchara; Böhmen, Wran a. Moldau].

Quedius gracilis Stephens, 1832: 215 [Type locality: London], **syn. rev.** *Quedius parallelus* Hatch, 1957: 216 [Type locality: Washington, Seattle]

References. GRIDELLI (1924): 79 (characters), SCHEERPELTZ (1933): 1441 (characters), HANSEN (1952): 141 (characters); SMETANA (1958): 362 (characters and ecology); (1962): 133, (1965b): 38 (characters); (1971a): 129 (characters, synonymy of *Q. parallelus*); (1965a): 12, (1970): 62, (1990): 98, (1993): 50 (distribution); (1978a): 826 (biology); KORGE (1962b): 332 (suspected synonymy of *Q. parallelus*); (1964): 119 (distribution); PALM (1963): 141 (characters); LOHSE (1964): 211 (characters); DVOŘÁK (1965): 89 (distribution); HORION (1965): 272 (distribution); SZUJECKI (1968): 735 (distribution); FRANK (1969): 267 (biology); BORDONI (1974b): 10, (1976b): 92 (characters); POPE (1977): 31 (distribution); COIFFAIT (1978): 191 (characters); OUTERELO (1978): 281 (pupal characters); BURAKOWSKI et al. (1980): 134 (distribution); TÓTH (1984): 118 (characters); DRUGMAND (1987): 312 (distribution); NOWOSAD (1990): 145 (biology); BORGES (1990): Table II (distribution); CICERONI & ZANETTI (1995): 32 (distribution); OWEN (1997): 149 (distribution); OUTERELO et al. (1998): 129 (biology); ASSING (2001): 75

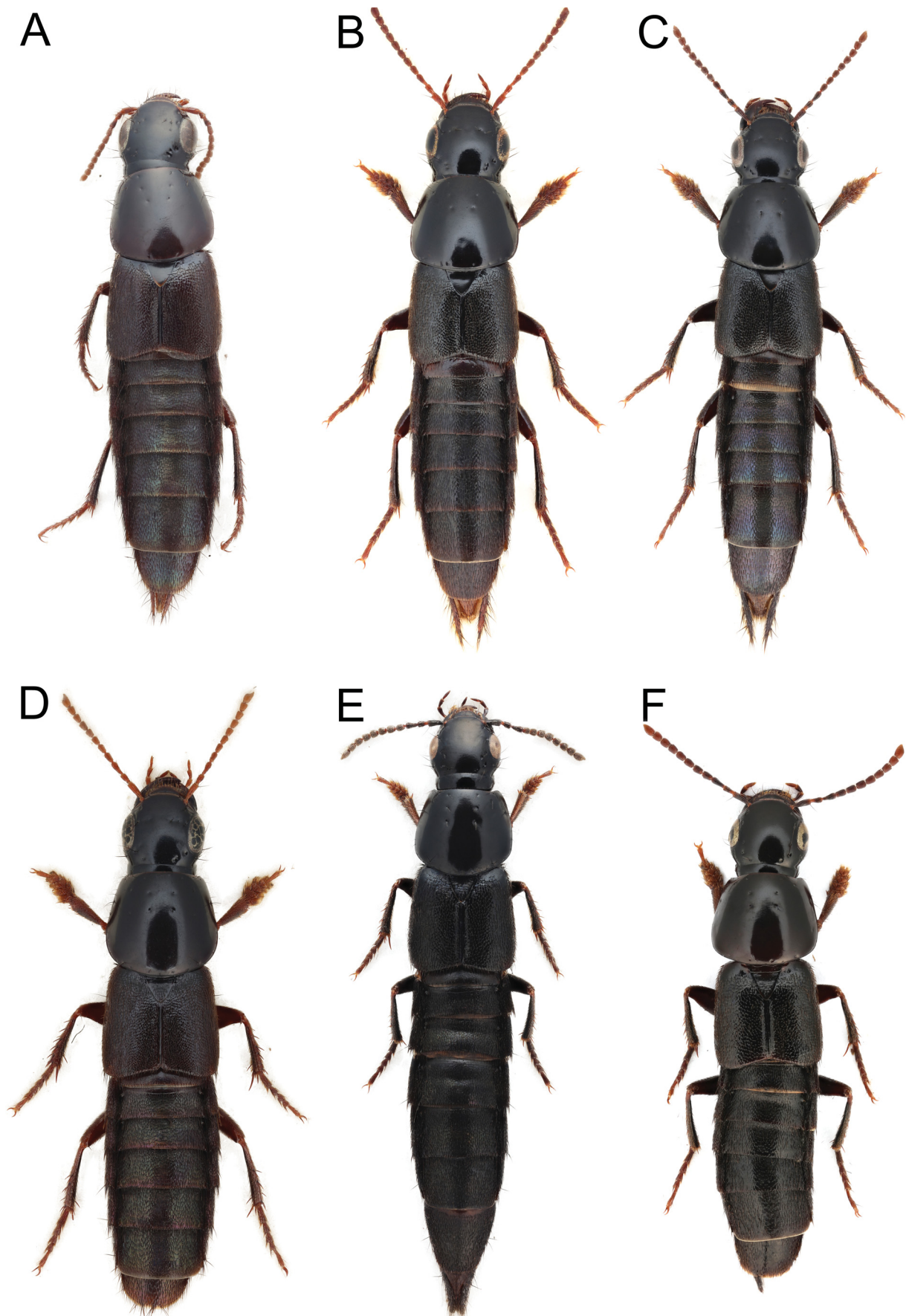


Fig. 7. Habitus of *Quedius* s. str. A – *Q. afrofuliginosus* Gusarov, 1991; B – *Q. curtipennis* Bernhauer, 1908; C – *Q. fuliginosus* (Gravenhorst, 1802); D – *Q. levicollis* Brullé, 1832; E – *Q. unicolor* Kiesenwetter, 1847; F – *Q. subunicolor* Korge, 1961.

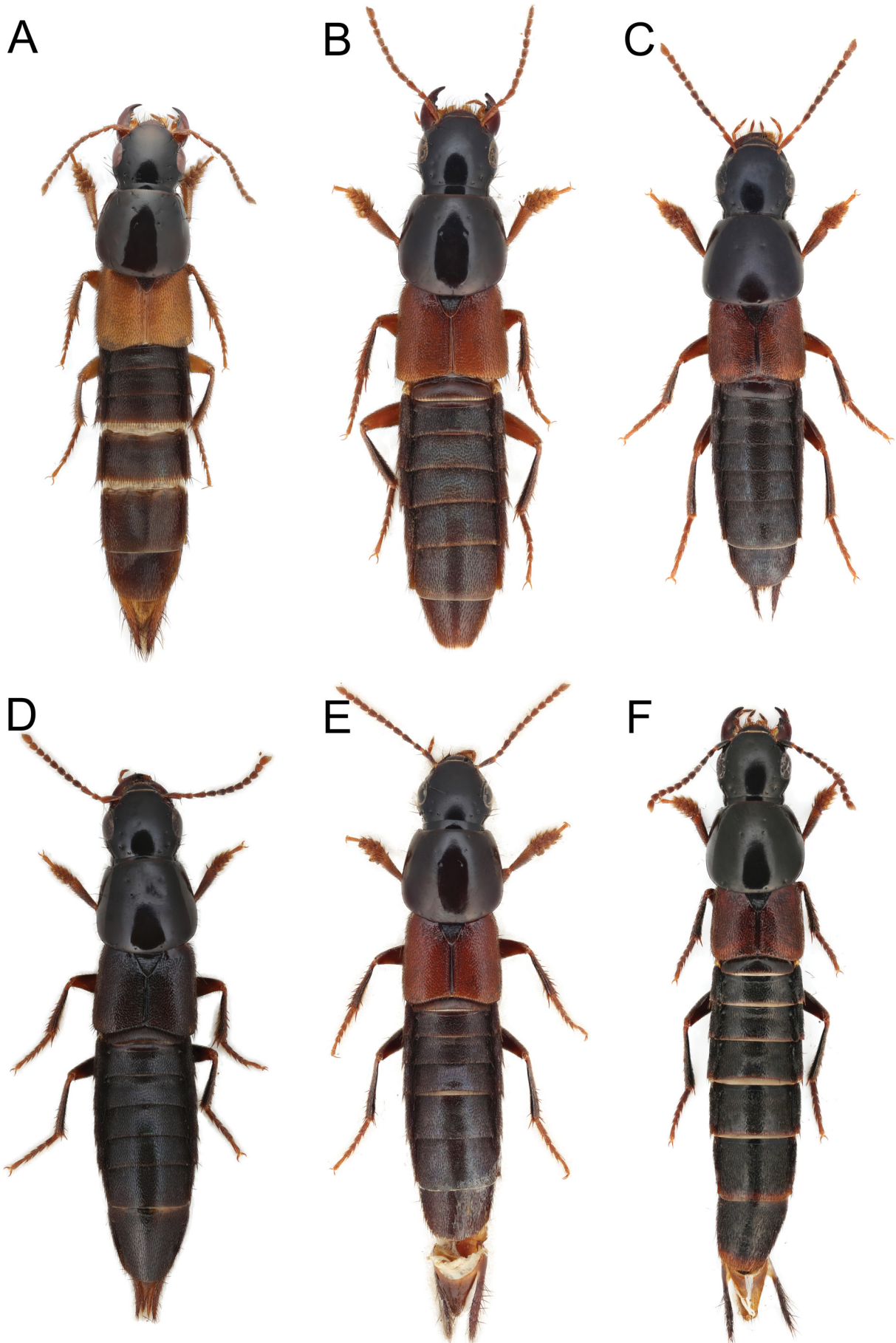


Fig. 8. Habitus of *Quedius* s. str. A – *Q. vicinus* (Ménétriés, 1832); B – *Q. meridiocarpaticus* Smetana, 1958; C – *Q. molochinus* (Gravenhorst, 1806) (red elytra variant); D – *Q. molochinus* (black elytra variant); E – *Q. balticus* Korge, 1960; F – *Q. sundukovi* Smetana, 2003.

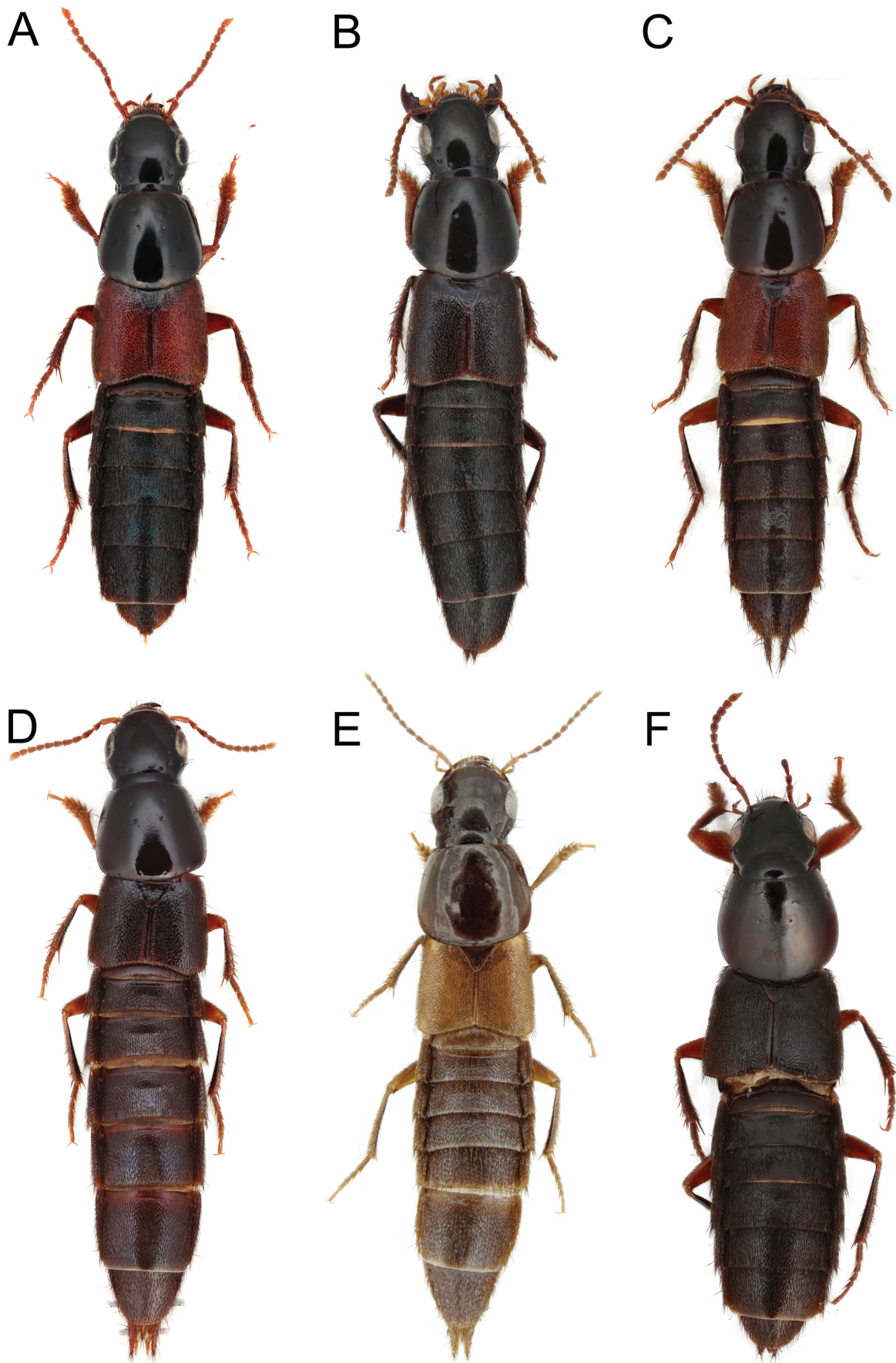


Fig. 9. Habitus of *Quedius* s. str. A – *Q. hispanicus* Bernhauer, 1898; B – *Q. hispanicus* (pale sutures variant); C – *Q. pallipes* Lucas, 1846; D – *Q. laticollis* (Gravenhorst, 1802) (black elytra variant); E – *Q. laticollis* (red elytra variant); F – *Q. strenuus* Casey, 1915.

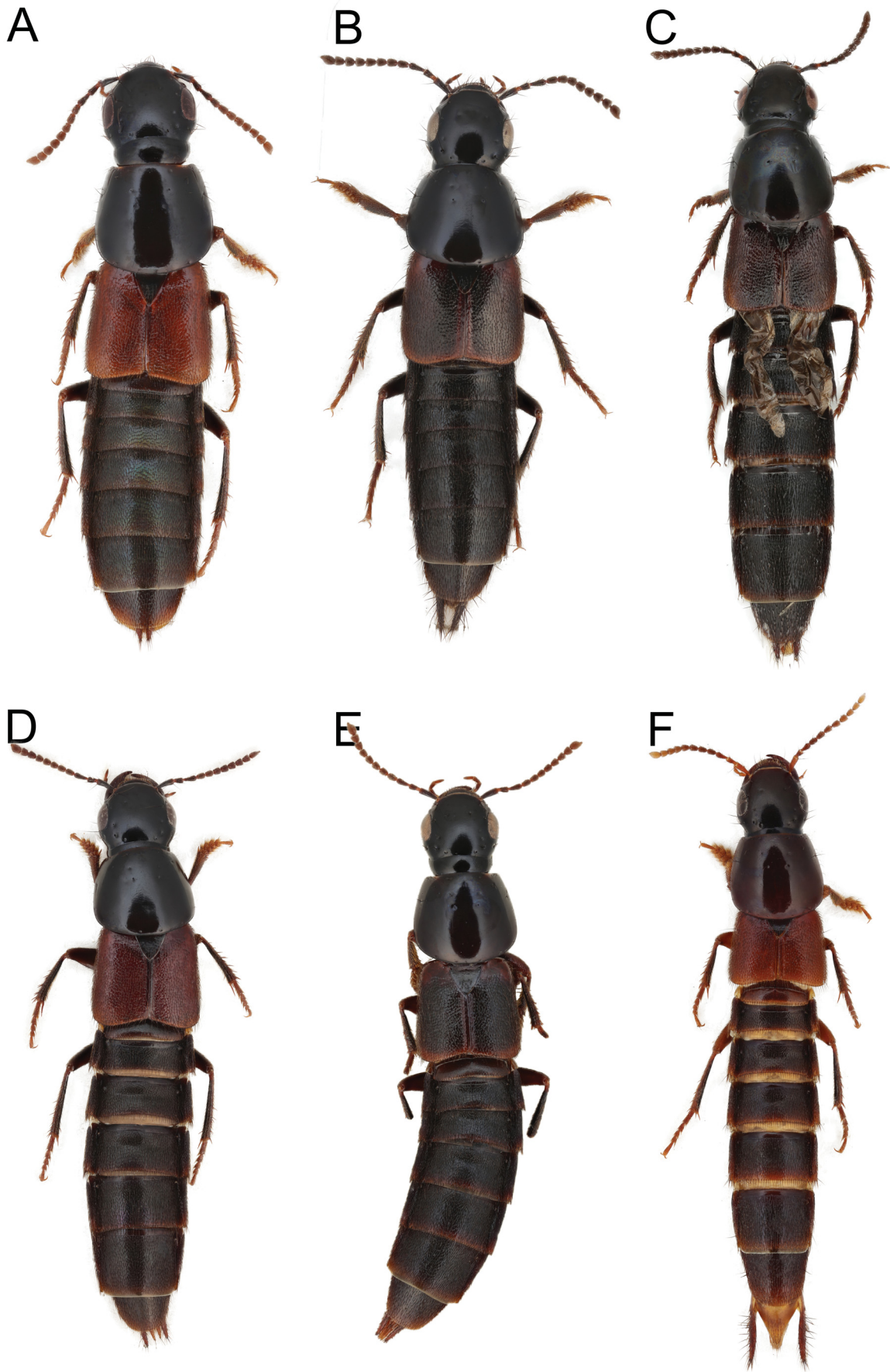


Fig. 10. Habitus of *Quedius* s. str. A – *Q. horni* Hatch, 1957; B – *Q. lanei* Hatch, 1957; C – *Q. altanai* Hansen & Brunke, sp. nov.; D – *Q. molochinoides* Smetana, 1965 (red elytra variant); E – *Q. molochinoides* (black elytra variant); F – *Q. labradorensis* Smetana, 1965.

(biology); UHLIG et al. (2006): 54 (distribution); TRONQUET (2006): 102 (distribution); MAJKA & SMETANA (2007): 429 (characters and distribution); ÖZGEN (2011): 204 (distribution); BRUNKE & MARSHALL (2011): 59 (characters and distribution); WEBSTER et al. (2012): 313 (distribution); MAGURA et al. (2013): 719 (biology); TÓTHMÉRÉSZ et al. (2014): 688 (biology); SEMENOV et al. (2015): 127 (distribution); SEMIONENKOV et al. (2015): 330 (distribution); SALNITSKA & SOLODOVNIKOV (2018a): 125 (notes on types and distribution); (2019): 48 (distribution).

Type material examined. *Quedius curtippennis*: LECTOTYPE: (♂, here designated): “Suderö Faroer Ins./ Dr. Cornu 1907/ v. curtippennis Brh. Typus / fuliginosus Grav. Scheerp. / Chicago NHMus M. Bernhauer Collection / D. Drugmand det. 1994 *Quedius* (s. str.) curtippennis Brnh. / Lectotype *Quedius curtippennis* Bernhauer, 1908 A.K. Hansen & A. Solodovnikov des. 2021” (FMNH). PARALECTOTYPES: “Nördl. Faroer Ins. / Dr. Cornu 1907 / v. curtippennis Brh. Typus / fuliginosus Scheerp. [sic!] det. [illegible] / Chicago NHMus M. Bernhauer Collection / D. Drugmand det. 1994 *Quedius* (s. str.) curtippennis Brnh. / Paralectotype *Quedius curtippennis* Bernhauer, 1908 A.K. Hansen & A. Solodovnikov des. 2021” (1 ♂ FMNH); “v. curtippennis Buchara Bang Haas det. Bernh. / Chicago NHMus M. Bernhauer Collection” (1 ♂ FMNH).

Quedius parallelus: HOLOTYPE: “Seattle, Wash. U.W. Campus IV-12-1949 / Del. 1954 H. Houk / Type ♂ *Quedius* (s. str.) parallelus - 1951 M. Hatch / *Quedius* (s. str.) fuliginosus Grav. M. Hatch - 1947” (1 ♂ UWBM). PARATYPES: “Seattle, Wash. April 12, 1934” (1 ♂ UWBM); “Seattle, Wash. U.W. Campus, IV-11-1947” (1 ♂ UWBM, N. Vowles coll.); “Vancouver, B.C., 5 March, 1949, G.B. Rich” (1 ♂ CNC); “Wash. Seattle, Feb. 15, 1954, B. Malkin” (1 ♀ FMNH, ex coll. B. Malkin).

Additional material examined. **ARMENIA:** Arzakanskaja dolina, Aghveran, [40.51, 44.56], 3.VII.1978, leg. R. Rous (1 ♀ MCZ); NE Dilizhan nr. Haghartsin Monastery, 40.8013, 44.8919, 1450 m, 21.V.2001, leg. Shaverdo & Schillhammer (4 ♂♂ NMW); 18 km E Dilizhan, 3 km Gosh, 40.7405, 45.0191, 1850 m, 27.V.2001, leg. Shaverdo (1 ♂ NMW); 21 km N Hrazdan, Ankavan, 40.6286, 44.5533, 1000 m, 22.V.2001, leg. Shaverdo & Schillhammer (1 ♂ NMW); Teghut, Akhtala, 41.0901, 44.8120, 1009 m, 28.VI.2016, leg. J. Müller (1 ♂ cSch); same locality, 41.0911, 44.8131, 1020m, 20.V.2016, leg. A. & J. Müller (2 ♀♀ ZMHB). **AUSTRIA:** Bisamberg, [48.33, 16.36], leg. Luze (1 ♀ NMW); S Steiermark, [46.91, 15.60] (1 ♂ NMW); Tirol, Musau, [47.53, 10.67], litter, moss, and grass, 28.C.1995, leg. M.Uhlig (1 ♂ ZMHB); Wolfpassing, [48.08, 15.06], VI.1965, leg. Wewalka (1 ♀ NMW). **BULGARIA:** Rila Monastery, [42.13, 23.34], 1150 m, 14.VII.1965, leg. P. Jorum (1 ♂ NHMD). **BOSNIA AND HERZEGOVINA:** Zeleznica [Zeljeznica] n. Foinica, [43.89, 17.95], 500-700m, 13.IV.1969, leg. U. Heinz (1 ♂ ZMHB). **CANADA:** **BRITISH COLUMBIA:** Stanley Park, Vancouver, [49.30, -123.14], 9.VI.1954, leg. D. Lazorko (1 ♂ 1 ♀ NMW). **CZECH REPUBLIC:** Brandeis, [50.18, 14.65], leg. Skalitzky (2 ♂♂ NMW). **DENMARK:** Vigsø Bugt, 1 km E of Vigsø, 57.0950, 8.7394, pine forest, pitfall traps, 16.-18.VI.2014, leg. A.Hansen, M.Justesen, A.Solodovnikov & L.Kræmer (1 ♂ NHMD). **LÆSØ:** Læsø Klitplantage, 57.3082, 11.0081, mixed forest, sifting litter, 28.V.2013, leg. A. Solodovnikov & M. Justesen (1 NHMD). **FAROE ISLANDS:** Suderö [Suðuroy], [61.51, -6.83], 1907, leg. Cornu (1 ♂ FMNH). **FRANCE:** Ain, Torcieu n. Amberieu, [45.91, 5.39] (1 ♂ ZMHB); Bretagne, Locronan, [48.09, -4.21], VII.1983, leg. H.Korge (1 ♂ ZMHB); Chigny n. Oise, [49.91, 3.76], leg. Gelchert (1 ♀ ZMHB); Morlaix, Bretagne, [48.57, -3.82], 1.VIII.1950, leg. A. Nilsson (2 ♂♂ MZLU). **GEORGIA:** Borzhom Distr., Bakuriani, [41.75, 43.52], 27.VII.1947, leg. Bogachev (1 ♂ 1 ♀ ZIN); Kartliskij Chreb. [Kartalinskij Khrebet], Sabaduris Tye [Sabaduri Pass] [41.91, 44.91], 1800m, 8.VI.1987, leg. Wrase (1 ♂ cSch); same locality, 25.VI.1988, leg. Wrase (1 ♂ ZMHB); Trialjetski, Khrebet Bakuriani, [41.74, 43.83], 1800-2200m, 4.-7.VII.1986, leg. Wrase & Schülke (8 ♂♂ 4 ♀♀ ZMHB); Zchneti [Tskneti], [41.69, 44.69], 1200m, 26.VI.1986, leg. Wrase (1 ♂ cSch). **GERMANY:** Bayern, Garmisch, [47.48, 11.08], 27.IV.1932, leg. Ihssen (1 ♂ ZMHB); Bonn, [50.72, 7.09], X, leg. Verhoeff (1 ♀ ZMHB); Bayern, Eschenlohe, [47.58, 11.18], 3.VIII.1937, leg. Ihssen (1 ♂ ZMHB); Brandenburg, Strausberg, [52.52, 13.85], 17.IV.1987, leg. M. Schülke (1 ♂ ZMHB); Dresden, Kötschenbroda, [51.11, 13.61], moss, 23.I.1920, leg. Dahl (1 ♂ ZMHB); Düsseldorf Unterbach, [51.20, 6.89], 27.VII.1974, leg. H.Bremer (1 ♀ ZMHB); Marburg, [50.80, 8.76], 16.IV.1904, leg. Strand (1 ♀ ZMHB); Sarstadt, [52.24, 9.85], 12.IX.1960, leg. Kuntze (1

♂ ZMHB). **ITALY:** Aniene, Lazio, [41.95, 12.82], 1200 m, 18.III.1964, leg. A. Vigna-Taglianti (1 ♂ cBor); Barni, Lombardia, [45.91, 9.26], 11.II.2001, leg. Diotti (1 ♂ 1 ♀ NHMD); Moliterno, Basilicata, [40.24, 15.86], 30.IX.2000, leg. F. Angelini (1 ♀ NHMD); Pignola, Basilicata, [40.57, 15.78], 700 m, 19.IV.1998, leg. F. Angelini (1 ♂ NHMD); Querciola, Toscana, [43.84, 11.32], 13.IV.2005, leg. Bordoni (1 ♂ cBor). **LATVIA:** Curonia Libau [Liepāja], [56.49, 21.01], 4.IV.1910 (1 ♂ 1 ♀ ZMHB). **MOROCCO:** Cirque du Jaafar, [32.55, -4.91], 4.III.1964 (1 ♂ NMW) [potentially mislabelled or introduced specimen clearly belonging to this species]. **MYANMAR:** Mountains, Tenasserim, Siam Border, [11.79, 99.62], II.-V.1913, leg. K.G. Gairdner (1 ♂ BMNH) [potentially mislabelled or introduced specimen clearly belonging to this species]. **POLAND:** Dunajec River n. Sromowce Nizne, [49.39, 20.39], 18.VII.1977, leg. F. Hieke (3 ♂♂ 4 ♀♀ ZMHB); Wyspawy, Krzozonowka River n. Poin, [49.69, 20.24] 300m, 26.VIII.1980, leg. Hieke (1 ♂ ZMHB). **PORTUGAL:** **AZORES:** Santa Maria, 2 km ENE Almagreira, Mirador dos Picos, [36.97, -25.07], 440 m, 19.III.1957, leg. Brinck & Dahl (1 ♂ MZLU); São Miguel, 500 m E of Lagoa do Pau Pique, [37.83, -25.74], pond, 7.III.1957, leg. Brinck & Dahl (1 ♂ MZLU); São Miguel, Pico de Vara, 37.8119, -25.2105, 1050m, boggy slope 24.VII.2013, leg. V. Assing (4 ♀♀ ZMHB). **MADEIRA:** Levada da Serra do Faial, [32.68, -16.85], creek, 820m, 11.IX.2014, leg. A. Kleeberg (1 ♂ cSch). **ROMANIA:** Klausenburg [Cluj-Napoca], [46.76, 23.62], leg. Verhoeff (1 ♂ ZMHB); Hermannstadt, Siebenbürgen [Sibiu], [45.79, 24.15], leg. Skalitzky (1 ♂ NMW); Piatra, Virful Tiganului, Sighetu Marmătiei, Maramureş, [47.99, 23.53], 1300 m, pasture, in rotten logs of beech, 14.VI.2006, leg. A. Grabant, Z. György, O. Merkl & A. Podlussany (1 ♂ NHMD). **RUSSIA:** **KARACHAY-CHEKKESSIA:** Teberda, [43.44, 41.74], VI.1912, leg. Roubal (1 ♀ SNMC). **MOSCOW OBLAST:** Bykovo village, VNIICR institute territory, [55.61, 38.05], 16.X.2013, leg. S. A. Kurbatov (3 ♂♂ ZIN); Odintsovsky Distr., near Zhavoronki vill., [55.64, 37.10], 6-13.VIII.2017, leg. E. M. Veselova & A. B. Ryvkin (1 ♂ ZIN). **NIZHEGORODSKAJA OBLAST:** near Gorodets town, [56.64, 43.47], mixed forest, 17.VIII.1989, leg. A. Klimenko (1 ♂ ZIN). **NOVGORODSKAJA OBLAST:** Torbino, Novgorod, [58.58, 32.87], 10.IV.1914, leg. A. Filiniev (1 ♂ cBor). **NORTH OSSETIA REP.:** Caucasus, Skalisty Khrebet, Fiagdon River, [42.87, 44.32], 1700-2200 m, VI.1976, leg. R. Rous (3 ♂♂ 1 ♀ MCZ). **SLOVAKIA:** Belá River n. Pribylina, [49.09, 19.81], 600m, 18.VIII.1981, leg. Hieke (1 ♂ 3 ♀♀ ZMHB). **SPAIN:** Bera de Bidasoa, Navarra, [43.27, -1.68], 1.-7.I.2001, leg. A. Anichtchenko (1 ♂ NHMD); Caldetas n. Barcelona, [41.57, 2.52], leg. G. Heine (1 ♂ ZMHB); La Molina, Pyrenees, [42.33, 1.93], 11.-16.VII.1963 (1 ♂ MZLU); O Rial, Serra do Mirador, [42.74, -7.83], 450m, 3.VI.2003, leg. J. P. Valcárcel (1 ♂ cSch); Picos de Europa, Camping El Redondo [Fuente Dé], [43.14, 4.81], forest, 1100 m, 14.-17.VII.1996, leg. Wrase (1 ♂ cSch); Plaiaundi, Irun, Guipuzcoa, [43.34, -1.79], V.2006, A. Anichtchenko (1 ♂ 1 ♀ NHMD); Pyrenees, Toses, 42.3502, 1.9955, 1660m, fir-spruce forest with moss, 9.X.1997, leg. Zerche (1 ♂ SDEI); Sierra Ancares, [42.81, -6.86], 20.X.1984, leg. J. C. Otero (6 ♂♂ 3 ♀♀ ZMHB); Sierra Caurel, [42.59, -7.18], 20.VII.1985, leg. J. C. Otero (5 ♂♂ 4 ♀♀ ZMHB); Sierra de Gredos, Hoyos de Collado, [40.35, -5.21], 1600m, 14.IV.1991, leg. Heinz (2 ♀♀ ZMHB); Sierra Guadarrama, [40.85, -3.95], 1.VI.1980, leg. C. Otero (2 ♂♂ ZMHB); Sierra de la Demanda, Val de Zcaray [Ezcaray], [42.32, -3.02], forest, 1650m, 23.07.1996, leg. Zaballos & Wrase (1 ♂ cSch). **SWEDEN:** Brönnestad, [56.08, 13.70] (1 MZLU); Omberg, [58.33, 14.64] (1 MZLU); Strömholm, [59.52, 16.23] (1 MZLU); Visseltofta, [56.42, 13.85] (1 MZLU); **ÖLAND:** Vickleby, [56.57, 16.46] (1 MZLU). **SWITZERLAND:** Wolfenschiessen, [46.91, 8.39], 5.VIII.1963, moss (1 ♂ ZMHB). **TURKEY:** Abant n. Bolu, [40.61, 31.27], 30.V.1964, leg. H.Korge (1 ♂ ZMHB); Akkus n. Ünye, [40.79, 37.01], 28.V.1964, leg. H.Korge (1 ♂ 2 ♀♀ ZMHB); Ilgaz Dağları, [41.11, 33.90], 17.-21.VI.1960, leg. F. Schubert (1 ♀ NMW); n. Ismetpasa & Cerkes, [40.75, 32.82], 05.IV.1979, leg. Heinz (1 ♂ NMEG); Kulakakaya n. Giresun, [40.69, 38.33], 1450m, 27.VII.1963, leg. H. Korge (2 ♀♀ ZMHB). **UKRAINE:** Tausban Bazar, [44.97, 34.59], 20.VI.1907, leg. B. Grigoriev (1 ♂ ZIN). **UNITED KINGDOM:** **ENGLAND:** Barnstaple, Devon, [51.07, -4.06], 12.-31.V.1954, leg. Lindroth (1 ♂ MZLU); Devon, Bidefort [51.01, -4.21], leg. H. Korge (2 ♀♀ ZMHB); Kent, Knockholt, 51.3124, 0.1191, 2.IV.2011, leg. J.J. Shaw (1 ♂ cJen); Shrops, Edgmond Harper Adams Uni. Campus, [52.77, -2.42], 6.III.2015, leg. J.J. Shaw (1 ♂ cJen); **SCOTLAND:** Loch Hope, [58.44, -4.62], 19.VII.1987, leg. G. Gillerfors (1 ♂ MZLU). **USA:** Maine: Booth Bay, [43.85, -69.62],

15.VIII.1982, leg. Wewalka (1 ♀ NMW). **UZBEKISTAN:** Buchara, [39.77, 64.42], leg. Bang Haas (1 ♂ FMNH).

Redescription. Measurements ♂♂ (n = 6): HW = 1.89–1.96 (1.93); HL = 1.53–1.71 (1.61); HL/HW 0.81–0.88 (0.84); PW = 2.36–2.56 (2.49); PL = 2.16–2.36 (2.29); PL/PW 0.87–0.94 (0.92); EW = 2.51–2.67 (2.61); EL = 2.36–2.49 (2.44); EL/EW 0.92–0.96 (0.93); EL/PL 1.04–1.10 (1.06); PW/HW 1.31–1.60 (1.49); forebody length 6.04–6.56 (6.34). ♂♀ (n = 4): HW = 1.78–2.00 (1.89); HL = 1.51–1.64 (1.58); HL/HW 0.82–0.85 (0.84); PW = 2.22–2.56 (2.41); PL = 2.07–2.40 (2.18); PL/PW 0.86–0.94 (0.91); EW = 2.44–2.62 (2.52); EL = 2.20–2.49 (2.33); EL/EW 0.90–0.95 (0.92); EL/PL 1.03–1.15 (1.07); PW/HW 1.47–1.55 (1.52); forebody length 5.78–6.53 (6.10).

Very large species; body black (Fig. 7B).

Head black, slightly transverse; eyes large (EyL/TL = 3.00–4.10 (3.55)) not protruding; microsculpture of transverse waves, four punctures between anterior frontal punctures (Fig. 6B); antennae and palpi pale reddish, antennae long, all antennomeres clearly elongate.

Thorax: pronotum black, slightly wider than long, clearly wider than head, microsculpture of transverse waves, three punctures in dorsal row and two in sublateral row with posteriormost puncture reaching level of middle puncture of dorsal row; scutellum smooth and glabrous; elytra black, uniformly pubescent, wider than long, of equal length as pronotum; legs dark brown with inner face of tibia darkened and tarsi paler.

Abdomen black, tergites uniformly punctured, slightly iridescent.

Male. Aedeagus (Fig. 11C): paramere broad, rather parallel-sided, reaching apex of median lobe, with sensory peg setae forming two single rows following parameral lateral margins for 2/3 of their length; median lobe with apical part dorsoventrally flattened to form a plate-like structure; internal sac with two pairs of sclerites.

Differential diagnosis. Within the *fuliginosus*-group *Q. curtipennis* is very close to *Q. fuliginosus*. Both species are very frequently encountered, often co-occurring, nearly non-distinguishable from each other based on external morphological characters alone. Our study of hundreds of specimens across their entire distribution ranges revealed that *Q. curtipennis* always have pale antennomeres 1–3, whereas *Q. fuliginosus* have them at least slightly darkened. A negligible fraction (ca. 2 %) of *Q. fuliginosus* with pale basal antennomeres are mostly teneral. Antennae are generally more elongate in *Q. curtipennis*, as opposed to being stouter in *Q. fuliginosus* (Fig. 7). Also *Q. curtipennis* has an almost smoothly rounded head with the eyes protruding while *Q. fuliginosus* has eyes clearly protruding and thus making its head seem more quadrate (Fig. 6). Only some rare specimens, maybe hybrids, faded and very old museum specimens, or actual rare intraspecific variants, do not fit these trends and their identity can be ascertained only through examination of the aedeagi. In *Q. curtipennis*, contrary to *Q. fuliginosus*, the paramere lacks clear medial attenuation, the apical part of median lobe dorso-ventrally flattened, and internal sac with 2 pairs of clear sclerites.

The examined material for both species clearly shows that *Q. curtipennis* is much more common in the south and west and becomes increasingly rare towards the north and east of its range, while *Q. fuliginosus* shows an opposite trend. *Quedius curtipennis* seems to be more common in warmer and drier areas with more sandy soils, where *Q. fuliginosus* seems to prefer wetter, colder and more humus rich soils.

Quedius curtipennis is also very similar to *Q. afrofuliginosus*, from which it is easily recognized by having no additional punctures between anterior and posterior frontal punctures. Besides, distributions of *Q. curtipennis* and *Q. afrofuliginosus*, as far as known, are allopatric.

From *Q. levicollis*, *Q. curtipennis* is easily recognized by unpunctured and glabrous scutellum.

Lectotype designation. BERNHAUER (1908) described *Q. curtipennis* as a variety of *Q. fuliginosus* without giving any exact data on the type material. He had stressed that it is very common at Faroe Islands and mentioned its occurrence in Central Europe as well as in ‘Romania’ and even ‘Buchara’. Here (see above), we have listed specimens from Faroe Islands and ‘Buchara’ at the FMNH which qualify as syntypes of *Q. curtipennis* and which we recorded long ago but were unable to re-examine in detail recently. There is no doubt about the identity of the syntypes from Faroe Islands. However, a syntype from ‘Buchara’ must be carefully checked. Given, additionally, some ambiguity about the geographic origin of that Middle Asian syntype (see Distribution), a syntype male from Faroe Islands is here designated as a lectotype for *Q. curtipennis*.

Synonymic notes. *Quedius parallelus* was described by HATCH (1957) in his work on beetles of the Pacific Northwest of North America without reference to European species. Based on the description of *Q. parallelus*, KORGE (1962b) suspected it to be identical to the European *Q. curtipennis*. This was confirmed by SMETANA (1971a) who studied the type material of *Q. parallelus* and found them conspecific with 2 male syntypes of *Q. curtipennis* from Faroe Islands at the FMNH. It is now firmly known that *Quedius curtipennis* occurs in the North American West (SMETANA 1971a) and East Coasts (SMETANA 1990, BRUNKE & MARSHALL 2011).

Quedius gracilis Stephens, 1832 was described from London, UK. Later, STEPHENS (1837) had it as a variety of *Q. tristis* (now *Q. levicollis*). In more recent works it was cited as a synonym of *Q. fuliginosus*. Based on examination of its two syntypes by Roger Booth (BMNH, pers. comm.) on our request, it was established that these specimens are conspecific with *Q. curtipennis*. As the name is older than *Q. curtipennis* we here establish the prevailing use of *Q. curtipennis* as opposed to the rule of priority (ICZN Article 23.9). *Quedius curtipennis* has been used at least 26 times in the last 50 years by more than ten authors (BORDONI 1974b, 1976b; POPE 1977; COIFFAIT 1978; OUTERELO 1978; BURAKOWSKI et al. 1980; TÓTH 1984; DRUGMAND 1987; NOWOSAD 1990; BORGES 1990; CICERONI & ZANETTI 1995; OWEN 1997; OUTERELO et al. 1998; ASSING 2001; UHLIG et al. 2006; TRONQUET 2006; MAJKA & SMETANA 2007; ÖZGEN 2011; BRUNKE & MARSHALL 2011; WEBSTER

et al. 2012; MAGURA et al. 2013; TÓTHMÉRÉSZ et al. 2014; SEMENOV et al. 2015; SEMIONENKOV et al. 2015; SALNITSKA & SOLODOVNIKOV 2018a, 2019). On the other hand, *Q. gracilis* has only been used once after its description as a valid species which was more than 150 years ago (CURTIS 1837). This deems the name *Quedius gracilis* Stephens, 1832 a nomen oblitum in relation to *Quedius curtippennis* Bernhauer 1908 (nomen protectum). *Quedius gracilis* Stephens, 1832 syn. rev. is thus moved from synonymy with *Quedius fuliginosus* (Gravenhorst, 1802) to synonymy with *Quedius curtippennis* Bernhauer 1908.

Bionomics. Based on published data as well as our observations, *Q. curtippennis* is a polytopic, somewhat thermophilous species found in a large range of habitats and various ground-based microhabitats with a tendency to occur in open woodlands. For example, in Central and Eastern Europe it was found under stones in dry pastures in Poland (DVOŘÁK 1965), in xerothermous grassland in Germany (ASSING 2001), and in closed oak forest with extensive ground vegetation and shrub cover in Hungary (TÓTHMÉRÉSZ et al. 2014). We have collected this species in a mixed forest on the sandy dry island of Læsø in Denmark. There are also records from mole (*Talpa europaea*) nests built from grasses and reeds on wet meadow in Poland (NOWOSAD 1990). In south-western Europe it was recorded from under rock in pine forest at an altitude of 1550 m in Central Spain (OUTERRELO 1978) and from a cave in Northern Spain (OUTERRELO et al. 1998). On the Azores (SMETANA 1970) it was found under rocks at the shore of a freshwater lake at an elevation of 400–500 m. Presumably, the nest or cave-based subterranean records are accidental occurrences, as there is no evidence of the species preferring these habitats. The species is found within the wide range of elevations from sea level in the northern part of its range up to about 2.000 m the southern part.

As an introduced species in North America, it was found especially around human settlements in various debris, under rocks, and in greenhouses. Some specimens were also collected by sifting barnyard litter on a pasture in Oregon (SMETANA 1978a) and in natural habitats away from settlements (in moss, in leaf litter, etc.).

Pupae of the species are described in OUTERRELO (1978). Adult females from Wytham, UK were observed to contain eggs between October and January (FRANK 1969).

Distribution. *Quedius curtippennis* is distributed from the Atlantic coast of Europe to Asia Minor, east to the Ural Mountains and Middle Asia (Fig. 18). It is also present on the islands of Madeira, the Azores, and the Faroe Islands. One specimen, which we studied was found in the central Moroccan mountains, and one old specimen from the type series is from 'Buchará', Uzbekistan. These are the only specimens we know from North Africa and Middle Asia, respectively. The species' occurrence in these areas needs confirmation to rule out possible mislabelling. Most previous records of *Q. curtippennis* (and *Q. fuliginosus*) from North Africa could be assigned to *Q. afrofuliginosus*, which is externally very similar. As *Q. curtippennis* does not seem to occur in southern Spain, Corse and Sardinia, it is very likely absent from North Africa too.

Quedius curtippennis is also known as introduced to at least four regions of North America (Fig. 12). The presence of *Q. curtippennis* in the Nearctic was first recognized by SMETANA (1971a) when he reviewed specimens of *Q. parallelus*, a newly described species from the Nearctic. *Quedius parallelus* was found to be identical to the Palearctic *Q. curtippennis*, something already hinted by KORGE (1962b). One specimen from the type series of *Q. parallelus* was collected in 1934 near the city of Seattle in Washington, which is currently the oldest known record of the species from North America. In 1971, the species was already found in a relatively large area along the Pacific coast of Oregon, Washington, and British Columbia (SMETANA 1971a), suggesting that it may have been established in North America even prior to 1934. Currently, *Q. curtippennis* in western North America is still known only from these states and provinces, where it is found as far East as Cranbrook, British Columbia in the Canadian Rockies (from web www.boldsystems.org) (teal in Fig. 12). One to three additional introductions of *Q. curtippennis* were later reported from the East Coast, in New Hampshire, USA, as well as Ontario and Nova Scotia, Canada. Specimens from near Guelph in Ontario were collected in 1976 (BRUNKE & MARSHALL 2011), from New Hampshire in 1983 (SMETANA 1990) and from Nova Scotia in 1997 (MAJKA & KLIMASZEWSKI 2008).

Quedius fuliginosus (Gravenhorst, 1802)

(Figs 1, 2A,E, 3, 6C, 7C, 11D, 12, 18)

Staphylinus fuliginosus Gravenhorst, 1802: 34 [Type locality: Brunsviga].

Note: See lectotype designation by GUSAROV (1993)

Quedius granulipennis Motschulsky, 1858: 656 [Type locality: Autriche].

Note: See lectotype designation by GUSAROV (1993)

Quedius impunctifrons Delahon, 1915: 395. [Type locality: Mark Brandenburg]

Quedius jelineki Krása, 1904: 81 [Type locality: Vrané n. Vlt, Bohemia]

Quedius latus Hochhuth, 1851: 30 [Type locality: Kaukasien, Alagez-Gebirge], **syn. nov.**

Quedius molochinicolor Roubal, 1931: 1 [Type locality: RCS.: Harmanec]

Quedius picicornis Stephens, 1832: 215 [Type locality: London]

Quedius subfuliginosus Britten, 1944: 290 [Type locality: England: Cotterill Clough, Cheshire]

Quedius viduus Sawada, 1965: 17 [Type locality: Japan, Pref. Nagano, Mt. Jōnen], **syn. nov.**

References. MARSHAM (1802): 504 (characters); LATREILLE (1804): 319 (characters); GYLLENHAL (1810): 301 (as *tristis*; characters); MANNERHEIM (1830): 25 (distribution); (1831): 439 (distribution); NORDMANN (1837): 78 (distribution); ERICHSON (1839a): 490 (distribution); (1840): 537 (characters); HEER (1839): 276 (characters); DUFOUR (1843): 33 (characters); KOLENATI (1846): 22 (distribution); GRAVENHORST (1847): 232 (characters); HOCHHUTH (1849): 151 (characters); (1862): 46 (distribution); REDTENBACHER (1849): 710, (1857): 203, (1874): 200 (characters); KIESENWETTER (1851): 419 (distribution); HARDY (1851): 33 (biology); KÜSTER (1853): 62 (characters); FAIRMAIRE & LABOULBÈNE (1856): 539 (characters); KRAATZ (1857): 503 (characters); (1858): 58 (distribution); PEYRON (1858): 428 (distribution); FAUVEL (1865): 293 (biology); (1874): 289 (characters); SEIDLITZ (1875): 267 (characters); MULSANT & REY (1876): 686 (characters); SAHLBERG (1876): 24 (distribution); FOWLER (1888): 237 (characters); GANGLBAUER (1895): 403 (characters); POPPIUS (1905): 9 (distribution); PORTA (1907): 128 (characters); REITTER (1909): 111 (characters); JOHANSEN (1914): 363 (characters); EICHELBAUM (1914): 339, (1915): 91 (morphology); FIORI (1915): 16 (distribution); MUNSTER (1923): 195 (distribution); GRIDELLI (1924): 79 (characters); PORTEVIN (1929): 341 (characters); WÜSTHOFF (1938): fig. 21 (mor-

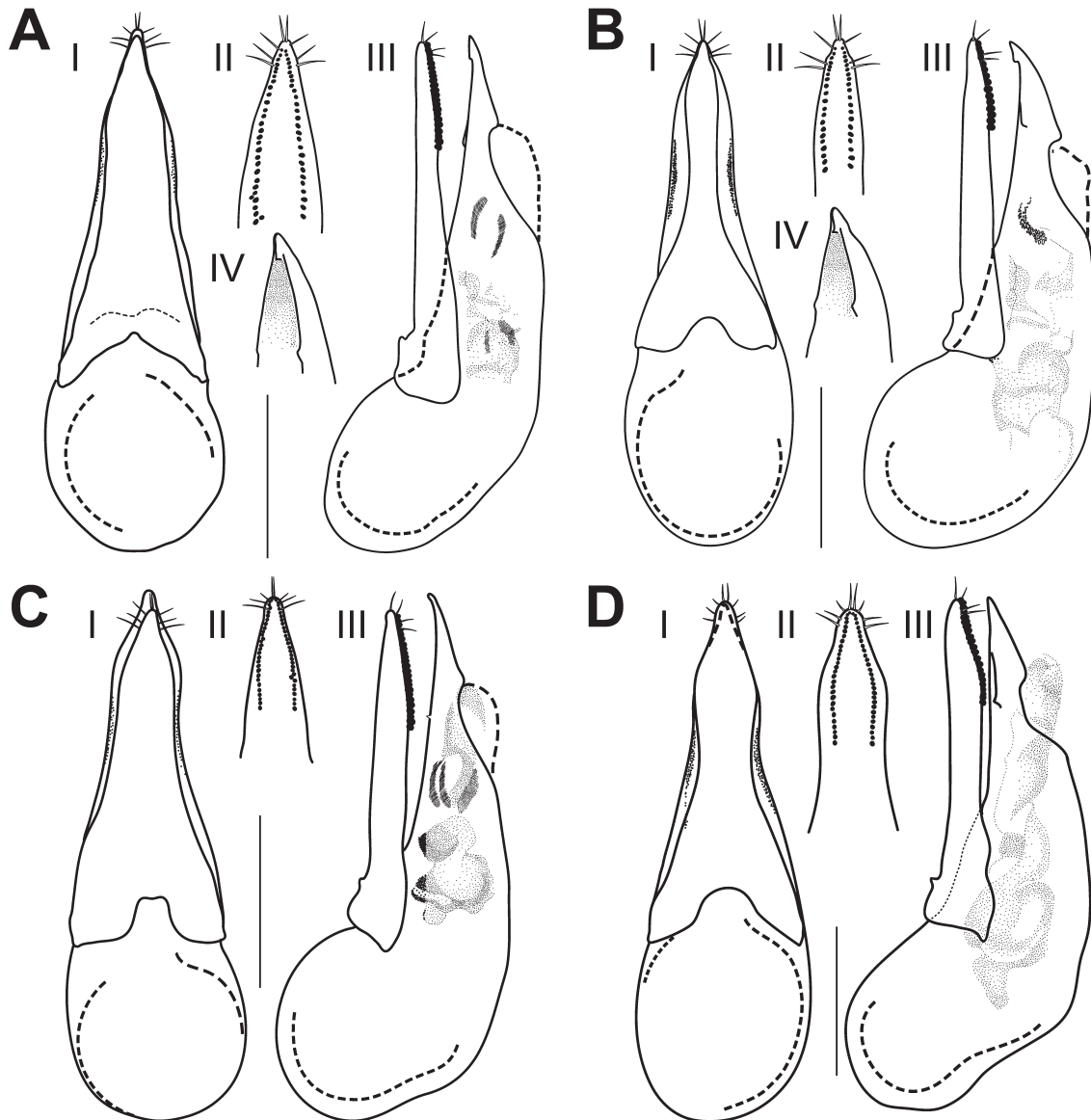


Fig. 11. Aedeagus of *Quedius* s. str. A – *Q. afrofuliginosus* Gusarov, 1991; B – *Q. levicollis* Brullé, 1832; C – *Q. curtipennis* Bernhauer, 1908; D – *Q. fuliginosus* (Gravenhorst, 1802). I – parameral view of whole aedeagus; II – apices of paramere in antiparameral view with peg setae; III – lateral view of whole aedeagus; IV – apices of median lobe at an angle between parameral and lateral view.

phology); PAULIAN (1941): 263 (larval characters); HINTON (1945): 70 (characters); FAGEL (1948): 196 (characters); JEANNEL & JARRIGE (1949): 378 (biology); HANSEN (1952): 140 (characters); SMETANA (1958): 361 (characters and biology); (1962): 133 (characters and distribution); (1964): 79 (distribution); (1976): 22 (distribution); (1978c): 85 (distribution); (1993): 50 (distribution); PALM (1963): 139 (characters); LOHSE (1964): 211 (characters); HORION (1965): 272 (distribution); POTOTSKAIA (1967): 84, 87 (larval characters); KASULE (1968): 53 (biology); (1970): 63 (larval characters); KORGE (1968): 52 (characters); SZUJECKI (1968): 735 (distribution); FRANK (1969): 266 (biology); (1982): 46 (list of parasites); BORDONI (1974): 12, (1976a): 89 (characters); (1976b): 238 (distribution); OSELLA & ZANETTI (1975): 120 (biology); POPE (1977): 31 (distribution); COIFFAIT (1978): 190 (distribution); TOPP (1979): 19 (development); BURAKOWSKI et al. (1980): 134 (distribution); TÓTH (1984): 117 (characters); NOWOSAD (1990): 143 (biology); ALLEN (1990): 4 (biology); WHITEHEAD (1991): 6 (biology); GUSAROV (1991): 9 (identity); (1993): 72 (synonymic notes, lectotype designation); WELCH (1993): 229 (morphology); HODGE & JONES (1995): 42 (characters); CICERONI & ZANETTI (1995): 32 (distribution); STANIEC (1996): 117 (pupal characters); (2010): 22 (distribution); OWEN (1997): 149 (biology); STANIEC (1999): 52 (characters of pupa); DERUNKOV (2005): 279 (distribution); UHLIG

et al. (2006): 54 (distribution); TRONQUET (2006): 102 (distribution); MAJKA & SMETANA (2007): 428 (distribution); MAZUR et al. (2007): 29 (distribution); STAN (2009): 242 (distribution); SEMENOV et al. (2015): 127 (distribution); SEMIONENKOV et al. (2015): 331 (distribution); SALNITSKA & SOLODOVNIKOV (2018a): 125, (2019): 48 (distribution); PUCHKOV et al. (2020): 43 (distribution).

Type material examined. *Quedius fuliginosus*: LECTOTYPE ♂ (ZMHB), labelled: “coll. Hellwig / Paratypus fuliginosus Grav.”.

Quedius granulipennis: LECTOTYPE ♂ (ZMMU), labelled: “Austria / *Quedius granulipennis* Motsch. Austria”.

Quedius latus: NEOTYPE ♂ (ZMHB), designated here, labelled: “ARMENIA (AR-16-19) 35 km NW Sisian, 39°40'59"N 45°46'50"E, 2070 m, stream valley, litter beneath bushes near stream sifted 3.VII.2016, leg. M.Schülke / *Quedius (Quedius) fuliginosus* (Gravenhorst) det. M. Schülke 2019 / Museum für Naturkunde Berlin Sammlung M. Schülke / Neotype *Quedius latus* Hochhuth, 1851 A.K. Hansen & A. Solodovnikov des. 2021”.

Quedius molochinicolor: SYNTYPE ♀ (SNMC), labelled: “Slovensko Harmanec Roubal 26.IX.1930 / f. molochinicolor mi [my] type / [red label] / fuliginosus f. molochinicolor cotypus”.

Additional material examined. ARMENIA: N Yerevan, NW Hrazdan, 40.6350 44.4602, grassy W slope with scattered *Salix*, litter and roots of grass sifted, 2500m, 26.VI.2016, leg. M. Schülke (1 ♀ cSch); same locality, 40.6944, 44.4878, stream valley, mixed deciduous forest, litter and grass roots sifted, 2110m, 28.VI.2016, leg. M. Schülke (1 ♀ cSch). **AUSTRIA:** Arbesbach; [48.49, 14.95], 1.-13.VII.1951, leg. Schubert (1 ♀ NMW); Brunnlust, Moosbrunn, Schwechat, [48.01, 16.45], 12.VI.1997, leg. Schillhammer (1 ♂ NMW); Faak, Kärnten, [46.56, 13.91], 5.VIII.1968, leg. Wewalka (1 ♀ NMW); Immerkrams, [46.96, 13.72], subalpine, 1400 - 2000 m, VI.1954, leg. Lindroth (1 ♀ MZLU); Plesch-Kogel n. Rein, [47.13, 15.28], 590m, sifting forest litter, 20.VI.1995, leg. Zerche & Behne (1 ♂ SDEI); Rekawinkel, [48.17, 16.02], leg. Briet (1 ♂ NMW). **BULGARIA:** Sofia, Tschernia [Cherni Vrah], [42.56, 23.27], 600m, 22.VI.1988, leg. Behne (1 ♂ SDEI); Sredna Gora, S Koprivshtiza, 42.8777, 25.0544, moss under *Picea*, 1000m, 29.VI.1997, leg. Zerche & Behne (1 ♀ SDEI); Stara Planina, 5km S Ribaritz, 42.75, 24.38, 750m, 7.VI.1997, Beech forest, sifting, leg. Zerche & Behne (1 ♂ SDEI); SW-Pirin, Kurort Popina Laka, 16 km NO Sandanski, [41.56, 23.27], ca. 1350m, *Pinus* and *Picea*, under snow remains, sifted, 8.IV.2005 leg. Zerche & Behne (1 ♂ SDEI); W Rhodopen, S Velingrad, Tschernowroh, [41.68, 24.05], 1600m 10.VI.1987, leg. Zerche & Behne (1 ♀ SDEI). **CZECH REPUBLIC:** Podyjí Nat. Park, forest at river Dyje valley ca. 2.5 km NW of Havraniky, 48.8300, 15.9804, h240m, sifted flood debris, 8.VI.2016, leg. A. Solodovnikov, J. Jenkins Shaw, A. Hansen (1 ♀ NHMD). **DENMARK:** Amager, Kalvebod Fælled, Store Høj Søen, 55.6159, 12.5606, sifting leaf litter, debris near lake, 17.III.2019, leg. A. K. Hansen (1 ♂ 1 ♀ NHMD); Lisjerg Forest, 8 km N of Aarhus, 56.2335, 10.1688, h85m, edges of forest lakes, hand collected in leaf litter and moss, 17.IV.2019, leg. A. K. Hansen (4 ♂♂ 4 ♀♀ NHMD); Nors Sø, S of Nors Sø, 57.0197, 8.6197, pitfall trap, dry pine forest, 16-18.VI.2014, leg. Solodovnikov, Hansen, Kræmer, & Justesen (1 ♂ NHMD). **GEORGIA:** N of Sviri, [41.73, 42.99], pitfall traps, 14.IV.-11.VI.2018, leg. D. Formynikh (1 ♂ cSch); Tusheti, n. Omalo, Abanos Pass, [42.27, 45.51], river valley, 1700m, 14.-17.VII.2016, leg. Heinz (1 ♂ NMEG). **GERMANY:** Bayern, Eschenlohe, [47.58, 11.18], 3.VIII.1937, leg. Ihssen (1 ♂ 1 ♀ SDEI); Berlin-Blankenfelde, [52.62, 13.39], 8.V.1994, leg. D. Wrase (1 ♂ SDEI); Biesenthal, [52.76, 13.61], 500m, field sandish-clayish ruderal, 1.IV.2002, leg. D. Wrase (1 ♀ SDEI); Brandenburg Kiesfläche 1km S Oderberg, [52.84, 14.04], 13.X.1990, leg. F. Hieke (1 ♂ SDEI); Brandenburg, Oranienburg, Briesetal, [52.71, 13.31], 12.IV.1992, leg. J. Ziegler (1 ♂ SDEI); Dars, Zingst, Freesenbruch, [54.43, 12.68], 20.VII.1987, leg. D. Wrase (1 ♀ SDEI); Erzgebirge, Prinzgehöhle, [50.63, 12.67], 29.IX.1921, leg. Uhmman (1 ♀ SDEI); Erzgebirge, W Teil, SW Kammweg & Morgenröthe, [50.43, 12.51], 4.V.1990 leg. O. Sorge (1 ♂ SDEI); Finkenkrug n. Berlin, [52.56, 13.03], 12.IV.1898, leg. Dahl (1 ♂ SDEI); Kehlheim Dürnbacher Forst, [48.74, 11.75], (1 ♀ SDEI); Liepnitzsee, n. Wandlitz, [52.74, 13.51], 01.X.1989, leg. M. Uhlig (1 ♂ SDEI); Marburg i Hess, [50.81, 8.77], 16.IV.1904, leg. Strand (1 ♂ 1 ♀ SDEI); n. Märkische Buchholz, Königs Wusterhausen, [52.11, 13.76], 12.VI.1980, leg. H. Wendt (1 ♀ SDEI); Martinfeld, Krs. Heiligenstadt, [51.28, 10.18], 21.-29.VI.1990, leg. M. Uhlig (1 ♂ SDEI); München-Grünwald, [48.04, 11.53], 3.VII.1931, leg. Ihssen (1 ♀ SDEI); Nauen, [52.61, 12.87], 19.III.1910, leg. M. Ude (1 ♂ SDEI); Sächsischen Schweiz, Rathen, [50.95, 14.08], 1.V.1977, leg. K. H. Mohr (1 ♀ SDEI); Schwäbisch Gmünd, Röben, [48.79, 9.81], 4.V.1953 (1 ♂ SDEI); Seilershof, Gransee, [53.06, 13.18], 22.V.1988, leg. M. Schülke (1 ♀ SDEI); Suekow, [53.07, 11.79], XI.1974, leg. M. Moritz (3 ♂♂ SDEI); Wandlitz, Liepnitzsee, [52.74, 13.51], 6.I.1981, leg. M. Uhlig (1 ♂ 2 ♀♀ SDEI); Wildeschütz n. Deuben Silbersee Schilfgürtel, [51.12, 12.07], 11.X.1987, leg. M. Uhlig (1 ♀ SDEI). **ITALY:** Alpie Orobie, Bergamo Castione & Passo della Presolana, 45.9202, 10.1001, 1170m, 18.-21.VI.2006, leg. P. Schnitter (1 ♂ NMEG); Basilicata, Pognola Ris. L. Pignola, [40.58, 15.74], 700 m, 23.XII.1996, leg. F. Angelini (1 cBor); Trentino, Lago di Tenno, N Riva, [45.93, 10.81], 560m, 2.VII.1994, leg. L. Zerche (1 ♀ SDEI). **KAZAKHSTAN:** Altai, Bukhtarma riv., Chingistai, [49.19, 85.88], 30.VIII.2010, leg. V. A. Kastcheev (1 ♂ ZIN); Akshatau Mt., NW Ayaguz, Semipalat, [48.25, 79.64], forest leaf litter, 17.VII.1962, leg. L. V. Arnoldi (1 ♂ ZIN); Ivanovsky Mt. Ridge, 32 km S Leninogorsk, [50.04, 83.51], 1300 m, 14.VIII.1986, leg. I. I. Kabak (1 ♂ ZIN). **RUSSIA: ALTAI KRAI:** Talmenskij Distr., E of vill. Litvinovka 53.6918, 83.7309, 200m, mixed forest, sifted leaf litter, 24.VI.2019, leg. A. Solodovnikov, A. K. Hansen & A. Tokareva (1 NHMD); Chemalskij Distr., SE of vill. Edigan 51.0546, 86.3791, 1030m, larch-fur forest, sifted

leaf litter, 27.VI.2019, leg. A. Solodovnikov & A. K. Hansen (1 NHMD); Chemalskij Distr., Verkhnij Berulu river, 51.3035, 86.1221, 790m, pine-birch forest, sifted leaf litter, 28.VI.2019, leg. A. Solodovnikov, A. K. Hansen & M. J. Justesen (1 NHMD). **BASHKOROSTAN REP.:** Buzdyakskij Distr., nr vill. Arslanovo 54.6485, 54.3789, 229m, at creek bank, 11.VI.2019, leg. A. Solodovnikov & A. Tokareva (1 NHMD); Mechetlinskij Distr., Oka river nr vill. Bolshaya Oka, 56.1085, 58.1977, 224m, debris and ground at river bank, 12.VI.2019, leg. A. Solodovnikov & A. Tokareva (1 NHMD). **IRKUTSK OBLAST:** Baikal, Chamar-Daban, Solsan Valley, [51.36, 104.15], 17.-21.VI.1978, leg. Schilencov (1 ♂ cSch); Baikal, Baikalsk, Solsan River near mouth, [51.47, 104.37], 20.VII.1989, leg. Hieke (1 ♂ 1 ♀ SDEI); Khamar-Daban Mts., valley of Snezhnaya River, [51.06, 103.99], 5.-8.VI.2007, leg. A. Shavrin (3 ♂♂ 6 ♀♀ cSha); Podvoloshino, Valley of Nizhnaya Tungka River, [58.25, 108.42], 4.-9.VIII.2008, leg. Shavrin & Enustschenko 18 km N Ust-Kut, Valley of Lena River, [56.95, 106.14], 26.-28.VII.2008, leg. Shavrin & Enustschenko (1 ♀ ZIN) Valley of Bodchakta River, [57.11, 106.61], 10.-11.VIII.2008, leg. Shavrin & Enustschenko (1 ♂ ZIN). **KALUGA PROV.:** 4-5 km SE from Chernaya Grayz, [54.96, 36.86], V.1988, leg. I. Ushakov (1 ♂ cRyv); Kozelsk Reg., Berezhich glass factory, Novaya Derevnaya village, NR "Ugra", [56.27, 40.25], broad leaved forest, leaf litter near stream (stagnant channel), 13.VII.2017, leg. M. Salnitska (1 ♀ ZIN). **KEMEROVSKAJA OBLAST:** Tashtagolsky Distr., Shorsky Nat. Park, 5 km SSE Tajmet [Verkhnij Tajmet] village, [52.48, 88.27], cedar forest, 8-18.VI. 2012, leg. L. A. Trilikauskas (1 ♂ 1 ♀ ZIN). **KRASNOYARSKIJ KRAI:** nr. Divnogorsk town, left tributary of Enissey river, [55.95, 92.38] cedar-birch forest, in leaf litter, 1.VI.1988, leg. A. B. Ryvkin (2 ♂♂ ZIN); Enissey distr., environs of vill. Ust-Pit, [58.98, 91.76], 02-10.VII.1995, leg. A. Rybalov (2 ♂♂ 1 ♀ ZIN); Nature Preserve 'Stolby' [Kranoyarskie Stolby], river Mana near Berly hut, [54.98, 94.00], stream edge, in moss and litter, 20.VI.1990, leg. A. B. Ryvkin (1 ♂ ZIN); Niznaya Lebedyanka river, [61.96, 89.45], 22.VI.1992, leg. V. S. (2 ♂♂ cRyv). **LENINGRAD OBLAST:** Kirovsky Distr., Turishkovo vill., Mga River, 59.684306, 31.2202, flood plain, meadow in forest, leaf litter, 02.VI.2018, leg. M. Salnitska, K. Fadeev (1 ♂ ZIN); Leningrad [Sankt Petersburg], in litter, 29.VII.1976, leg. Schilow (3 ♂♂ SDEI). **MOSCOW OBLAST:** Odintsovsky Distr., Zvenigorod Biological Station of MSU, [55.70, 36.72], soil sample, Betula forest, 7.VIII.1981, leg. K. G. Mikhailov (1 ♂ cRyv). **NOVGOROD OBLAST:** Staraja Russa, [57.99, 31.35], leg. Kessler (1 ♂ NMW). **PERM KRAI:** Perm town, ravine meadow on the right bank of Kama river, Motovilikha, [58.04, 56.30], 1989, leg. V. O. Kozminykh (1 ♂ ZIN). **REP. OF ADYGEA:** Caucasus, Adygeja, Guzeripl, Belaja River, [43.99, 40.13], 2000m, 23.VI.1999, leg. Putschkov (1 ♀ cSch). **REP. OF N. OSSETIA-ALANIA:** N Ossetia Nat. Res., mt. Kariuchoch, Kora pass. (Alansky), 42.8301, 44.2123, ~2200m, leaf litter Betula sp., 24.V.2017, leg. M. Salnitska (1 ♂ ZIN). **SVERDLOVSK OBLAST:** Visimskij Nature Res., 57.3733, 59.7734, 570m, spruce dominated forest, pitfalls, 18.VI.2019, leg. A. Solodovnikov, A. K. Hansen & A. Tokareva (1 NHMD); W of vill. Elan', 57.6406, 63.6220, 100m, mixed forest, sifted leaf litter, 20.VI.2019, leg. A. Solodovnikov, A. K. Hansen & A. Tokareva (1 NHMD). **TYUMEN OBLAST:** Uvatsky Distr., 8-14 km S from vill. Gornoslinskino, near Tobolsk station of IEE RAS, [58.68, 68.79], 11.VI.2004, leg. A. B. Ryvkin (2 ♂♂ 1 ♀ cRyv); Tyumenskij Distr., Tura river nr vill. Konyashina, 57.2925, 65.0281, 80m, flood forest, sifted leaf litter, 21.VI.2019, leg. A. Solodovnikov, A. K. Hansen & A. Tokareva (1 NHMD); nr Zavodoukovsk, 56.5329, 66.5689, 116m, pine-birch grove, sifted leaf litter, 21.VI.2019, leg. A. Solodovnikov, A. K. Hansen & A. Tokareva (1 NHMD). **SLOVAKIA:** Belá River n. Vavrisovo n. Lipt. Hrádek, [49.06, 19.77], 18.VII.1980, leg. Hieke (12 ♂♂ 1 ♀ SDEI); Gombasek n. Rožnava, [48.57, 20.45], 6.VIII.1981, leg. Hieke (1 ♀ SDEI); Harmanec, [48.79, 19.07], 26.IX.1930, leg. Roubal (1 ♀ SNMC); Pieninsky National Park, [49.38, 20.51], 18.VII.1993, leg. Zerche (1 ♂ SDEI); Rudohorie, Hnilec-Tal n. Švedlár, [48.83, 20.51], 8.VII.1981 leg. Hieke (1 ♀ SDEI). **SLOVENIA:** Triglav Nat. Park, river Soča valley, ca. 3 km SW Trenta; Občina Bovec, 46.3667, 13.7255, sifting flood debris and under stones, 03.VI.2016, leg. A. Solodovnikov, A. Hansen. & M. Salnitska (1 NHMD). **SWEDEN:** Månsatorp, 5km SW of Vittsjö, Skåne; 56.3105, 13.5955, hand collected in/under moss, 21.I.2018, leg. A. K. Hansen (1 ♂ 2 ♀♀ NHMD); Ödeshög V, Ekopark Ömberg, Storpissan nature reserve, 58.3344, 14.6508 sifting leaf litter on stream edge; 30.V.2017, leg. D. Żyła, K. Koszela, A. Solodovnikov (1 ♂ NHMD); Vegesjö, Skåne, 56.3031, 13.6473, banks of bog in wet sphagnum, 100 m, 22.IV.2018, leg. A. K.

Hansen (1 ♀ NHMD). **TURKEY:** Harçbeli Pass, Ordu, [40.59, 37.64], 1900 m, 28.V.1989, leg. Schönmann & Schillhammer (1 ♀ NMW); Süme-la, Altındere, [40.68, 39.65], 10.-11.VI.1969, leg. P. Brignoli (1 ♀ cBor). **UNITED KINGDOM:** ENGLAND: Norwich, Norfolk, UEA Campus, [52.62, 1.23], 3.III.2013, leg. C. Billet (1 ♂ cJen). **UKRAINE:** Kanev [Kaniv] near Kiev [49.75, 31.46], 28.I.1988, leg. Zerche (2 ♀♀ SDEI); Ivano-Frankovo, ca. 40 km WNW of Lvov, Rostochye, State Reserve, [49.94, 23.65] *Quercus, Pinus* etc. forest, 16-20.IX.1999, leg. S. Golovatch (1 ♂ cRyv); N Yablunytzia vill., S Gorgany Mnts., valley Prut riv., [48.34, 24.45], 800m, pitfalls, 22-24.V.2018, leg. Panin R. (1 ♂ cGon). **UZBEKIS-TAN:** Tashkent, [41.29, 69.25], near railway station, plant residues, 24.V.1986, leg. S. A. Kurbatov (1 ♂ 1 ♀ ZIN).

Redescription. Measurements ♂♂ (n = 5): HW = 1.78–1.89 (1.81); HL = 1.40–1.51 (1.46); HL/HW 0.79–0.83 (0.80); PW = 2.22–2.42 (2.31); PL = 2.04–2.20 (2.13); PL/PW 0.90–0.98 (0.92); EW = 2.44–2.51 (2.48); EL = 2.29–2.38 (2.32); EL/EW 0.91–0.96 (0.93); EL/PL 1.05–1.14 (1.09); PW/HW 1.54–1.60 (1.58); forebody length 5.78–6.09 (5.91). ♀♀ (n = 5): HW = 1.80–1.96 (1.84); HL = 1.42–1.51 (1.46); HL/HW 0.77–0.81 (0.80); PW = 2.22–2.42 (2.32); PL = 2.09–2.13 (2.10); PL/PW 0.88–0.94 (0.91); EW = 2.40–2.60 (2.50); EL = 2.29–2.44 (2.34); EL/EW 0.91–0.97 (0.94); EL/PL 1.08–1.15 (1.11); PW/HW 1.54–1.66 (1.59); forebody length 5.82–6.09 (5.90).

Large species; body black (Fig. 7C).

Head black, clearly transverse, with eyes very large (EyL/TL = 3.00–3.90 (3.54)) and clearly protruding, microsculpture of transverse waves, four punctures between anterior frontal punctures on frons (Fig. 6C); antennae and palpi darkened, except the joints, which are slightly paler, antenna with all antennomeres elongate. Thorax: pronotum black, slightly wider than long, wider than head, microsculpture of transverse waves, three punctures in dorsal row and two in sublateral row with the posteriormost puncture not reaching level of second puncture of dorsal row; scutellum smooth and glabrous, elytra black, uniformly pubescent, slightly wider than long, slightly longer than pronotum; legs dark brown to black with tarsi slightly paler.

Abdomen black, tergites uniformly punctured, clearly iridescent.

Male. Aedeagus (Fig. 11D): paramere broadly lanceolate, with clear medial attenuation, sensory peg setae forming two subapical, longitudinal rows along paramere edge apically but slightly turning inwards at half their length. Median lobe with two small but distinct teeth in front of basal part of parameral peg setae. Internal sac without clear sclerites.

Differential diagnosis. Even though *Quedius fuliginosus* differs from all other members of the *fuliginosus*-group by having the basal antennomeres at least slightly darkened, this is not always obvious in teneral or old museum specimens as coloration is altered. It is easily distinguished from *Q. levicollis* by the glabrous scutellum. It can be safely distinguished from *Q. curtipennis* by the aedeagi. In *Q. fuliginosus*, contrary to *Q. curtipennis*, the paramere has clear medial attenuation, a median lobe with the apical part being robustly pyramid-shaped and not laterally flattened, and an internal sac with no clear sclerotization. Subtle external difference between *Q. fuliginosus* and *Q. curtipennis* includes slightly stouter antennae, more tran-

sverse head, larger eyes clearly protruding thus making the head shape more quadrate, as well as slightly longer elytra in *Q. fuliginosus*. Also, *Q. fuliginosus* is very similar to *Q. afrofuliginosus*, but is easily recognized from the latter by having no additional punctures between anterior and posterior frontal punctures. It is also unclear if the two species have a distributional overlap.

Synonymic notes and neotype designation. *Quedius fuliginosus* was described from environs of Braunschweig, North Germany (GRAVENHORST 1802). Two syntypes from the collection of Johann Christian Ludwig Hellwig (1743–1831) were revised by GUSAROV (1993), who designated a lectotype to represent our current concept of *Q. fuliginosus*, while the paralectotype was identified as *Q. curtipennis*. GUSAROV (1993) also studied the type of *Quedius granulipennis*; he found it to be a junior subjective synonym of *Q. fuliginosus*.

Quedius latus was described from “Alagez-Gebirge” (HOCHHUTH 1851), the Aragatz mountain area in Armenia and has never been recorded since the original description. Based on the rather extensive faunistic knowledge of the Caucasus region, *Q. latus* could either be conspecific to *Q. fuliginosus* or *Q. curtipennis*, both common in the area (ASSING & SCHÜLKE 2019) and both fitting the original description of *Q. latus*. Since no type or any other authentic material of *Q. latus* was found in Hochhuth’s collection in Kyiv, Ukraine (S. Glotov, pers. comm.), apparently it is lost. To secure current and future stability of the name *Quedius latus* Hochhuth, 1851, in accordance with the ICZN, Article 75, we designate its neotype. For this, a male specimen of *Q. fuliginosus* collected in the vicinity of the original type locality (for details see Type Material section above) has been selected. The neotype fits the original description of *Q. latus* and thus allows us to consider the so far dubious name *Quedius latus* Hochhuth, 1851 syn. nov. as a junior subjective synonym of *Quedius fuliginosus* Gravenhorst, 1802.

The specimen we studied from the syntype series of *Quedius molochinicolor* Roubal, 1931 represents *Quedius fuliginosus* with slightly brownish elytra, thus confirming the currently accepted synonymy.

BRITTEN (1944) recognized that there were two closely related species of *Quedius* s.str. in Britain. Based on his descriptions and illustration, it is clear that *Q. fuliginosus* sensu Britten is *Q. curtipennis* while the new species he described, *Q. subfuliginosus*, is identical to *Q. fuliginosus*. This is in agreement with the currently accepted synonymy.

We were not able to check the types of *Quedius impunctifrons* Delahon, 1915 and *Quedius jelineki* Krása, 1904 from Germany and Czech Republic, respectively. Both names are currently in synonymy with *Q. fuliginosus*. Since the descriptions state that they lack the interocular punctures on frons characteristic of the *Q. fuliginosus*-group, they either represent variability in chaetotaxy – or more likely, they are dark variants of *Q. molochinus*, the latter possibility calling for a revised synonymy.

SAWADA (1965) described *Q. viduus* as being very similar to *Q. fuliginosus*, but different in the broader head, larger and more convex eyes, pronotum with lateral sides

less convergent anteriorly, broader elytra, and rougher punctation of abdomen. This original description based on the single female specimen is the only record of *Quedius* s. str. from Japan. In spite of the thorough searches in the collections of National Museum of Nature and Science, Tokyo (Shuhei Nomura), Osaka Museum of Natural History, Osaka (Shigehiko Shiyake), Nakane Collection at Hokkaido University (Masahiro Ohara), and Sawada personal collection (Yasuhiko Hayashi), all performed by respective curators upon our request, the holotype of *Q. viduus* could not be located. Based on the original description and lack of any other species of *Quedius* s. str. in Japan, we suspect this is either a mislabeled specimen not from Japan, or an introduced specimen of *Q. fuliginosus*, which was not established or recollected in Japan. Thus, *Q. viduus* Sawada, 1965 syn. nov. is considered as a junior subjective synonym of *Q. fuliginosus* Gravenhorst, 1802.

Bionomics. *Quedius fuliginosus* is widespread and eurytopic species found in a variety of forests (both deciduous and coniferous) and in the open habitats too. Usually, it occurs in moss and leaf litter or in various other kinds of ground debris (SOLODOVNIKOV 2012). We have commonly collected this species in moss near the edge of a lake in Denmark (Fig. 2A), in various forests often with dense fern or grassy undergrowth, across larger parts of Western Siberia (Fig. 2E), in flood debris of a forested mountain stream in Triglav, Slovenia and along river forested on either side in the southern Czech Republic. It seems to prefer mossy patches and moist litter, and is thus to some degree often associated with water bodies, although it is not found at the very edge of these. It has also been reported from mole (*Talpa europaea*) nests (NOWOSAD 1990), from bracket fungi (*Polyporus squamosus*) (SEMENOV et al. 2015), and from ant nests (GORESLAVETS 2010, 2016), all of which are presumably accidental occurrences, as there is no indication of the species preferring these habitats.

Larvae were described by PAULIAN (1941), POTOTSKAYA (1967) and KASULE (1970). Pupae of the species are described in STANIEC (1999); SZUJECKI (1966) described the egg. Adult females from Wytham, UK were observed containing eggs between May and June (FRANK 1969).

Distribution. *Quedius fuliginosus* can be found across a large part of the Palearctic region (Fig. 18). In Europe it is common in the North-East, but becomes rarer south-westwards and is probably absent from the southern parts of the Iberian Peninsula and Italy. It is found across most of Siberia from the Urals to at least the Baikal region. In the southern part of the range the species is confined to the forested zone in mountains. Here it is found along the Pyrenees, the Alps, the North Anatolian mountains, the Caucasus, and Transcaucasia. Eastwards it extends to the western forested regions of the Tian Shan Mountain Range in central Asia. The northern distributional border of the species seems to be determined by the forested boreal zone, as it does not continue into the tundra.

Records of *Q. fuliginosus* from Tunisia and Algeria (FAUVEL 1902) most likely refer to either *Q. levicollis* or *Q. afrofuliginosus*, as we did not come across any specimens of this species from northern Africa or nearby regions.

Moreover, *Q. fuliginosus* is apparently absent in the south Mediterranean coastal areas, which makes its presence in North Africa even more unlikely.

Introduced to eastern North America in an area of Nova Scotia where the first specimens were found in 1996 (MAJKA & SMETANA 2007) (Fig. 12).

Quedius levicollis (Brullé, 1832)

(Figs 1, 2B, 3, 6D, 7D, 11B, 19)

Staphylinus levicollis Brullé, 1832: 131 [Type locality: Morée: plaine de Modon]

Philonthus frontalis Nordmann, 1837: 76 [Type locality: Gallia; Symperopoli]

Quedius balthasari Mañan, 1935: 9 [Type locality: Knossos, Creta]

Staphylinus nigritarsis Ménétré, 1832: 144 [Type locality: Caucase]

References. GRAVENHORST (1802): 34, (1847): 231 (characters); STEPHENS (1832): 215, (1839): 389 (characters); FALDERMANN (1835): 123 (characters); LACORDAIRE (1835): 376 (characters); NORDMANN (1837): 75 (distribution); HOLME (1837): 63 (distribution); WESTWOOD (1838): 167 (larva and pupa); ERICHSON (1840): 537 (characters); KOLENATI (1846): 22 (characters); KIESENWETTER (1848): 34 (characters); HOCHHUTH (1849): 154, (1862): 46 (characters); REDTENBACHER (1849): 709, (1857): 201, (1874): 198 (characters); FAIRMAIRE & LABOULBÈNE (1856): 536 (characters); ROSENHAUER (1856): 71 (distribution); KRAATZ (1857): 502 (characters); FAIRMAIRE & COQUEREL (1860): 154 (distribution); FAUVEL (1865) (ecology); (1874): 289 (characters and distribution); (1878): 128, (1886): 58, (1902): 115 (distribution); MULSANT & REY (1876): 688 (characters); FOWLER (1888): 237 (characters); GANGLBAUER (1895): 403 (characters); SAINTE-CLAIRE DEVILLE (1906): 102 (distribution); PORTA (1907): 129 (characters); REITTER (1909): 111 (characters); JOHANSEN (1914): 363 (characters); MUNSTER (1923): 196 (distribution); GRIDELLI (1924): 80 (characters and distribution); PORTEVIN (1929): 341 (characters); WÜSTHOFF (1938): fig. 22 (characters); TOTTENHAM (1949): 376 (characters); HARDY (1851): 32 (distribution); HANSEN (1952): 142 (characters); SCHEERPELTZ (1956): 1102, (1965a): 407, (1965b): 511 (distribution); (1961): 133 (characters); SMETANA (1958): 362 (characters and ecology); (1962): 134 (characters and distribution); (1963): 39, (1967): 558, (1970): 62, (1993): 50 (distribution); (1978b): 121 (distribution and ecology); PALM (1963): 141 (characters and distribution); LOHSE (1964): 211 (characters); FOCARILE (1964): 61 (distribution); HORION (1965): 273 (distribution); COIFFAIT (1970): 62 (distribution); (1978): 192 (characters and distribution); BORDONI (1976a): 93 (characters); (1982): 140 (ecology); (1984): 342 (distribution); POPE (1977): 31 (characters and distribution); HINTON (1981): 662 (characters of egg); TÓTH (1984): 118 (distribution); FRANZ (1987): 70 (distribution); GUSAROV (1993): 73 (synonymy); WELCH (1993): 229 (ovary structure); CICERONI & ZANETTI (1995): 33 (distribution); NEWTON (1995): 51 (requested to ICZN to place *Q. levicollis* on the Official List of Specific Names in Zoology); ICZN (1996): 215 (*Q. levicollis* placed on Official List of Specific Names in Zoology); BLAND & SINCLAIR (1997): 204 (biology); MARCHAL & CHARDONNET (2000): 72 (distribution); OWEN (2000): 252 (ecology); ASSING & WUNDERLE (2001): 37 (distribution); UHLIG et al. (2006): 54 (distribution); TRONQUET (2006): 102 (distribution); ANLAŞ (2009): 229 (distribution); STAN (2009): 242 (distribution); VORST et al. (2009): 16 (distribution); MAJZLAN & BOHÁČ (2012): 182 (distribution); BEBERMANS et al. (2016): 135 (distribution); ÖZGEN et al. (2016): 620 (distribution); RUTA et al. (2016): 37 (distribution); SALNITSKA & SOLODOVNIKOV (2019): 49 (distribution).

Type material examined. *Staphylinus nigritarsis*: LECTOTYPE: designated by GUSAROV (1993) (ZIN), labelled: “[golden square] / Caucas. / nigritarsis Menet. Cauc”. PARALECTOTYPE: labelled: “[golden square] / Caucas.” (1 ♂ ZIN).

Additional material examined. ALBANIA: 13km SE Elbasan, Mali i Shpatit, Mt. Bukanikut, 41.0431, 20.2172, brook bank in beech forest, 1500m, 22.V.2010, leg. D.W. Wrase (1 ♂ cSch). BOSNIA AND HERZEGOVINA: Maklen-Pass, [43.85, 17.65], 1902, leg. O. Leonhard (1 SDEI); Prozor, [43.82, 17.61], 1902, leg. O. Leonhard (1 SDEI). BULGARIA: Arkutino, S of Burgas, [42.41, 27.65], 28.V-9.VI.1971, leg. Wallis (1 ♂ SDEI). CROATIA: Capela [Kapel], [44.89, 15.52], leg. Heyden (1

SDEI); Velebit Mountains, [44.52, 15.22], wine traps, V.2005 (1 ♂ cJen). **CYPRUS:** Agios Nikolaos, [34.86, 32.75], 16.IV.1995, leg. H. Schmid (1 ♂ NMW); Troodos Mountain, Stavros tis Psokas, [35.02, 32.63], 800–950m, 12.–18.IV.2010, leg. I. Wolf (1 ♂ cSch). **DENMARK:** Ovestrup Hede, 56.2412, 8.9297, pitfall trap, heathland grazed part, 7–22.VI.2017, leg. E. Kristensen, D. Byriell, & M. Justesen (1 ♂ NHMD). **FRANCE:** Avignon, [43.94, 4.81], 22.V.1949, leg. R. Skovgaard (1 ♂ NHMD); Chigny n. Oise, [49.91, 3.76], 19.X.1918, leg. Salchert (1 ♀ ZMHB); Paris, [48.83, 2.41], 19.V.1949, leg. R. Skovgaard (1 ♂ NHMD). **CORSE:** Bocognano, [42.08, 9.06], 1905, leg. O. Leonhard (1 SDEI); Col de Bavella, [41.79, 9.23], 1240m, East slope, 25.VII.1994 leg. L. Zerche (1 ♂ SDEI); Foret de Valdo-Niello, Evisa, [42.28, 8.91], 1000–1200 m, 27.VII.1967, leg. Langemark-Lomholdt (1 ♂ NHMD). **GERMANY:** Berlin-Marzahn, Hellersdorfer Berg, [52.53, 13.58], 8.VIII.1997, leg. Hieke (1 ♀ ZMHB); Berlin, Prenzlauerberg Hof, [52.53, 13.46], 29.V.1985, leg. I. Uhlig (1 ♂ ZMHB); Grunewald n. Zehlendorf, [52.48, 13.22], leg. Wagner (1 SDEI). **GREECE:** Attica, [38.05, 23.84], 17.IV.1922, leg. W. Liebmann (1 SDEI); Paleokastro, Halkidiki, [40.43, 23.42], 800m, 11.VII.1983, leg. A. Casale (1 ♀ cBor); 2 km W Panagia, Trikala, [39.79, 21.33], 15.VI.1982, leg. R. Danielsson (1 ♂ MZLU); Voria Pindos, Morfi, [40.21, 21.21], dry slope, 26.VI.1997, leg. Winkelmann (1 ♀ cSch); **CORFU:** Pandokratoras, 39.7492, 19.8701, N-slope with scattered pine, deciduous trees, and bushes, litter and roots between rocks sifted, 800 m, 4.VI.2017, leg. Schülke (1 ♂ cSch); Pantokrator, [39.74, 19.87], V.1964, leg. Palm (1 ♀ MZLU). **CRETE:** Georgioupouli, [35.36, 24.26], 24.–25.IV.1995, leg. B. Jaeger (1 ♀ cSch); Ida mts., ca. 6 km S Analipsis, 35.1752, 24.8391, Quercus forest, 1260m, 21.X.2006, leg. M. Schülke (1 ♂ cSch); Mt. Ida, 28km SW Iraklio, [35.23, 24.77], 1600m, 7.IX.1991, leg. N. Esser (1 ♀ NHMD). **KARPATOS:** Karpathos, 35.5097, 27.2189, 40 m, terraced grassy fallow, 01.I.2016, leg. V. Assing (ZMHB). **LESBOS:** SW Agiassos, road to Olympos peak, [39.06, 26.36], 700 m, 10.VI.1996, leg. Jäch (1 ♂ 1 ♀ NMW). **PELOPONNES:** Korinthia, Kyllini, Zoria, [37.94, 22.43], 2000 m, 3.VI.1995, leg. Giachino & Vailati (1 ♂ 3 ♀♀ cBor); Kyllini Mountain, [37.97, 22.39], 2100m, North side, below summit over valley, 9.VI.1996, leg. P. Wunderle (1 ♀ cSch); Sparta, [37.06, 22.43], 3.V.1962, leg. Skovgaard (1 ♂ NHMD); N Taygetos, 6 km NE Thouria, 37.1401, 22.1284, litter and soil under bushes, sifted, 584 m, 20.IV.2015, leg. M. Schülke (1 ♀ cSch). **RHODES:** Prophitis Ilias, 36.2734, 27.9287, pine forest, under stones & sifted from litter & moss, 685m, 17.V.2015, leg. Wrase & Laser (1 ♂ cSch). **IRAN:** Kohgiluyeh-Va-Boyer-Ahmad province, 20 km SW Yasuk, 10 km SE Sepidor, [30.56, 51.51], 5.–6.V.2007, leg. A. Anistshchenko (1 ♀ SDEI). **IRELAND:** Inch Dingle Eire, [52.14, -9.97], IX.2012, leg. J.J. Shaw (1 ♂ cJen); Pembury, Kent 51.1625, 0.3431, 24.VII.2011, leg. J.J. Shaw (2 ♂♂ cJen). **ISRAEL:** Upper Galilee, Har Avivim, W Avivim, 33.0833, 35.4923, open stony grazing land limestone, 768m, 21.IV.2006, leg. D.W. Wrase (1 ♂ cSch); Upper Galilee, Meron Mts. Har Meron, Kamin Rom, 32.9908, 35.4111, open stony grazing land, limestone, 1100m, 28.IV.2006, leg. D.W. Wrase (1 ♂ cSch). **ITALY:** Calabria Aspromonte, [38.21, 15.99], 1905, leg. Pagametti (1 SDEI); Calabria, Roseto Capo Spulico, [39.98, 16.61], 20 m, 6.X.1998 leg. F. Angelini (1 ♀ NHMD); Dicomano, Toscana, [43.89, 11.52], I.1971, leg. Bordoni (1 ♂ cBor); Macerata, [43.29, 13.45], 1.X.1955, leg. D. Caccamicelo (1 ♀ cBor); Marche, Montemonaco, Isola San Biagio, [42.91, 13.31], fields, 900 m, 27.VII.–1.IX.2004, leg. M. Rismondo & R. Fabbri (2 ♂♂ 2 ♀♀ NHMD); same locality, black hornbeam forest, 1.IX.–7.X.2004, leg. M. Rismondo & R. Fabbri (1 ♂ NHMD); Modena, Prignano sulla Secchia, La Quercia, [44.45, 10.73], pitfall traps, 400 m, 5.–18.VII.2006, leg. R. Fabbri (1 ♂ NHMD); Reggio di Calabria, river Sant'Agata, [38.09, 15.66], 11.III.1959 (1 ♂ cBor); Settecaminì, Rome, Lazio, [41.93, 12.62], 23.Xi.1969 (1 ♂ 1 ♀ cBor); Sovara, Anghiari, [43.53, 12.03], 19.V.1930, leg. A. Andreini (1 ♀ cBor). **SARDINIA:** Aritzo Mountain, Gennargentu, [40.01, 9.29], leg. C. Kruger (2 SDEI); Ottana, [40.23, 9.04], 15.X.1974 (3 ♂♂ 1 ♀ cBor); Oristano, [39.89, 8.59], 3.V.1975, leg. S. Ripze (2 ♀♀ cBor). **SICILY:** Ficuzza, [37.85, 13.38], 1906, leg. O. Leonhard (1 SDEI); Messina, [38.18, 15.54], leg. Schiödte (4 ♀♀ NHMD). **MOROCCO:** Ain Leuh, [33.28, -5.33], 17.V.1925, leg. M. Escalera (1 ♂ 4 ♀♀ MNCN); Ar Rif, Chefchaouen reg., env. Bad Bessen, 34.9913, -4.8555, 1124 m, 3.VI.2007, leg. P. Hlaváč (1 ♂ cSch); Ar Rif, Chefchaouen region, rd. Bad Berret - Bad Bessen, 1392 m, 35.0169, -4.0035, 3.–6.VI.2007, leg. P. Hlaváč (1 ♀ cSch); Taza, [34.22, -4.00], leg. F. Schubert (1 ♀ NMW). **PORTUGAL:** Penedo da Meditação, Coimbra, [40.224371, -8.40], 24.IV.1961, leg. R.N. F. (1 ♂ NMW). **MADEIRA:** Faja da Nogueira, [32.74, -16.90], laurisilva

with big *Ocoteas*, 750 m, 20.IX.1980, leg. H. Enghoff & O. Martin (2 ♂♂ 3 ♀♀ NHMD); Paul da Serra, [32.73, -17.05], 27.XII.1987, leg. Gillerfors (1 ♂ MZLU). **SPAIN:** Castanos de Calabazas, 1 km S Castanar de Ibor, Extremadura, 39.6235, -5.4128, 860 m, sifted mossy rock scree litter, chestnut and oak forest /w rock screes and small stream, 10.V.2019, leg. A. K. Hansen, J. J. Shaw, & J. Kypke (NHMD); Cavarrubias [Covarrubias], Burgos, [42.05, -3.51], 10.XI.1995, leg. A. Anichtchenko (1 ♂ cSha); Lloret de Mar, [41.69, 2.83], 17.IX.–6.X.1961, leg. Palm (1 ♂ MZLU); Sierra de Ancares, A Degrada vill., [42.81, -6.87], 1100–1250 m, 8.–9.VII.1996, leg. Wrase (2 ♂♂ cSch); Sierra de Guadarrama, Navacerrada, Arroyo de Peca [Peña] Cabrita, [40.77, -3.99], 1800 m, 5.IX.2001, leg. A. Anichtchenko (1 ♂ NHMD); Sierra Nevada, rio Lanjaron, Tello, [36.92, -3.47], 1500 m, 29.–31.III.2010, leg. Shavrin & Anichtchenko (1 ♂ NHMD); Toledo, El Pielago Navamorcuende, [40.15, -4.79], 4.VIII.2005 leg. Lencina & Andujar (1 ZMHB). **SYRIA:** Krak des Chevaliers, [34.75, 36.29], 600 m, 7.V.1982 (1 ♂ 1 ♀ MCZ); MashtalHelu [Mashta Al Hilu], E of Safita, [34.87, 36.26], 30.IV.2008, leg. Skoupý (1 ♂ cSch); Zainie, 45 km NE of Latakia, [35.78, 36.19], 4.V.1982, leg. M. Dvorák (3 ♀♀ MCZ). **SWEDEN:** FARÖ: Farön, [57.94, 19.14] (1 MZLU). **GOTSKA SANDÖN:** Sandön, [58.36, 19.24] (1 MZLU). **ÖLAND:** Stenåsa, [56.51, 16.59] (1 MZLU). **TURKEY:** Amanos [Nur Mountains], [36.74, 36.33], 24.V.1987, leg. Jäch (1 ♀ NMW); Bolu, [40.72, 31.61], leg. F. Schubert (1 ♀ NMW); Çikrikçi, Turgutlu, [38.47, 27.81], 15.II.2006, leg. S. Anlaş (1 ♂ NHMD); Çikrikçi, Turgutlu, [38.47, 27.81], 17.II.2006, leg. S. Anlaş (1 ♂ 3 ♀♀ NHMD); Danin-Danin, Hakkari Prov, [37.44, 42.86], 2200 m, 1.VI.1987, leg. Schönemann & Schillhammer (2 ♂♂ 7 ♀♀ NMW); Izmir, Boz daglari, Boz dag köy env., [38.34, 27.75], 1500–1700 m, 30.V–3.VI.2003, leg. R. Lohaj (1 ♂ 1 ♀ cSch); 50 km N Antalya, [37.33, 30.77], 18.IV.2015 leg. Snizek (1 ♀ NMEG); Sogukoluk, Belen, Hatay, [36.49, 36.14], 24.V.1987, leg. Schönemann & Schillhammer (1 ♀ NMW). **UNITED KINGDOM:** **SCOTLAND:** Bridge of Orchy, [56.51, -4.76], 23.VII.1987, leg. Gillerfors (1 ♂ 1 ♀ MZLU); Hawock [55.42, -2.78], VI.1964, leg. M. Paoletti (1 ♀ NMW).

Redescription. Measurements ♂♂ (n = 6): HW = 1.78–1.87 (1.81); HL = 1.47–1.56 (1.51); HL/HW 0.81–0.85 (0.83); PW = 2.27–2.36 (2.31); PL = 2.22–2.24 (2.23); PL/PW 0.94–0.98 (0.96); EW = 2.60–2.69 (2.63); EL = 2.49–2.60 (2.54); EL/EW 0.95–0.98 (0.96); EL/PL 1.12–1.16 (1.14); PW/HW 1.49–1.58 (1.53); forebody length 6.20–6.33 (6.28). ♀♀ (n = 4): HW = 1.80–1.87 (1.84); HL = 1.49–1.56 (1.52); HL/HW 0.81–0.86 (0.83); PW = 2.38–2.51 (2.44); PL = 2.27–2.36 (2.31); PL/PW 0.94–0.95 (0.95); EW = 2.73–2.89 (2.82); EL = 2.58–2.69 (2.64); EL/EW 0.92–0.97 (0.94); EL/PL 1.09–1.17 (1.14); PW/HW 1.53–1.69 (1.61); forebody length 6.42–6.56 (6.47).

Very large species; body black (Fig. 7D).

Head black, slightly transverse, with eyes large (EyL/TL = 3.64–4.78 (4.22)) following contour of head; microsculpture of transverse waves, 4 to 6 punctures between anterior frontal punctures on frons (Fig. 6D); antennae pale reddish, long, all antennomeres clearly elongate; palpi pale reddish.

Thorax: pronotum black, almost quadrate, as wide as long, clearly wider than head, microsculpture of transverse waves, three punctures in dorsal row and three in sublateral row with the most posterior one reaching the level of third puncture of dorsal row; scutellum punctured and setiferous, elytra black, densely punctured and pubescent, slightly wider than long, slightly longer than pronotum; legs dark brown with inner face of tibia darkened and tarsi paler.

Abdomen black, tergites uniformly punctured, slightly iridescent.

Male. Aedeagus (Fig. 11B): Paramere slender, lanceolate, reaching apex of median lobe, sensory peg setae forming two clear rows; median lobe with protrusion at

apices and two small but distinct teeth near lower level of parameres peg setae; internal sac with two small distal medial sclerites.

Differential diagnosis. *Quedius levicollis* is easily distinguished from other members of the *fuliginosus*-group by the punctured and setiferous scutellum and three punctures in the sublateral row of pronotum with the posteriormost one reaching the level of the third (basalmost) puncture of the dorsal row. It can be additionally distinguished from *Q. fuliginosus* by the pale antennae, and from *Q. curtippennis* by the slender paramere and median lobe with apical protrusion. *Quedius levicollis* is mainly found in drier habitats and rarely co-occurs with any of the other species in the species group.

Synonymic notes. The name *Quedius tristis* (Gravenhorst, 1802) has long been applied to this species. GRAVENHORST (1802) did not describe *Staphylinus tristis* as a new species but attributed it to Fabricius. The Fabrician species is now in *Ocyopus* (*Pseudocyopus*). NEWTON (1995) made an appeal to the International Commission of Zoological Nomenclature requesting that the species takes the name *Quedius levicollis*, as this was the next available name associated with this species. As a result, *Quedius levicollis* (Brullé, 1832) was accepted on the Official List of Specific Names in Zoology (ICZN 1996: 215).

BERNHAEUER & SCHUBERT (1916) placed *Staphylinus nigratarsis* Ménériés, 1832 in synonymy to *Philonthus splendens*. GUSAROV (1993) revised the type series of *S. nigratarsis* and designated a lectotype. He found *S. nigratarsis* to be conspecific with *Q. levicollis* (Brullé, 1832) based on both external characters and the shape of the aedeagus. We confirm Gusarov's identification through examination of photos of the type from ZIN provided by M. Salnitska (see supplementary Fig. S1).

We were not able to examine the types of *Philonthus frontalis* Nordmann, 1837 and *Quedius balthasari* Mařan, 1935, both currently accepted synonyms of *Q. levicollis*.

Based on the original descriptions, both synonymies appear to be correct. *Philonthus frontalis* was described from Italy and Greece and fits the description of *Q. levicollis*, with interorbital punctures and punctate scutellum. *Quedius balthasari* Mařan, 1935, described from central Crete as a species different from *Q. levicollis* in sparser punctation and reddish margins of elytra is likely a color aberration because *Q. levicollis* is also known from Crete.

Bionomics. *Quedius levicollis* is a clearly thermophilous eurytopic species, which prefers sandy soils and is found in both open habitats and dry forests. It occurs in various ground debris and under rocks, e.g., it has been found in forest litter at different elevations (200–1900 m) in Cyprus (ASSING & WUNDERLE 2001), under rocks in Corse (MARCHAL & CHARDONNET 2000), and from sifted wet leaf-litter under oleander trees, at 500–1100 m in Israel (SMETANA 1978b). We have encountered this species under rocks in open oak and chestnut forest in Spain (Fig. 2B), and between the roots of *Erica* in a heathland in Denmark. It has been recorded from caves in Sardinia (BORDONI 1982), although this most likely represents an accidental occurrence.

WELSH (1993) found this species to contain six ovaries with a fasciculata type of structure.

Distribution. *Quedius levicollis* is widely distributed across the Western Palearctic from the Atlantic coast, including British Islands through the Mediterranean, including North Africa, in the west to the Russian Black Sea coast and the Middle East (Fig. 19). In the Middle East the species extends into the Levant region, but not into the Nile delta. The south-easternmost record of *Q. levicollis* is from South Iran. The species is found on all major Mediterranean islands, including Cyprus, Crete, Corse and Sardinia, as well on the island of Madeira in the Atlantic Ocean. It is most common in the southern part of its distribution range gradually becoming rarer towards the north-east where it

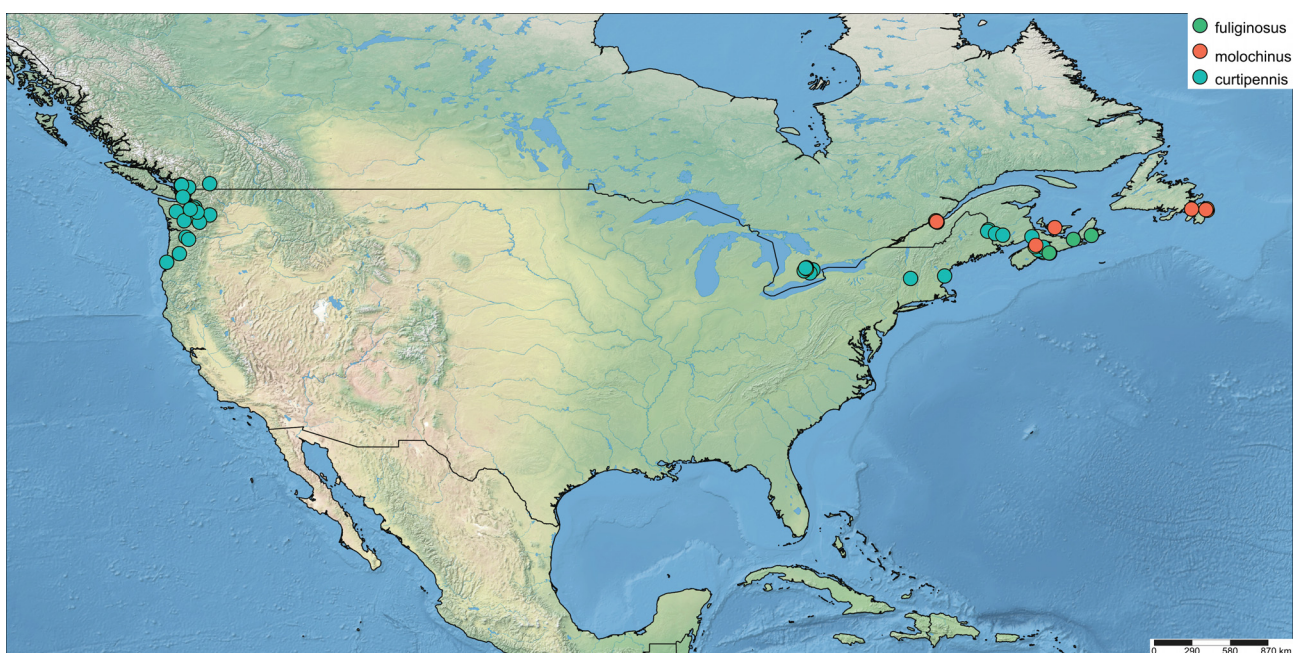


Fig. 12. Distribution of Eurasian species introduced to North America: *Quedius curtippennis* Bernhauer, 1908 (teal), *Q. fuliginosus* (Gravenhorst, 1802) (green), and *Q. molochinus* (Gravenhorst, 1806) (orange).

occurs at xerothermic sites reaching its northernmost limit on the Swedish island of Gotland in the Baltic Sea.

Quedius molochinus-group

Diagnosis. Species of medium size. Coloration variable from completely dark to dark with brown, reddish, or yellowish pale elytra and appendages. Eyes smaller, temples larger, with temporal puncture separated from posterior margin of eye by a distance equal to the diameter of the puncture. Frons without interocular punctures (cf. Fig. 6F). Scutellum punctate and pubescent. Pronotum without puncture(s) in the posterior part of sublateral row. Palearctic; *Q. molochinus* introduced to North America.

Comments. The *Quedius molochinus*-group is composed of four species (*Q. molochinus*, *Q. meridiocarpaticus*, *Q. vicinus*, and *Q. balticus*) that usually have red elytra, although some variants have them darkened. All of these are distributed within the Palearctic Region – although *Q. molochinus* has been introduced to the Nearctic (SMETANA 1981). Among others of the subgenus, these species are characterized by usually having reddish-brown to orange elytra, frons without interocular punctures, scutellum punctate and pubescent, and sublateral rows on pronotum without punctures on the posterior half (Fig. 8). The species are externally very similar and have been confused for a long time, rendering their real distributions unknown. They have also been confused with the red elytral species of the *Q. pallipes*-group, from which they are distinguished by sublateral rows on pronotum without punctures in posterior half. Thorough investigation of representative material here demonstrates that *Q. molochinus*, *Q. meridiocarpaticus* and *Q. vicinus* are almost entirely allopatric (Fig. 20). *Quedius molochinus* is a more northern species, distributed in Europe from the UK and European Russia to the Alps and the Czech Republic, in Asia it is widespread from the Urals to Transbaikalia. In southern Europe it is replaced by *Q. meridiocarpaticus*, which is found in the Italian and Balkan peninsulas and continuing eastwards through Hungary to the Black Sea coast of Ukraine and Russia. *Quedius vicinus* is confined to Eastern Transcaucasia along the Caspian Sea, southeastern Anatolia, and the northern Middle East across to central Asia. The only overlap is in Anatolia where both *Q. meridiocarpaticus* and *Q. vicinus* can co-occur. In this area the species can be most easily distinguished by differences in male genitalia (Fig. 13). Another minor difference includes the antennal coloration, where the middle antennomeres (from fourth to sixth) are slightly lighter in *Q. vicinus* compared to *Q. meridiocarpaticus* (Fig. 8). *Quedius meridiocarpaticus* in turn has slightly lighter middle antennomeres as compared to *Q. molochinus* (Fig. 8). All three species are found in similar habitats, mainly in various types of moist litter or under rocks either near creeks and rivers or in forests. *Quedius balticus* is found across a large part of the Palearctic and thus has an overlapping distribution with the other three species in parts of their ranges (Fig. 19). Unlike the three former species, *Q. balticus* is almost exclusively found in bogs and on floodplains, to which it is highly adapted. Also, it is externally easy to recognize based on the darkened

basal three antennomeres, which are pale in the three other species (Fig. 8). If there is any doubt in external characters, these four species in the *Q. molochinus*-group can most easily be identified through differences in male genitalia (see descriptions).

Quedius balticus Korge, 1960

(Figs 1, 4, 8E, 13E, 19)

Quedius balticus Korge, 1960a: 52 [Type locality: Südspitze der Insel Hiddensee bei Rügen]

References. LAST (1952): 148 (characters; cited as *Q. molochinus*, but misidentified according to KORGE 1960a); (1963): 43 (characters); KORGE (1960a): 67 (characters and notes); (1963): 87 (biology); COIFFAIT (1961): 50 (characters); (1978): 192 (characters, distribution and biology); SMETANA (1962): 135 (characters); HANSEN (1962): 319 (characters); PALM (1963a): 160, (1963b): 117 (characters); LOHSE (1964): 212 (characters); HORION (1965): 277 (distribution); SZUJECKI (1966): 36 (distribution); POPE (1977): 31 (distribution); TÓTH (1984): 119 (characters); LUCHT (1987): 109 (distribution); GUSAROV (1989): 12 (distribution); JANÁK (1992): 91 (distribution); SMETANA (1993): 50 (distribution); HYMAN (1994): 194 (distribution); HODGE & JONES (1995): 41 (characters); MORAVEC & VONIČKA (2000): 39 (distribution and biology); JELÍNEK (2001): 200 (distribution); KOMOSIŃSKI (2001): 19 (distribution); FÜLÖP (2005): 144 (distribution); UHLIG et al. (2006): 41 (distribution); NASH (2009): 23 (distribution and biology); CUPPEN et al. (2011): 12 (distribution); MONSEVIČIUS (2013): 27 (distribution); MAJZLAN & LITAVSKÝ (2017): 19 (distribution and biology); HOFFMANN et al. (2018): 199 (biology).

Material examined. AUSTRIA: Purbach, Burgenland, [47.90, 16.70], 6.VIII.1985, leg. V. Kovits (1 ♂ NMW). BULGARIA: Sozopol, Black Sea coast, [42.42, 27.68], 16.VI.1972, leg. M. Uhlig (1 ♂ ZMHB). CZECH REPUBLIC: Poděbrady, [50.13, 15.12], 3.IX.1936 (1 ♂ NHMD). DENMARK: Bognæs Skov på Tuse Næs, 55.7511, 11.7695, sifted from sea debris on saline marsh, 30.XII.2013, leg. K.B. Nielsen (1 ♂ NHMD); Engestofte, [54.76, 11.56], 20.VIII.1976 (2 ♂♂ 1 ♀ NHMD); Sundby Storeskov, [54.78, 11.81], 29.VII.1962, leg. V. Hansen (9 ♂♂ 2 ♀♀ NHMD); Vålse Vesterskov, 54.9592, 11.7728, sifted from fresh sea debris on saline marsh, 7.XII.2013 leg. K.B. Nielsen (1 ♀ NHMD). FINLAND: Kiiminki, [65.13, 25.78], 2011, leg. M. Mutanen (1 ♀ ZMUO). GERMANY: Degensmoor, Wesenberg, [53.27, 13.03], 31.VII.1978, leg. Stöcke (1 ♀ ZMHB); Döbitzer Heide, Ferbitzer Bruch, [52.50, 13.01] (1 ♂ 1 ♀ ZMHB); Federsee, Württemberg, [48.08, 9.62], 28.VII.1977 (2 ♀♀ ZMHB); Korswandt n. Wolgast, [53.92, 14.16], 25.VIII.1989, leg. Kleeberg (1 ♂ 1 ♀ NMW); Lübars, Berlin, [52.62, 13.36], 14.VII.1969, leg. H. Korge (3 ♂♂ 4 ♀♀ ZMHB); Müritz, Waren, [53.44, 12.74], sifting, sphagnum with grass and leaf litter, 17.VI.1976, leg. M. Uhlig (2 ♂♂ ZMHB); Teufelbruch n. Spandau, [52.57, 13.21], 22.VIII.1964 (1 ♂ ZMHB). HUNGARY: Pest nr. Mariabesnyő, [47.61, 19.41], 23.VIII.1931, leg. J. Fodor (1 ♀ NHMD); Pest nr. Pécel, [47.49, 19.34], IX. -XI.1929 leg. J. Fodor (1 ♂ NHMD). ITALY: Zeccone n. Pavia, [45.26, 9.19], 17.X.1977, leg. P. Kanaar (1 ♂ ZMHB). KAZAKHSTAN: Karatal river, [45.41, 77.81], 1.VII.2004, leg. V.A. Kastcheev (2 ♂♂ ZIN); Kyrgyz Alatau, Koshirme konezanod, [43.04, 76.84], 9.VII.2010, leg. V.A. Kastcheev (2 ♂♂ ZIN). NORTH MACEDONIA: Ohrid Lake, n. Struga, [41.17, 20.66], 7.VI.1980, leg. F. Hieke (1 ♂ 2 ♀♀ ZMHB). SWEDEN: Arlöv, [55.64, 13.05], grass roots on mossy soil near sea, 3.X.1962, leg. Palm (1 ♂ MZLU); Fotevik, [55.45, 12.95] (1 MZLU). UKRAINE: Peter & Paul, VII-VIII., leg. A. Spaney (1 ♂ ZMHB).

Redescription. Measurements ♂♂ (n = 5): HW = 1.64–1.78 (1.68); HL = 1.38–1.47 (1.41); HL/HW 0.81–0.88 (0.84); PW = 2.13–2.38 (2.22); PL = 1.98–2.00 (1.98); PL/PW 0.84–0.93 (0.89); EW = 2.11–2.40 (2.21); EL = 1.91–2.27 (2.07); EL/EW 0.88–0.96 (0.93); EL/PL 0.97–1.13 (1.04); PW/HW 1.48–1.65 (1.57); forebody length 5.36–5.71 (5.46). ♀♀ (n = 5): HW = 1.62–1.71 (1.66); HL = 1.33–1.44 (1.40); HL/HW 0.82–0.87 (0.84); PW =

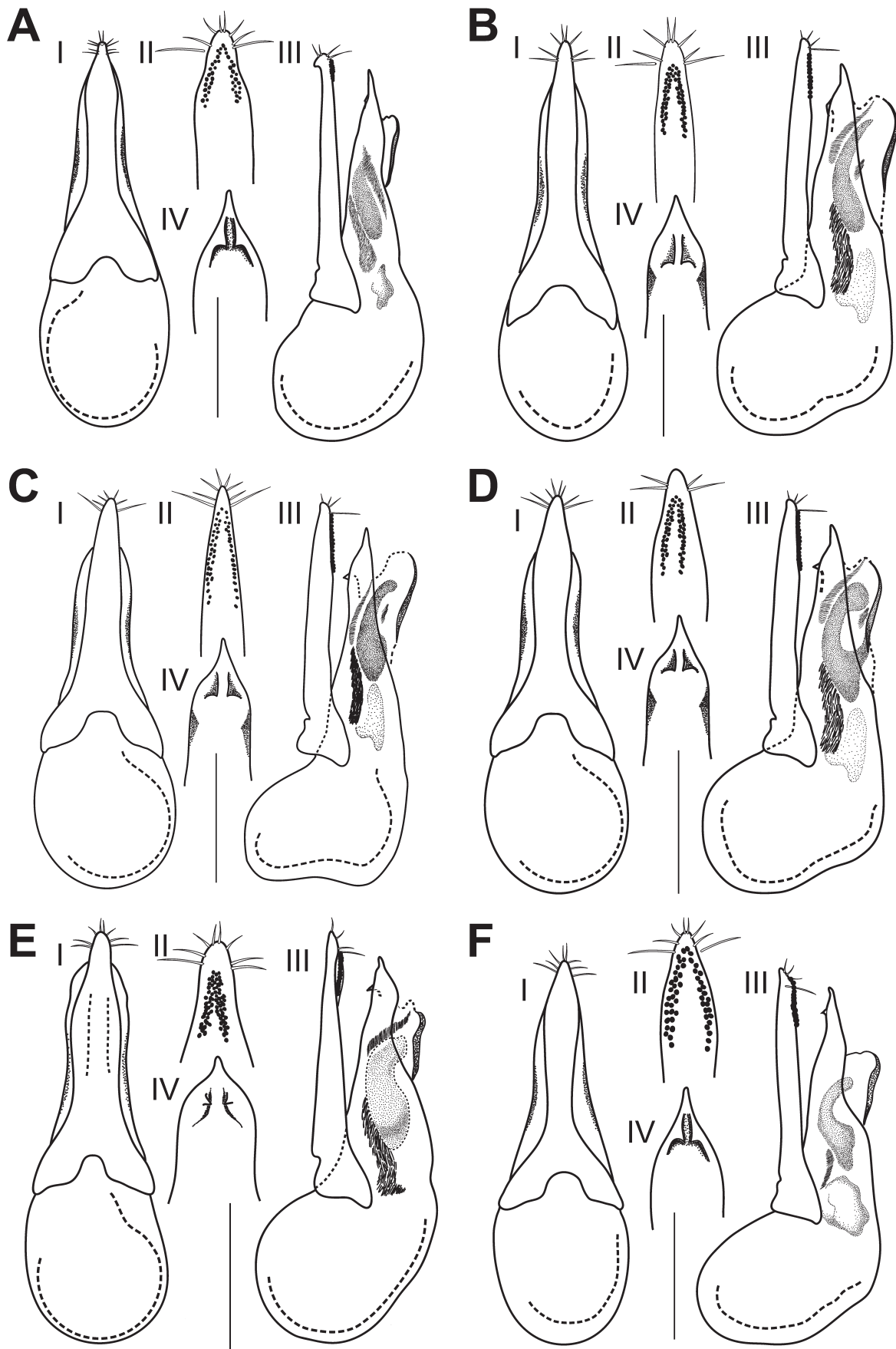


Fig. 13. Aedeagus of *Quedius* s. str. A - *Q. vicinus* (Ménétriés, 1832); B - *Q. sundukovi* Smetana, 2003; C - *Q. subunicolor* Korge, 1961; D - *Q. molochinus* (Gravenhorst, 1806); E - *Q. balticus* Korge, 1960; F - *Q. meridiocarpaticus* Smetana, 1958. I - parameral view of whole aedeagus; II - apices of paramere in antiparameral view with peg setae; III - lateral view of whole aedeagus; IV - apices of median lobe in parameral view.

2.00–2.22 (2.13); PL = 1.78–2.00 (1.88); PL/PW 0.86–0.90 (0.89); EW = 2.13–2.24 (2.20); EL = 2.02–2.18 (2.08); EL/EW 0.90–0.98 (0.94); EL/PL 1.01–1.15 (1.10); PW/HW 1.29–1.56 (1.47); forebody length 5.18–5.51 (5.36).

Medium sized, robust species; body dark brown to black (Fig. 8E).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 2.00–2.27 (2.14)); microsculpture of transverse waves; no interocular punctures between anterior frontal punctures (cf. Fig. 6F); antennae pale reddish with base of antennomeres 1–3 clearly darkened, all antennomeres elongate; palpi pale reddish.

Thorax: pronotum dark brown to black, slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond the first puncture of dorsal row; scutellum punctured and pubescent; elytra most often reddish brown rarely fully darkened, uniformly pubescent, with punctures clearly separated, slightly wider than long, roughly as long as pronotum; legs reddish brown with inner face of tibia and femur darkened, tarsi paler.

Abdomen dark brown to black, tergites uniformly punctured, without clear iridescence.

Male. Aedeagus (Fig. 13E): paramere rather broad, with clear medial expansion and extending into a point at apex, reaching just beyond apex of median lobe, with sensory peg setae forming two short broad rows fusing together towards apex, in lateral view peg setae are easily seen on protruding medial part of parameral apex; median lobe broad with sudden constriction to a point at apex, on parameral side with two well-defined teeth directed almost medially, positioned at level near end of peg setae rows of paramere; internal sac without extension of the C-sclerite.

Differential diagnosis. *Quedius balticus* is very similar to *Q. molochinus*, *Q. meridiocarpaticus* and *Q. vicinus*, but can be distinguished by the antennomeres 1–3 being at least partially darkened. For confident identification genitalia should be examined, especially when specimens are teneral or faded (from old collections) and thus with unnatural coloration. The aedeagus of *Q. balticus* differs from *Q. molochinus* in the absence of an extension of the C-sclerite in the internal sac, in the broad median lobe suddenly constricted at tip and in the medial broadening of paramere. It can be distinguished most easily from *Q. meridiocarpaticus* by the shape of the paramere, which is medially broadened in *Q. balticus* and broadened towards apex in *Q. meridiocarpaticus*. *Quedius balticus* can be confused with *Q. picipes* from the subgenus *Raphirus*, which may occur in similar environments. It can be readily distinguished from the latter by the labrum being entire, the darkened base of antennomeres 1–3 and the abdomen being more parallel-sided.

Color variation. *Quedius balticus* var. *funebis* Coiffait, 1971 was described from a female specimen from ‘Sarthe, La Ferté-Bernard’ as a variant of *Q. balticus* with black elytra (COIFFAIT 1971). Based on the images of that specimen kindly made on our request by Vinicius Ferreira at the MNHP, it is *Q. molochinus* with dark elytra. According to the ICZN Article 45.6 *Quedius funebis* is unavailable name.

Quedius picipennis ab. *nigribasis* Korge, 1960, another unavailable name, was described from a female from Germany (“Sweertia Weise Bin Lübaus”) and characterized by darkened antennomeres. So far, the form has been considered a color form of *Q. molochinus* (e.g., HERMAN 2001), but we are inclined to believe that this is indeed *Q. balticus*. At the time of description H. Korge considered *Q. balticus* restricted to an area near the Baltic Sea, but it is now known that the species is much more widespread. **Bionomics.** *Quedius balticus* was originally considered a littoral species found only in sea debris (KORGE 1960a, HANSEN 1962) and litter washed up on beaches (PALM 1963). Later it was discovered in reed litter in swamps, moors, wet meadows, as well as riverine areas subject to flooding (KORGE 1963, MORAVEC & VONIČKA 2000, NASH 2009, MAJZLAN & LITAVSKÝ 2017). Based on the earlier published data and our observations, *Q. balticus* is not common.

KORGE (1963) noted that specimens, which he kept in a terrarium were hiding in wet meadow litter and could not even be expelled from it by flooding. While other beetles, including closely related representatives of the same genus, quickly moved out when debris were flooded, *Q. balticus* stayed behind. In a study conducted in a valley of the river Peene in NE Germany, HOFFMANN et. al (2018) found *Q. balticus* to live only near natural fens and be the strongest indicator of these natural habitats. Given these observations the species seems to be highly adapted to environments subject to flooding and it can be a good indicator of a natural hydrology of an area.

Distribution. *Quedius balticus* is currently known to occur across large parts of Europe except the Iberian and the Italian peninsulas (Fig. 19). The species is currently known from Southern Finland and Sweden in the north to Italy, Bulgaria and Macedonia in the south, and from the British Isles and Northern France in the west to Kazakhstan in the east. Newly studied material herein extends the range north- and southwards, from Finland to Italy and Macedonia.

Quedius meridiocarpaticus Smetana, 1958

(Figs 1, 2C, 4, 8B, 13F, 20)

Quedius meridiocarpaticus Smetana, 1958: 365 [Type locality: Slovensko, Kamenný Most, Slanec]

Quedius dalmatinus Korge, 1960b: 68 [Type locality: Dalmatia: Castelnuovo]

References. COIFFAIT (1961): 53 (characters); KORGE (1962): 153 (synonymy of *Q. dalmatinus*); SMETANA (1962): 138 (characters); LOHSE (1964): 212 (characters); HORION (1965): 277 (distribution); SMETANA (1967): 558 (distribution); BORDONI (1976): 99 (characters); COIFFAIT (1978): 195 (characters); TÓTH (1984): 129 (characters); SMETANA (1993): 50 (distribution); CICERONI & ZANETTI (1995): 32 (distribution); LÁSZLÓ (1998): 137 (distribution); ANLAŞ (2009): 230 (distribution); SOLODOVNIKOV (2012): 33 (distribution); PETRENKO (2015): 80 (distribution); SALNITSKA & SOLODOVNIKOV (2019): 49 (characters and distribution).

Type material examined. *Quedius meridiocarpaticus*: LECTOTYPE ♂ (cSme), designated by SOLODOVNIKOV (2012), labelled: “Slovakia mer. Kamen. Most 5.5.1955 Smetana 1955 / *Quedius meridiocarpaticus* s. Smetana det. 1957 / Lectotype *Quedius meridiocarpaticus* Smetana A. Solodovnikov des. 2009 / *Quedius meridiocarpaticus* Smetana A. Solodovnikov det. 2009”.

PARALECTOTYPES: 1 ♂, labelled: "Slovakia mer. Kamen.most 3.5.1955 Smetana / *Quedius meridiocarpaticus* Smetana det. 1957 / *Quedius meridiocarpaticus* A. Solodovnikov det. 2009 / PARALECTOTYPE *Quedius meridiocarpaticus* Smetana A. Solodovnikov des. 2009/NHMD 00523118" (NHMD); 1 ♀, labelled: "Slovakia mer. Kamen.most 3.5.1955 Smetana / *Quedius meridiocarpaticus* Smetana det. 1957 / *Quedius meridiocarpaticus* A. Solodovnikov det. 2009 / PARALECTOTYPE *Quedius meridiocarpaticus* Smetana A. Solodovnikov des. 2009/NHMD 00523117".

Additional material examined. **ALBANIA:** Kolonjë, 3 km ENE Leskovik, 40.1586, 20.6216, flooded pasture, 990 m, 28.V.2010, M. Schülke (1 ♂ cSch). **BOSNIA AND HERZEGOVINA:** Jajce, [44.34, 17.27], 12.-23.VI.1967, leg. Baderle (1 ♂ 3 ♀♀ NMW); Trebinje, [42.71, 18.35], 1903 O. Leonhard (1 ♀ SDEI). **BULGARIA:** Burgas, Black Sea coast, [42.50, 27.48], 8.-19.V.1985, leg. D.W. Wrase (1 ♂ 5 ♀♀ ZMHB); Kiten, [42.24, 27.77], 29.V.1982, leg. H. Wendt (1 ♂ ZMHB); Melnik, [41.52, 23.38], 12.-20.V.1981 (2 ♀♀ ZMHB); Nessebar, [42.66, 27.71], 6.-7.VI.1982, leg. H. Wendt (1 ♂ 2 ♀♀ ZMHB); Pomorie, Black Sea coast, [42.58, 27.62], 9.-18.V.1985, leg. D.W. Wrase (1 ♂ cSch); Primorsko, [42.26, 27.75], VII.1980, leg. I. Pokorný (1 ♀ cSch); Rupite, General Todorov, [41.43, 23.24], 5.V.1984, leg. Hieke (1 ♀ ZMHB); nr. Sandanski, [41.55, 23.23], 28.IV.1985, leg. B. Jaeger (1 ♂ 1 ♀ ZMHB); Slivno, [42.67, 26.32] (1 ♂ NHMD); Veliko Tarnovo, [43.08, 25.63], 25.VII.1984, leg. U. Opitz (2 ♀♀ ZMHB). **CROATIA:** Castelnuovo [Kaštel Novi], [43.55, 16.31], 1895, leg. F. Müller (1 ♀ SDEI); nr. Plitvice, [44.86, 15.58], 19.VII.1910, leg. Hochetlinger (1 ♀ NHMD); nr. Zagreb, [45.78, 15.98] (1 ♂ NMW). **GREECE:** Alexandroupolis, [40.85, 25.87], 20.-30.IV.1967, leg. Krättschmer; 4 km NO of Anthili, Thessalia, Lamia, 38.8655, 22.5224, 6.II.2015, leg. T. Wolsch (1 ♂ cSch); Essymi [Aesymi], [41.01, 25.95], 700 m, 25.IV.1978, leg. Heinz (1 ♂ 1 ♀ ZMHB); Ioannina, Metsovo, Lago O Pigon, [39.81, 21.11], 18.V.2005, 1500m, leg. Angelini (2 ♀♀ NHMD); Janina [Ioannina], [39.66, 20.85], IV.1927, leg. C. Purkyne (2 ♂♂ NHMD); Keramidi, Thessalia, Palamas, 39.5627, 22.0801, 5.II.2015, leg. T. Wolsch (1 ♀ cSch); Lavrio, 60 km S Athina, [37.71, 24.06], 10.IV.1993, leg. P. Jørum (1 ♀ NHMD); Parnass. [Parnassos], [38.53, 22.62] (3 ♂♂ NHMD); Skarfia, 20 km WSW Lamia, 38.8405, 22.6988, salt meadows, 6.II.2015, leg. T. Mainda (1 ♂ cSch). **CORFU:** Val di Ropa, [38.24, 21.73], 1905, leg. O. Leonhard (1 ♀ SDEI). **CRETE:** Crete [35.41, 24.75], leg. Paganetti (1 ♂ NMW) [potentially mislabelled or introduced specimen clearly belonging to this species]. **KEFALONIA:** Paranetti, [38.21, 20.58], leg. F. Müller (1 ♀ SDEI). **PELOPONNES:** 3 km E Kalogria, 20 km NW of Varda, [38.19, 21.39], 15.IV.1993, leg. P. Jørum (1 ♀ NHMD); Nomos Lakonias, Near Fokiano, 37.0741, 22.9676, 0 m, sifting, waters edge, stagnant water, salt marsh, 02.IV.2019, leg. M. J. Justesen & A. K.Hansen (1 ♂ NHMD). **ZAKYNTHOS:** Kalamaki, [37.74, 20.89], 1909, leg. M. Hilf (1 ♀ ZMHB). **HUNGARY:** Hódmezővásárhely, [46.41, 20.34], 16.-22.VI.1995, leg. Probst (2 ♀♀ NMW); Rapnitz [Rábca] river, Neusiedler See, [47.67, 16.81], V.1994 (1 ♂ ZMHB); Velencei, Dinnyes, [47.17, 18.54], salt lake with gravel banks, 15.VI.1979, leg. M. Uhlig (1 ♂ 1 ♀ ZMHB). **ITALY:** Albareto, Emilia, [44.53, 10.40], 8.II.1994, leg. A. Fiori (2 ♀♀ ZMHB); NE of Bibione, left bank of Canale di Lugugnana mouth at Bibione, Veneto, 45.6259, 12.9791, sifting flood debris and litter, 29.V.2016, leg. A. Solodovnikov & M. Salnitska (2 ♂♂ 1 ♀ NHMD); Casinalbo, Emilia, [44.53, 10.40] 25.VII.1996, leg. A. Fiori (2 ♂♂ ZMHB); Cascine Del Riccio, Riva Ema [43.73, 11.25], 14.I.1970, leg. Mascagnia (1 ♂ cBor); Comacchio, [44.69, 12.17], 28.III.1974, leg. P. Garaghahi (2 ♀♀ cBor); Firenzuola, [44.12, 11.37], VII.1970, leg. Mascagnia (1 ♂ cBor); Lido di Jesolo, [45.51, 12.62], 10.VIII.1962, leg. Salvato (1 ♀ cBor); Noghera Istria, [45.58, 13.81] (1 ♂ NHMD); Padova, [45.39, 11.90], IX.1969 (1 ♂ ZMHB); Roma, Portonaccio, [41.90, 12.54], IX.1937, leg. G. Sacca (1 ♂ 4 ♀♀ cBor); Tencarola, [45.39, 11.80], 10.XII.1961, leg. Salvato (1 ♀ cBor). **NORTH MACEDONIA:** Bitola, Jugoslavina, [41.02, 21.32], 1962, leg. J.T. Skovgaard (1 ♀ NHMD); Katlanovo nr. Skopje, [41.89, 21.68], 17.IX.-12.X.1966, leg. Gruber (1 ♂ 1 ♀ ZMHB); Treska River, Sara, [41.97 21.30], 3.VI.1980, leg. F. Hieke (1 ♂ ZMHB); Vardar River, n. Skopje, [41.98, 21.49], 26.V.1980, leg. F. Hieke (1 ♂ 3 ♀♀ ZMHB). **ROMANIA:** Predeal, [45.49, 25.57], 20.VI.1977 (1 ♀ MZLU). **RUSSIA:** KRASNODAR KRAI: 15 km S of vill. Taman, [45.21, 36.70], 15.V.1995, sandy sea shore, under logs (2 ♂♂ NHMD); Temruk, mud volcano Gefest, 45.2566, 37.4326, leaf litter in meadows,

12.VI.2017, leg. M. Salnitska (1 NHMD) Karabetova Gryada 5 km SE of vill. Taman, [45.12, 36.76], in litter at the bank of the permanent pond (1 ♀ NHMD); Mt. Tkhab, valley of river Zhene, [44.58, 38.35], in forest litter, 21.VI.1992, leg. M. Savitsky (1 ♂ NHMD). **SLOVENIA:** 9 km SE Piran, [45.48, 13.59], 26.VI.1981, leg. F. Hieke (1 ♀ ZMHB). **TURKEY:** Adapazarı, [40.79, 30.40], flooding, 15.VII.1965, leg. Korge & Heinz (1 ♂ ZMHB); SW Arnavutköy and Yassiören, [41.17, 28.65], 60 m, 19.IV.1990, leg. Heinz (1 ♂ ZMHB); Caykasi River, Erfelek, Sinop, [41.89, 34.92], 26.V.1989, leg. Schönmann & Schillhammer (1 ♂ 3 ♀♀ NMW); 6 km E Gebze, Izmit, [40.78, 29.49], IV.1983, leg. Heinz (1 ♂ 2 ♀♀ ZMHB); 20 km W Gebze, [40.87, 29.22], IV.1989, leg. Heinz (2 ♂♂ 1 ♀ ZMHB); Gelibolu, [40.41, 26.67], 10 m, 3.V.1982, leg. Boffa (2 ♀♀ cBor) İnönü, Eskişehir, [39.82, 30.14], 850 m, 3.IV.1986, leg. Heinz (1 ♀ ZMHB); Keşan, [40.85, 26.62], 22.IV.1978, leg. Heinz (2 ♂♂ ZMHB) E Pamucak, Selcuk, [37.96, 27.27], swamp, 28.III.1986, leg. Heinz (1 ♂ ZMHB); 2 km E Sarısaltık, 39.1241, 39.2475, 1594 m, 19.V.2011, leg. Anlaş (1 ♀ NHMD); Saray, 30 km W Ankara, [40.07, 32.61], 23.II.1973, leg. Exp. Nat. Mus. Praha (1 ♂ NHMD); Söğüt, SE of Bilecik, [40.02, 30.18], 1200 m, 4.IV.1992, leg. Heinz (1 ♂ 2 ♀♀ ZMHB); Susuz-Dag, Dokuz-Göl, Elmalı, [36.50, 29.76], 1700-2000 m, 20.VII.1971, leg. Heinz (1 ♂ ZMHB). **UKRAINE:** Environs Odessa, right bank of Kujalnikij estuary, [46.57, 30.73], 10.VI.2005, under stones, leg. A. Gontarenko (3 ♂♂ 1 ♀ NHMD); Nikitsky botanical garden, [44.50, 34.23], by the sea, stones, 16.IX.1966 (1 ♂ cRyv).

Redescription. Measurements ♂♂ (n = 7): HW = 1.73–1.82 (1.78); HL = 1.47–1.56 (1.51); HL/HW 0.82–0.88 (0.85); PW = 2.27–2.47 (2.36); PL = 2.09–2.31 (2.19); PL/PW 0.89–0.95 (0.93); EW = 2.27–2.47 (2.36); EL = 2.09–2.24 (2.17); EL/EW 0.87–0.99 (0.92); EL/PL 0.92–1.05 (0.99); PW/HW 1.50–1.66 (1.56); forebody length 5.71–6.02 (5.86). ♀♀ (n = 3): HW = 1.64–1.76 (1.71); HL = 1.33–1.51 (1.43); HL/HW 0.81–0.86 (0.83); PW = 2.07–2.36 (2.21); PL = 1.96–2.13 (2.05); PL/PW 0.91–0.95 (0.93); EW = 2.16–2.38 (2.28); EL = 1.98–2.24 (2.12); EL/EW 0.90–0.97 (0.93); EL/PL 1.00–1.09 (1.03); PW/HW 1.52–1.56 (1.54); forebody length 5.27–5.78 (5.60).

Medium sized, robust species; body light to dark brown (Fig. 8B).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.50–1.67 (1.56)); microsculpture of transverse waves; no interocular punctures between anterior frontal punctures (cf. Fig. 6F); antennae pale reddish, antennomeres elongate; palpi pale reddish.

Thorax: pronotum light to dark brown, slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond the level of first puncture of dorsal row; scutellum punctured and pubescent; elytra most often reddish brown rarely fully darkened, uniformly pubescent, slightly wider than long, roughly same length as pronotum; legs reddish brown with inner face of tibia darker.

Abdomen light to dark brown, tergites uniformly punctured, without clear iridescence.

Male. Aedeagus (Fig. 13F): paramere spatulate with clear proximal to medial attenuation and extending into paddle-like structure near apex, reaching just beyond apex of median lobe, with sensory peg setae forming a broad horseshoe shaped band of relatively large peg setae; median lobe broad with gentle constriction to a point at apex, on parameral side with two small teeth pointing slightly basad,

positioned at level near basal level of peg setae band of paramere; internal sac without a continuation of C-sclerite.

Differential diagnosis. *Quedius meridiocarpaticus* is very similar to other species in the *molochinus*-group with red elytra, viz *Q. molochinus*, *Q. balticus*, and *Q. vicinus*. It can be distinguished from *Q. balticus* by the pale base of the basal three antennomeres. Generally, it has paler middle antennomeres compared to *Q. molochinus*. Compared to *Q. vicinus* it is generally slightly darker, elytra brownish red (pale red to yellowish in *Q. vicinus*), abdomen dark brown (light brown in *Q. vicinus*). For confident discrimination of these species, their genitalia should be checked: the aedeagus of *Q. meridiocarpaticus* differs from *Q. molochinus* in the absence of an extension of the C-sclerite in the internal sac, in the spatula-shaped paramere with clear proximal to medial attenuation, and larger peg setae. It can be distinguished most easily from *Q. balticus* by the shape of the paramere, which is medially broadened in *Q. balticus* and broadened towards apex in *Q. meridiocarpaticus*. It differs from *Q. vicinus* in the absence of a blunt apical hook on the paramere (parameral side). *Quedius meridiocarpaticus* can be confused with *Q. picipes* of the subgenus *Raphirus*, which may occur in similar environments. It can be readily distinguished from the latter by more parallel-sided abdomen and entire labrum.

Synonymic notes. Independent of each other, SMETANA (1958) and KORGE (1960b) recognized that a species very similar to *Q. molochinus* was present in Southeastern Europe. KORGE (1962) himself synonymized *Q. dalmatinus* Korge, 1960 with *Q. meridiocarpaticus* Smetana, 1958. Based on the description and illustration of *Q. dalmatinus*, it clearly agrees with the concept of *Q. meridiocarpaticus* herein.

Bionomics. *Quedius meridiocarpaticus* appears to be found most frequently in wet debris and under rocks near water bodies, both fresh and saline. We (AKH and AS) have collected this species in the flood debris of a salt lagoon near Bibione, Italy, in debris around the stagnant salt pond near the beach of Fokiano, Greece (Fig. 2C) and on the marsh debris near the Gefest Mud Volcano in the Taman Peninsula in southern Russia. Like many other *Quedius* s. str., the species is found at lower elevations in the northern part of its range and at much higher elevations (up to 2000 m) towards the southern part of its range.

Distribution. *Quedius meridiocarpaticus* is distributed from Italy through Southeastern Europe to the Crimea, Western Caucasus and Anatolia (Fig. 20). There seem to be rather well defined distributional boundaries between this species, and *Q. molochinus* and *Q. vicinus*. The northern range of *Q. meridiocarpaticus* is roughly delimited by the Alps and Carpathians, where it is replaced by *Q. molochinus* to the North of these mountain chains. The species continues north around the Black Sea to the western foothills of the Caucasus. To the South it extends to northern and western Anatolia, mainly along the coast, but it is also found more inland in some sites. In southern and eastern Anatolia *Q. meridiocarpaticus* is gradually replaced by *Q. vicinus*, with which it seems to co-occur to some extent in southern Anatolia.

Quedius molochinus (Gravenhorst, 1806)

(Figs 1, 4, 9, 8C,D, 12, 13D, 20)

Staphylinus molochinus Gravenhorst, 1806: 56 [Type locality: Brunsviga]
Quedius demudatus Stephens, 1832: 216 [Type locality: London; Suffolk]
Quedius lathburii Stephens, 1832: 218 [Type locality: London; Suffolk, Orwell]

Quedius niger Sahlberg, 1876: 229 [Type locality: Muonioniska]
Quedius maculicornis Mulsant & Rey, 1876: 694 [Type locality: les montagnes du Lyonnais, à la Grande Chartreuse, dans les Pyrénées]
Raphirus picipennis Stephens, 1833: 243 [Type locality: London]
Staphylinus laevicollis Runde, 1835: 6 [Type locality: Halae]
Staphylinus lapponicus Zetterstedt, 1838: 61 [Type locality: Lapponia Umensis, Lycksele; Wilhelmina; Gaskelougt]

References. GYLLENHAL (1810): 302, (1827): 477 (characters); SAHLBERG (1830): 314 (characters); (1876): 24 (distribution); MANNERHEIM (1830): 25, (1831): 439 (distribution); (1843): 232 (characters); RUNDE (1835): 5 (characters); LACORDAIRE (1835): 377 (characters); CURTIS (1837): pl. 638 (characters); NORDMANN (1837): 76 (distribution); ERICHSON (1839): 489, (1840): 535 (characters); HEER (1839): 276 (characters); STEPHENS (1839): 390 (characters); LAPORTE (1840): 177 (characters); KIESENWETTER (1848): 52 (characters); (1851): 419 (distribution); GRAVENHORST (1847): 227 (characters); REDTENBACHER (1849): 709, (1857): 201, (1874): 198 (characters); HARDY (1851): 32 (biology); FAIRMAIRE & LABOULBÈNE (1856): 537 (characters); KRAATZ (1857): 500 (characters); WATERHOUSE (1858): 23 (synonymy); THOMSON (1859): 25 (notes on types); (1860): 173 (synonymy); GEMMINGER & HAROLD (1868): 570 (synonymy); FAUVEL (1874): 290 (characters and distribution); SEIDLITZ (1875): 267 (characters); MULSANT & REY (1876): 692 (characters); FOWLER (1888): 237 (characters); REITTER (1909): 112 (characters); JOHANSEN (1914): 364 (characters); GRIDELLI (1924): 81, (1962a): 320 (characters); PORTEVIN (1929): 341 (characters); MÉQUIGNON (1937): 3 (synonymy); HANSEN (1952): 142 (characters); SMETANA (1958): 364 (characters and biology); (1962a): 136, (1965a): 38 (characters); (1962b): 134 (larval characters); (1964): 80, (1976a): 172, (1978a): 85, (1981): 638, (1990): 98, (1993): 50 (distribution); (1971): 133 (distribution; introduction to Nearctic); (1973): 1427 (introduction to Nearctic); KORGE (1960b): 53 (characters); COIFFAIT (1961): 52, (1963): 423, (1978): 194 (characters); PALM (1963a): 141 (characters); LOHSE (1964): 212 (characters); DVOŘÁK 1965: 89 (distribution); POTOTSKAIA (1967): 82 (larval characters) KASULE (1968a): 66 (biology); (1970): 61 (larval characters); SZUJECKI (1968): 736 (distribution); OSELLA & ZANETTI (1975): 120 (biology); BORDONI (1976a): 95 (characters); SHILOV (1975): 376 (distribution); POPE (1977): 31 (distribution); TÓTH (1984): 120 (characters); SEGERS (1987): 182 (morphology); WELCH (1993): 229 (morphology); CICERONI & ZANETTI (1995): 32 (distribution); STANIEC (1996): 117 (pupal characters); DOWNIE & ARNETT (1996): 391 (characters); OWEN (2000): 252 (biology); ASSING (2001): 75 (biology); UHLIG et al. (2006): 55 (distribution); MAJKA (2007): 949 (distribution); DAPKUS & TAMUTIS (2008): 33 (distribution); CUPPEN et al. (2011): 15 (distribution); SEMIONENKOV et al. (2015): 335 (distribution).

Type material examined. *Staphylinus molochinus*: SYNTYPE ♂ (ZMHB), labelled: "6230 / Braunsberg Dahl leg. / molochinus gr. gyll. / (Para)?typus Grav. / det. H. Korge *Quedius molochinus* Grav. Typus!".

Quedius niger: SYNTYPE ♀ (MZH), labelled: "Tjudi / J. Sahlbg. / 1617. / Mus. Zool. H:fors Spec. typ. No 157 *Qued. molochinus* var. *niger* J. Sbg. / Syntype / http://id.luomus.fi/GZ.83 / Photographed 2020 Pekka Malinen".

Additional material examined. AUSTRIA: Arbesbach, [48.49, 14.95], 13.VII.1957, leg. Schubert (1 ♀ NMW); Admont, [47.56, 14.45], leg. H. Franz (1 ♀ NMW); Prater, [48.21, 16.39], 19.IX.1964 (1 ♂ NHMD). CZECH REPUBLIC: Iser [Jizera] River, n. Benešov u Semil, [50.60, 15.36], 350 m, 24.VII.1982, leg. Hieke (1 ♀ ZMHB); Pastviny n. Žamberk, [50.09, 16.56], 31.VII.-3.VIII.1982, leg. Hieke (1 ♀ ZMHB); Podyji Nat. Park, forest, at river Dyje valley ca. 2.5 km NW of Havraníky, 48.83, 15.98, 240 m, sifted flood debris, 08.VI.2016, leg. A. Solodovnikov, J. Jenkins Shaw, & A. Hansen (1 ♂ NHMD); Silesia Altwater [Praděd], [50.08, 17.23], leg. Letzner (1 SDEI); Teplice nad Metují, [50.59, 16.16], 3.-5.VIII.1992, leg. Hieke (1 ♀ ZMHB); Vysoká Hůla, NW Karlov, Malá Morávka, [50.08, 17.23], sifting litter of *Pinus mugo*, 25.VII.1993, leg. Zerche (1 SDEI). DENMARK: Hjelm Hede, [56.49, 8.91], 20.VII.1951, leg. J. Petersen (2 ♀♀ NHMD). BORNHOLM: Øle Å, 19.IV.1965, [55.05, 15.02], leg. F.

Bangsholt (1 ♀ NHMD). **FUNEN:** Bjergsted, [55.66, 11.35], 1.VI.1981, leg. M. Hansen (1 ♂ NHMD); Ristinge Klint, [54.82, 10.61], 14.VII.1978, leg. M. Hansen (2 ♂ NHMD). **ZEALAND:** Furesøstien, [55.81, 12.41], 27.IX.1954, leg. J. Petersen (3 ♀♀ NHMD); Holmegårds Mose, [55.29, 11.82], 26.VI.1975, leg. M. Hansen (1 ♂ NHMD); Ormø, [55.21, 11.45], 13.IX.1997, leg. O. Martin (1 ♀ NHMD); Rude Skov, [55.83, 12.47], 19.VIII.1948, leg. J. Petersen (1 ♀ NHMD). **FINLAND:** Kilpisjärvi, [69.04, 20.81], 21.-22.VII.1985, leg. Hieke (1 ♀ ZMHB); Kiuruvesi, [63.65, 26.62], 6.VII.1951, leg. Linnavuori (1 ♂ 2 ♀♀ ZMUO); Mutenia, Sodankylä, [68.02, 27.41], 13.IX.2001, leg. J. Itämiies, O. Nenonen (1 ♀ ZMUO); Rymättylä, [60.37, 21.94], leg. Linnavuori (1 ♀ ZMUO); Saana, Enontekiö, [69.04, 20.85], 10.VII.2013, M. Pentinsaari (1 ♂ ZMUO). **FRANCE:** Chigny, Oise River, [49.91, 3.77], Selchert (1 ♂ ZMHB). **GERMANY:** Bayern, Schleissheim, [48.24, 11.59], 15.V.1931, leg. Ihssen (1 ♂ ZMHB); Berlin-Marzahn, Hellersdorfer Berg, [52.53, 13.58], 8.VIII.1997, leg. Hieke (1 ♂ ZMHB); Brunn, Dosse, [52.91, 12.51], 16.III.1980, leg. E. Rössner (2 ♂♂ SDEI); Engolling, Auerbach, [48.79, 13.10], 5.IX.1978, leg. K. Kouf Frauen (1 ♂ 1 ♀ ZMHB); Erzgebirge, Flohtelberg, [50.42, 12.95], 2.VI.1925, leg. Uhmman (1 ♂ SDEI); Finkenkrug nr. Berlin, [52.56, 13.03], 12.IV.1898, leg. Dahl (1 ♀ ZMHB); Flessenow, Schwerin, [53.75, 11.49], 4.VII.1968, leg. Uhlig (1 ZMHB); Hainleite, SW Günseroda and Seega, [51.32, 11.02], 10.VIII.1993, leg. F. Hieke (1 ♂ ZMHB); Marburg in Hess, [50.81, 8.77], 16.IV.1904, leg. Strand (1 ♂ ZMHB); Neuendorf, Teupitz, [52.11, 13.58], 30.IV.1992, leg. Renner (1 ♂ ZMHB); Sarnow n. Anklam, [53.75, 13.63], 29.IX.1964, leg. F. Hieke (1 ♂ ZMHB); Strausberg, 23.VII.1981, [52.56, 13.88], leg. H. Wendt (1 ♀ ZMHB); Thüringer Wald nr. Scheibe, [50.48, 11.05], under stones, 8.I.1957, leg. Dieckmann (1 SDEI); Willersdorf, [51.02, 8.85], VII (1 ♀ ZMHB). **ITALY:** Gello, [43.96, 10.45], VI.1922, leg. A. Strand (1 ♂ NHMD); Zeccone n. Pavia, [45.26, 9.19], 17.X.1977, leg. P. Kanaar (1 ♂ ZMHB). **NORWAY:** Hemnesberget, [66.22, 13.61], 8.-14.VII.1903, leg. E. Strand (2 ♂♂ ZMHB); Kongsvinger Eis, [60.19, 12.01], 27.X.1980, leg. F. Midtgaard (1 ♂ NHMD); Pasvik Lake, Sydvaranger, [69.34, 29.53], VI.1994, leg. G. Nietsch (1 ♂ NMW); Utgardsjön, Rønningen, Austmarka, [60.01, 12.37], 28.VI.-10.VII.1975, leg. P. Kanaar (1 ♀ ZMHB). **POLAND:** Misdroy, [53.91, 14.44] (1 ♂ ZMHB); Pölit [Police], Pommern, [53.55, 14.57], 13.VI.1920, leg. E. Hanau (1 ♀ ZMHB); Riesengebirge [Krkonoše], [50.79, 15.57], 750m, moss, 16.X.1902, leg. Dahl (1 ♂ ZMHB); Tamsel, [52.62, 14.70], 20.V.1920, leg. Kuntzen (1 ♀ ZMHB). **RUSSIA: CHITA OBLAST:** Malkhanskij Khrebet, pass to Maleta, 20 km S Maloarkhangel'sk, 50.2352 108.916, 19.-25.VIII.1998, leg. A. Shavrin (NHMD). **KHANTY-MANSI AUTONOMOUS DISTRICT:** Sovetsky region, Malaya Sosva Nature Reserve, near Cordon Hangokurt, road to Belaya Gora, 61.9504, 64.2489, 81 m, nr a roadside puddle with *Polytrichum* sp. on clay, 28.VI.2017, leg. A.B. Ryvkin (1 ♂ cRyv). **KOMI REP:** Ukhta surrounding, [63.57, 53.71], 29.VI.1974, leg. V. Shulov (6 ♂♂ 6 ♀♀ ZMHB). **KRASNOYARSK KRAI:** Niznaya Lebedyanka river, [61.96, 89.45], 23.VI.1992, leg. V.S. (1 ♂ cRyv); Turukhanskij Distr., Mirmoye, [62.28, 89.03] 6.-17.VII.1990, leg. L.B. Rybalov (1 ♂ 1 ♀ cRyv). **LENINGRAD OBLAST:** Saint-Petersburg, Sestroretsk, Rzhavaya kanava, [60.12, 29.96], 16.VIII.2009, leg. V.N. Prasolov (1 ♂ ZIN); Stary Petergof, [59.87, 29.87], forest, 7.VI.1997, in leaf litter, leg. A. Solodovnikov (1 ♂ NHMD) Yaschera, [58.92, 29.98], 18.V.1996, leg. L. Anisutkin (1 ♂ NHMD). **MOSCOW OBLAST:** Moscow, Izmajlovskij Park, [55.75, 37.62], 7.VII.1983, leg. A. Isaev (1 ♂ NHMD); Odintsovskij Distr., Zvenigorod Biological Station of MSU, [55.70, 36.72], mixed forest, 22.VIII.1984, leg. K.G. Mikhailov (2 ♂♂ cRyv). **MURMANSK OBLAST:** Kyndomys [Kindo] Peninsula, [66.65, 33.22], forest floor, 16.VII.1992, leg. Wegner (1 ♂ ZMHB). **PERM KRAI:** Perm city, [58.01, 56.22], pitfall, 29.VIII.1978, leg. S.L. Esunin (1 ♂ NHMD). **REP. OF BURYATIA:** Barguzinsky Distr., Barguzin valley, 20 km E Ust-Barguzin, Gusikha, [53.42, 109.42], aspen forest, pitfalls, leg. V. Shilenkov (1 ♂ NHMD); Vitimsky Nat. Preserve, lake Oron, mouth of Labaznyj creek, Oron hut, [54.82, 112.26], 27-30.VII.2000, leg. A. Shavrin (2 ♂♂ NHMD). **RYAZAN OBLAST:** Ryazan Prov., Spassky Distr., Oka nature reserve, [54.71, 40.85], leaf litter, 26.VI.1981, leg. Kormylutyn & Eskov (1 ♂ 1 ♀ cRyv). **SVERDLOVSK OBLAST:** Ural, Visim Nature Reserve, [57.37, 59.77], 25.I.1985, leg. L.P. Titova (2 ♂♂ cRyv). **TYUMEN OBLAST:** Surgutsky Distr., Yugansky Nature Reserve, Ai-Magromsy River Basin, near 'Medvezhii Ugol', [59.59, 74.71], 22.IX.2002, leg. A.B. Ryvkin (1 ♂ cRyv). **ULYANOVSKAJA OBLAST:** Inzenskij Distr., Argash village, [53.96, 46.25], birch forest, 9.VII.1995, leg. A. Isaev (2 ♂♂ NHMD). **SLOVAKIA:** Inovec, [48.77, 18.04], IX.1931, leg. Čepelák (1 ♂ ZMHB). **SWEDEN:**

Dagsås-trakten, Hall, [57.06, 12.48], 26.X.1953, leg. J.T. Skovgaard (2 ♂♂ 3 ♀♀ NHMD); Södermanand, Ornö, [59.05, 18.41], 15.V.1946, leg. J.T. Skovgaard (1 ♂ 1 ♀ NHMD); Stockholm, Djurgården 23.III.1945, leg. J.T. Skovgaard (1 ♀ NHMD); Vitamölle, [55.69, 14.21], 1.VIII.1926, leg. Stephensen (1 ♂ NHMD). **GOTLAND:** Lau, [57.28, 18.61], 25.VI.1950, leg. J.T. Skovgaard (1 ♂ NHMD). **SWITZERLAND:** Reussdelta, Seedorf, [46.89, 8.61], 435 m, VIII.1998, leg. Herger & Rezb. (1 ♂ ZMHB). **UNITED KINGDOM: ENGLAND:** Stanford le Hope, Essex, [51.51, 0.42], 7.IX.1969, leg. Wewalka (1 ♀ NMW). **SCOTLAND:** Bridge of Orchy, [56.51, -4.76], 23.VII.1987, leg. Gillerfors (1 ♀ MZLU); S Braemar, [56.99, -3.39], 15.VII.1987, leg. Gillerfors (1 ♀ MZLU).

Redescription. Measurements ♂♂ (n = 5): HW = 1.60–1.78 (1.68); HL = 1.36–1.53 (1.44); HL/HW 0.83–0.88 (0.85); PW = 2.09–2.24 (2.20); PL = 1.93–2.11 (2.04); PL/PW 0.91–0.94 (0.93); EW = 2.00–2.18 (2.11); EL = 1.73–2.07 (1.92); EL/EW 0.87–0.95 (0.91); EL/PL 0.90–1.02 (0.94); PW/HW 1.32–1.57 (1.47); forebody length 5.02–5.58 (5.40). ♀♀ (n = 5): HW = 1.60–1.69 (1.64); HL = 1.38–1.51 (1.45); HL/HW 0.86–0.93 (0.89); PW = 2.07–2.22 (2.13); PL = 1.91–2.09 (2.00); PL/PW 0.90–0.98 (0.94); EW = 2.04–2.18 (2.11); EL = 1.84–1.93 (1.91); EL/EW 0.88–0.95 (0.91); EL/PL 0.91–1.01 (0.96); PW/HW 1.40–1.53 (1.47); forebody length 5.22–5.51 (5.35).

Medium sized, robust species; body dark brown to black (Figs 8C,D).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.67–2.13 (1.76)); microsculpture of transverse waves; no interocular punctures between anterior frontal punctures (cf. Fig. 6F); antennae pale reddish with antennomeres 3–5 slightly darkened, all antennomeres elongate; palpi pale reddish.

Thorax: pronotum dark brown to black, slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond level of first puncture of dorsal row; scutellum punctured and pubescent; elytra most often reddish brown rarely fully darkened, uniformly pubescent, slightly wider than long, roughly same length as pronotum; legs reddish brown with inner face of tibia and inner femur darkened.

Abdomen dark brown to black, tergites uniformly punctured, with slight iridescence.

Male. Aedeagus (Fig. 13D): paramere lanceolate with slight medial attenuation and extending into a slight expansion broadest below slightly asymmetric apex, reaching just beyond apex of median lobe, with sensory peg setae forming two long rows fusing together towards apex; median lobe broad with gentle constriction to a point at apex, on parameral side with two small teeth pointing slightly basad, positioned at level near basal level of peg setae band of paramere; C-shaped sclerite of internal sac with spine-like basal extension.

Differential diagnosis. *Quedius molochinus* is very similar to the other species with red elytra in the *molochinus*-group: *Q. meridiocarpaticus*, *Q. balticus*, and *Q. vicinus*. It can be distinguished from *Q. balticus* by the pale base of the basal three antennomeres. In most cases it has darker middle antennomeres and is generally slightly darker with abdomen black to dark brown (dark to light brown in *Q. meridiocarpaticus* and *Q. vicinus*). For confident discrimination of these species genitalia should be examined: ae-

deagus of *Q. molochinus* has an extension of the C-sclerite in the internal sac. *Quedius molochinus* with black elytra can be confused with *Q. subunicolor* where their ranges overlap. Usually, the lighter colored appendages and the coarser microsculpture of *Q. molochinus* are sufficient to distinguish it from *Q. subunicolor*. *Quedius molochinus* can be confused with *Q. picipes* from the subgenus *Raphirus*, which may occur in similar environments. It can be readily distinguished from the latter by more parallel-sided abdomen and entire labrum. In North America the species can be confused with *Q. laticollis*, from which it can be distinguished by stouter antennae with slightly darker middle antennomeres. Also, in *Q. molochinus* elytra are more often brick red or almost black, whereas in *Q. laticollis* they are most often dark brown.

Synonymic notes. *Quedius picipennis* Stephens, 1832 from London, Norfolk, Suffolk, Devonshire, and Somerset and *Raphirus picipennis* Stephens, 1833 from London have recently been mixed up as the same species in both HERMAN (2001) and NEWTON (2020). Based on the original descriptions, *Raphirus picipennis* clearly belongs in the *Quedius* subgenus *Raphirus*, whereas *Quedius picipennis* fits *Q. molochinus*. Original descriptions of *Staphylinus laevicollis* Runde, 1935 described from Halle in Central Germany and *Staphylinus lapponicus* Zetterstedt, 1838 described from Finland fit *Q. molochinus*, consistently with the currently accepted synonymy.

Bionomics. *Quedius molochinus* is found in meadows, heaths and grasslands, as well as in mainly coniferous forests. Most records are from under rocks or in moss. We have encountered it in flood debris near a river forested on either side in Czech Republic, in *Sphagnum* moss of a bog in Southern Sweden, and from pitfall traps set in a heathland in Denmark. Records from Russia (SEMIONENKOV et al. 2015), Switzerland (UHLIG et al. 2006) and the Netherlands (CUPPEN et al. 2011) are from meadows. In North America it seems to be in more ruderal habitats as well, having been found in e.g., potato fields on Prince Edward Island (MAJKA 2007).

Distribution. Among the closest congeners, *Quedius molochinus* is a more northern species widely distributed from France and British Isles through Central and Northern Europe, across European Russia and western Siberia to Transbaicalia (Fig. 20). In the southern areas of its distribution, it gradually moves to higher elevations, for example in the Alps extending into the Apennines. More thorough sampling in Russia may widen its distribution significantly.

Quedius molochinus is introduced in North America, where it is currently found in three separate areas in Canada: around the Avalon Peninsula of Newfoundland (SMETANA 1981), in the Canadian Maritime Provinces (Nova Scotia, New Brunswick and Prince Edward Island, MAJKA 2007) and around Quebec City (SMETANA 1981) (Fig. 12).

Quedius subunicolor Korge, 1961

(Figs 1, 2F, 4, 7F, 13C, 20)

Quedius subunicolor Korge, 1961: 81 [Type locality: Schweden, Häggenäs, Jämtland]

Quedius altaicus Korge, 1962: 152 [Type locality: Zentral-Altai], **syn. nov.**

References. PALM (1962): 187, (1963): 142 (characters); TIKHOMIROVA (1973): 189 (distribution); SHILOV (1975): 376 (distribution); COIFFAIT (1978): 193 (characters); LOHSE & LUCHT (1989): 172 (biology); SALNITSKA & SOLODOVNIKOV (2018a): 128–130 (redescription, suspected synonym of *Q. altaicus*); (2019): 47 (key and characters).

Type material examined. *Quedius subunicolor*: PARATYPES (MZLU): 1 ♂, labelled: “Häggenäs s-n Jtl. T. Palm 4–8, 8 1945 / det. H. Korge *Quedius subunicolor* Korge / Paratypus *subunicolor* Korge / *Quedius subunicolor* Korge / Type no. 1202:2 MZLU/ 2016 189 MZLU”; 3 ♀♀, same data, but last two labels “Type no: 1202:3 MZLU/ 2016 190 MZLU”.

Quedius altaicus: HOLOTYPE: ♀ (FMNH), labelled: “Zentral-Altai, Ig. Leder, det. Bang-Haag / unicolor Kies. det. Bernhauer / ♀ Holotypus *Quedius* s. str. *altaicus* H. Korge / Chicago NHMus M. Bernhauer Collection / Holotype teste D.J. Clarke 2014 GDI Imaging Project / Photographed Kelsey Keaton 2014 Emu Catalog / FMNHINS 2819427 Field Museum”.

Additional material examined. FINLAND: Kuusamo, [65.96, 29.17] (1 ♀ ZMUO); Savukoski, [67.29, 28.15], 15.-25.VI.2006, leg. M. Mutanen, P. Välimäki & M. Penttisaari (1 ♂ ZMUO). KAZAKHSTAN: Altai, Listvyaga, SSW Gora Tesninskiy Belok, Seredchikha River, [49.51, 85.25], 1200–1500 m, 27.VII.1997, R. Dudko & V. Zinchenko (1 ♂ NHMD); Bukhtarma riv., Uryl-Chingistai, [49.19, 85.88], 13.VI.1987, leg. V.A. Kastcheev (1 ♂ ZIN); Rahmanovskie Kluchi, [49.53, 86.50] 14.-16.VI.1980, leg. V.A. Kastcheev (1 ♂ ZIN); Saur ridge, Uidene riv., [47.20, 85.32], 1600–1800 m, 15.VII.2011, leg. V.A. Kastcheev (10 ♂♂ 2 ♀♀ ZIN). RUSSIA: ALTAI REP.: Source of Kuma river, 50.9989, 84.1647, 1479 m, mixed forest, under stones, 4.VII.2019, leg. A. Solodovnikov, A. K. Hansen, & M. J. Justesen (2 NHMD); Source of Kuma river, 50.9806, 84.1652, 1800 m, under stones, timber line, 3.VII.2019, A. Solodovnikov, A. K. Hansen, & M. J. Justesen (1 ♂ NHMD). REP. OF BURYATIA: Lake Baikäl, Svyatoy Nos, [53.69, 108.86], 9.VIII.1997, leg. A. Shavrin (1 ♂ NHMD). SWEDEN: Barsele, [65.04, 17.45], leg. Alan Dufberg (1 MZLU); Revsund, [62.89, 15.12], 27.V.1970, leg. R. Bergvall (3 MZLU).

Redescription. Measurements ♂♂ (n = 6): HW = 1.67–1.78 (1.74); HL = 1.42–1.56 (1.49); HL/HW 0.80–0.89 (0.86); PW = 2.24–2.40 (2.32); PL = 2.04–2.20 (2.12); PL/PW 0.90–0.96 (0.91); EW = 2.22–2.56 (2.46); EL = 2.29–2.47 (2.36); EL/EW 0.92–1.03 (0.96); EL/PL 1.06–1.17 (1.11); PW/HW 1.50–1.64 (1.56); forebody length 5.78–6.04 (5.97). ♀♀ (n = 3): HW = 1.67–1.76 (1.73); HL = 1.44–1.49 (1.47); HL/HW 0.82–0.88 (0.85); PW = 2.13–2.33 (2.25); PL = 1.89–2.02 (1.97); PL/PW 0.83–0.94 (0.88); EW = 2.11–2.47 (2.30); EL = 2.00–2.36 (2.24); EL/EW 0.95–1.01 (0.97); EL/PL 1.00–1.25 (1.14); PW/HW 1.45–1.62 (1.54); forebody length 5.47–5.82 (5.67).

Medium sized, robust species; body black (Fig. 7F).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.88–2.13 (2.02)); microsculpture of fine transverse waves, in some areas almost meshed; no interocular punctures between anterior frontal punctures (cf. Fig. 6F); antennae brown with antennomeres 1–5 clearly darkened, all antennomeres elongate; palpi brown.

Thorax: pronotum black, slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond level of first puncture of dorsal row; scutellum punctured and pubescent; elytra black, uniformly pubescent, slightly wider than long, roughly as long as—slightly longer than pronotum; legs dark brown to black, tarsi usually lighter pale brown.

Abdomen black, tergites uniformly punctured, with slight iridescence.

Male. Aedeagus (Fig. 13C): paramere lanceolate with

no or very slight medial attenuation, reaching just beyond apex of median lobe, with rather large sensory peg setae forming two long single rows fusing together towards apex; median lobe broad with gentle constriction to a point at apex, on parameral side with two small teeth pointing slightly basad, positioned at level near basal level of peg setae band of paramere; internal sac without a continuation of C-sclerite.

Differential diagnosis. *Quedius subunicolor* is very similar to the species of the *molochinus*-group with dark elytra – *Q. unicolor*, *Q. sundukovi* – and to the dark forms of *Q. molochinus*. It differs from *Q. unicolor* by the microsculpture of head consisting of transverse waves and rarely becoming meshed (clearly meshed frons appearing dull in *Q. unicolor*). Also, genitalia are clearly different in both species, and they have completely non-overlapping distributions. *Quedius subunicolor* can be clearly distinguished from *Q. sundukovi* by the presence of the palisade fringe of tergite VII, which is missing in *Q. sundukovi*. It usually differs from the dark forms of *Q. molochinus* in the darker colored appendages and finer microsculpture. If in doubt the internal sacs are also clearly different in both species: in *Q. subunicolor* C-sclerite lacking an extension, which is present in *Q. molochinus*.

Synonymic notes. KORGE (1961) described *Quedius subunicolor* from Sweden for fully darkened specimens that originally were assigned to *Q. unicolor*, a species which is actually restricted to the central and southern European mountains. Additional records showed that *Q. subunicolor* was rather widespread in Scandinavia (PALM 1962, 1963; ТИХОМИРОВА 1973). Nearly at the same time, KORGE (1962) described *Q. altaicus* based on two females from an unspecified locality in ‘central Altai’. SALNITSKA & SOLODOVNIKOV (2018a) made a thorough morphological comparison between *Q. altaicus* and *Q. subunicolor*, including type material and demonstrated that the external characters claimed by KORGE (1962) as unique for *Q. altaicus* compared with *Q. subunicolor* (microstructure of the head, proportions of the pronotum, chaetotaxy of the head and pronotum) vary continuously between both species. They suspected a synonymy and suggested that molecular comparisons of the two species should be conducted. The results of such an analysis here, that included newly collected material, suggest that specimens from Northern Europe and Altai are identical based on COI barcode (0.6% intraspecific variation among them in one clade; Table 2; Fig. 4). Since there is continuous morphological variation and no clear separation in COI, there is no evidence for separate species. We therefore propose that *Quedius altaicus* Korge, 1962 syn. nov. is placed in synonymy with *Quedius subunicolor* Korge, 1961.

Quedius subunicolor has historically been confused with *Q. unicolor*. Many older specimens from Scandinavia and Northern Russia have been assigned to *Q. unicolor*, although these belong to *Q. subunicolor*. More recently, it has been erroneously reported from the Bohemian Forest in Central Europe, e.g., BOHÁČ & MATĚJČEK (2004).

Bionomics. In Northern Europe *Q. subunicolor* is almost exclusively found in bogs and fens. This is a type of habitat

that historically has often been drained for agriculture and peat gathering, thus the species may be rarer now than it used to be. In the Altai Mountains all hitherto known specimens were collected at the elevations 1200–2000 m. We (AKH and AS) have spent six days in the western Altai mountains in the early summer of 2019 searching for this species. There we sifted many types of debris, but without any luck. It was not until we started turning stones just below the timber line that we found the first specimen. In spite of six days of focused collecting, we encountered only three specimens, all collected from under rocks near streams in forested areas (Fig. 2F). The low number of specimens we encountered is in agreement with the very few numbers of specimens available in museums. The species is likely very rare and patchily distributed across its range. Contrary to the morphological and molecular homogeneity of this species, we see a clear difference in habitat preference between the Scandinavian populations restricted to bogs and Altaian populations confined to the banks of mountain creeks at higher altitudes. Such variation in habitat preference within the distribution range is not unique and is also found in other members of *Quedius* sensu stricto, e.g., *Q. labradorensis*. Presumably, these different habitats provide the same or similar parameters of temperatures and moisture for a species within a wide range.

Distribution. *Quedius subunicolor* currently displays a disjunct distribution between Northern Europe and Altai Mountains, with few specimens known from the Ukhta District in the Komi Region of Russia (SHILOV 1975) and from Lake Baikal listed herein (Fig. 20). It is still unknown if *Q. subunicolor* represents a species continuously distributed from Northern Europe to Altai, or if it is a hitherto unrecorded case of a boreo-montane disjunction between Northern Europe and Siberian mountains. Further sampling should be done in the areas of the apparently large distributional gaps.

Quedius sundukovi Smetana, 2003

(Figs 1, 4, 7, 8F, 13B, 15, 20)

Quedius sundukovi Smetana 2003: 189–193 [Type locality: Badshalskiy Khrebet mountains]

References. SMETANA & SHAVRIN (2018): 834 (distribution); SALNITSKA & SOLODOVNIKOV (2018a): 130–131 (distribution); (2019): 50 (characters and distribution).

Material examined. KAZAKHSTAN: SW Altai, East of Narymskij Mt. Ridge, upper course of Ozernaja River, 49.0478, 85.1614, 1900–2300 m, supalpine zone, 18.VII.1997, leg. R.Yu. Dudko & V.K. Zinchenko (ZIN). RUSSIA: JEWISH AUTONOMOUS REG.: Kuldur vill., 49.1854, 131.6171, pitfall trap, stream, 480m, 14.–15.VII.2017, leg. A. Bergmann (1 ♂ cSch). EAST YAKUTIA: Suntar-Khayata Mts, Valley of Tyry river valley, Kidyarki river near Khalya, [62.35, 138.46], 800–950 m, 14.–19.VIII.1991, leg. Alexeev (NHMD). KHABAROVSK TERR.: Badshalskiy chr., Omot lake, [50.54, 134.26], tundra, 1850–2050 m, 7.–19.VII.1997, leg. A. Plutenko (2 ♂♂ 2 ♀♀ cSch); Levaja Bureya riv., estuary Don riv., [51.68, 134.51], 24.–25.VII.2006, leg. U. Valainis (ZIN); Levaja Bureya riv., the left bank of the Imganakh river near the mouth, 51.7355, 134.572, 650–670 m, sloppy rocky hills with burrow pits, litter and mosses of *Picea ajanensis*, *Abies nephrolepis*, *Larix gmelinii*, *Rhododendron dauricum*, *Betula platyphylla*, *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Dicranum* sp., *Polytrichum* sp., *Sphagnum girgensohnii*, *Sph.* sp., 26.VI.2011, leg. A.B. Ryvkin (ZIN); Verkhnobureinsky natural park, Ust-

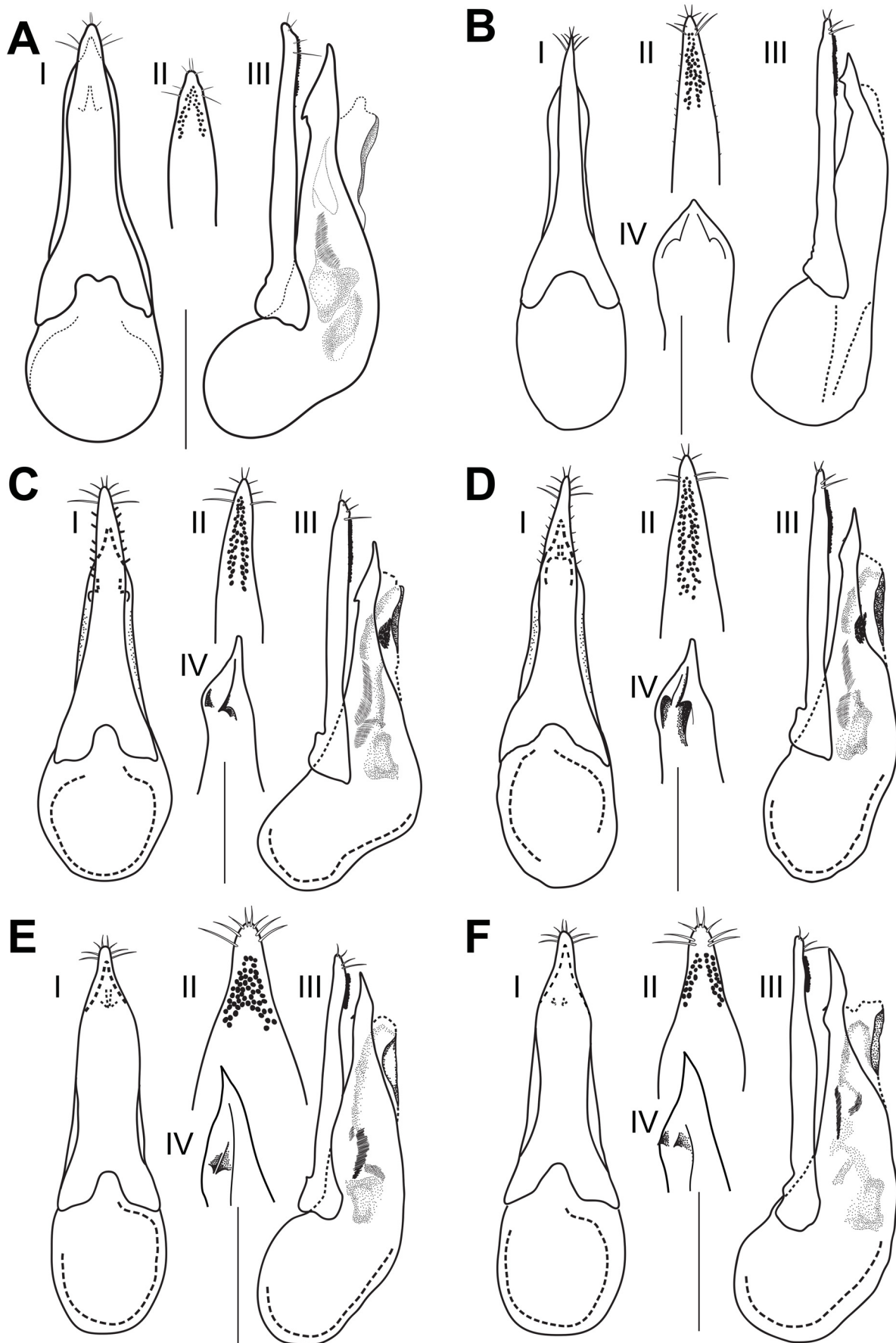


Fig. 14. Aedeagus of *Quedius* s. str. A – *Q. unicolor* Kiesenwetter, 1847; B – *Q. levasseuri* Coiffait, 1964 (syn. of *Q. pallipes* Lucas, 1846); C – *Q. hispanicus* Bernhauer, 1898; D – *Q. pallipes* Lucas, 1846; E – *Q. laticollis* (Gravenhorst, 1802); F – *Q. strenuus* Casey, 1915. I – Parameral view of whole aedeagus, II – apices of paramere in antiparameral view with peg setae, III – lateral view of whole aedeagus, IV – apices of median lobe at an angle between parameral and lateral view.

-Urgal project gauging station Ust-Niman Topolevnik, 51.3995, 132.733, 1.IX.2009, leg. L.A. Trilikauskas (NHMD); Verkhnebureinsky natural park, Ust-Urgal project gauging station Ust-Niman Topolevnik, 51.3995, 132.733, 315 m, *Padus, Alnus, Salix, Picea, Plagiomium*, 4.VIII.2009, leg. A.B. Ryvkin (ZIN). **SAKHALIN ISLAND:** 13 km N from Korsakov, 2 km N from Solovyovka, [46.74, 142.73], *Acer, Betula*, 5.VIII.1992, leg. V. Gusarov, (CNC); 13 km N from Korsakov, 2 km N from Solovyovka, [46.74, 142.73], *Abies, Larix, Ledum, Betula*, 6.VIII.1992, leg. V. Gusarov (CNC). **ZABAYKALSKY KRAI:** Stanovoy Highlands, W part of Kodar, top Chara River, 50 km WSW River Novaya Chara, [56.65, 117.54], 1700–2000 m, 27.VII.1995, leg. A. & R. Dudko, D. Lomakin (ZIN); Stanovoy Highlands, top Chara River, Lake Leprindo, 56.636, 117.537, 1000 m, 23.VII.1995, leg. A. & R. Dudko, D. Lomakin (ZIN).

Redescription. Measurements ♂♂ (n = 5): HW = 1.40–1.69 (1.53); HL = 1.22–1.40 (1.29); HL/HW 0.79–0.89 (0.85); PW = 1.82–2.22 (2.00); PL = 1.71–2.07 (1.81); PL/PW 0.80–0.96 (0.91); EW = 1.80–2.09 (1.88); EL = 1.44–1.71 (1.60); EL/EW 0.80–0.89 (0.85); EL/PL 0.83–0.95 (0.89); PW/HW 1.46–1.67 (1.55); forebody length 4.38–5.18 (4.70). ♀♀ (n = 5): HW = 1.58–1.73 (1.67); HL = 1.33–1.42 (1.38); HL/HW 0.78–0.87 (0.83); PW = 1.93–2.24 (2.04); PL = 1.80–2.11 (1.88); PL/PW 0.90–0.94 (0.92); EW = 1.89–2.09 (1.96); EL = 1.69–1.78 (1.72); EL/EW 0.83–0.91 (0.88); EL/PL 0.82–0.96 (0.92); PW/HW 1.39–1.58 (1.48); forebody length 4.82–5.27 (4.99).

Small sized species; body dark brown to black (Fig. 8F).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.73–2.00 (1.83)); microsculpture of fine transverse waves; no additional punctures between anterior frontal punctures (cf. Fig. 6F); antennae dark internally becoming continuously lighter, all antennomeres slightly elongate; palpi pale with apical palpomere slightly darkened.

Thorax: pronotum black, wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond level of first puncture of dorsal row; scutellum sparsely punctured and pubescent; elytra most often fully darkened but occasional

dark reddish brown, short uniformly pubescent, clearly shortened wider than long, clearly shorter than pronotum; legs dark with tarsi lighter.

Abdomen black, tergites sparsely and uniformly punctured, without palisade fringe of tergite 7, without clear iridescence.

Male. Aedeagus (Fig. 13B): paramere lanceolate with slight medial attenuation and extending into a slight expansion broadest below apex, apex slightly asymmetric, reaching just beyond apex of median lobe, with sensory peg setae forming two long rows fusing together towards apex (Fig. 15); median lobe broad with gentle constriction to a point at apex, on parameral side with two small teeth pointing slightly basad, positioned at level near basal level of peg setae band of paramere; internal sac without a continuation of C-sclerite.

Differential diagnosis. *Quedius sundukovi* is most similar to *Q. unicolor*, *Q. subunicolor*, and *Q. molochinus*. It can easily be distinguished from all these species by its smaller size and brachypterous habitus with shortened elytra and absent palisade fringe on tergite VII. If in doubt, the aedeagus can be checked for characters listed in the diagnosis. It is also similar to Siberian species *Q. (Raphirus) jennisensis* Sahlberg, 1880, from which it is easily distinguished by the entire labrum (medially incisioned in *Q. jennisensis*).

Comments. *Quedius sundukovi* was described by SMETANA (2003) based on 13 specimens from the Badshalskiy Khrebet mountains in Khabarovsk Krai in the Far East of Russia. SMETANA & SHAVRIN (2018) reported additional specimens from Vitimskiy Nature Reserve and the Udokan Plateau extending the species range significantly westwards in Russia to Transbaikalia. SALNITSKA & SOLODOVNIKOV (2018a) reported a number of records of this species from the Altai Mountains in Kazakhstan. SALNITSKA & SOLODOVNIKOV (2019) reported the occurrence of this species in Buryat Republic in Transbaikalia and in the Russian Far East regions of Amur Oblast and Sakhalin Island (Fig. 20). Here we add detailed information on many of these

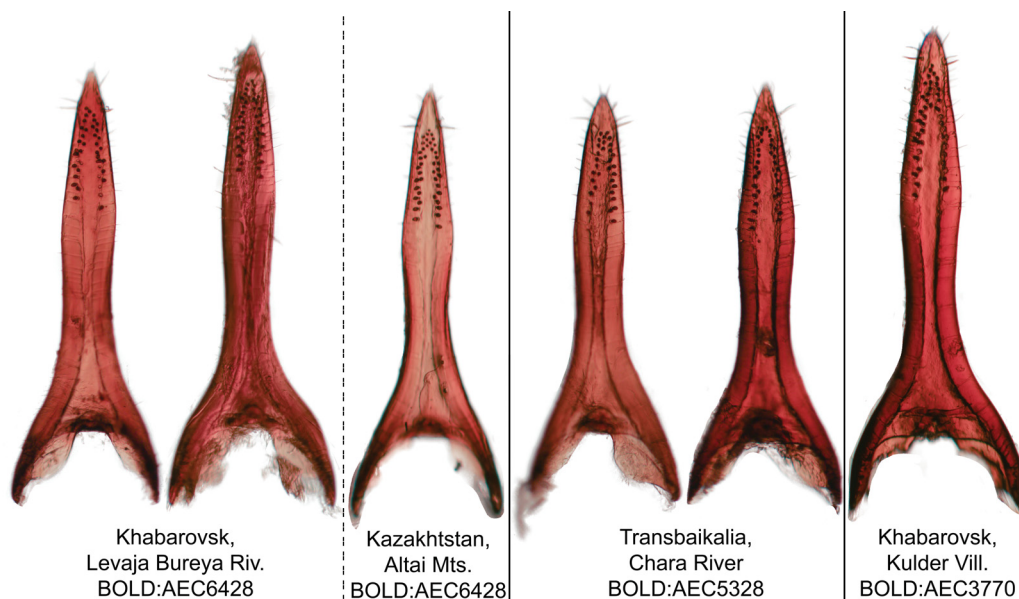


Fig. 15. Variation of the shape of the paramere of *Quedius sundukovi* Smetana, 2003. Locality and BOLD BIN number are indicated under respective specimens.

records along with COI barcodes from specimens across the range (Fig. 4). The barcodes showed high variation as we recovered five OTUs (four BINs) with as high as 7.7% divergence between the OTUs (Table 2). Morphological studies of the specimens also revealed some variation in size – but not in the shape – of the paramere (Fig. 15). We found no differences to correspond to any of the molecular clusters, which also did not cluster geographically. Lack of a clear congruence between the molecular and morphological variation, as well as no hiatus between different morphological variants, suggests that they all represent a single species. The species is known across a large area with complex montane orography and it is flightless, with the palisade fringe of abdominal segment VII absent and clearly shortened elytra. Apparently, the high degree of the intraspecific variation can be related to the flightlessness of the species leading to low dispersal abilities of members of different populations and accelerated rates of divergence in the barcode region (MITTERBOECK & ADAMOWICZ 2013).

Bionomics. Little is known about the specific habitat requirement of *Q. sundukovi*. Based on the examined material, the species appear to occur in various leaf litter, both coniferous and deciduous, and is commonly associated with talus debris and moss, often near streams or rivers. Specimens are found within a wide range of elevations from 315 to 2300 m, at higher elevation at lower latitudes.

Distribution. *Quedius sundukovi* is currently known from relatively few specimens scattered across a large range comprising the Altai Mountains, Transbaikalia, Bureya and the Suntar-Khayata Range (Fig. 20). It is also found on Sakhalin Island. Although currently known from only a few localities, the species distribution is most likely continuous. The range maybe poorly known because it spans through an area with very little recent and historical entomological activity, especially for leaf-litter dwelling organisms.

Quedius unicolor Kiesenwetter, 1847

(Figs 1, 2G, 4, 7E, 14A, 21)

Quedius unicolor Kiesenwetter in KIESENWETTER & MÄRKEL (1847: 75).
[Type locality: Riesengebirge]

References. KIESENWETTER (1848): 53 (characters); REDTENBACHER (1849): 825, (1857): 202, (1874): 199 (characters); FAIRMAIRE & LABOULBÈNE (1856): 536 (characters); FAUVEL (1874): 291 (characters); MULSANT & REY (1876): 697 (characters); GANGLBAUER (1895): 403 (characters); PORTA (1907): 132 (characters); REITTER (1909): 112 (characters); GRIDELLI (1924): 80 (characters); PORTEVIN (1929): 341 (characters); WÜSTHOFF (1938): fig. 24 (characters); SMETANA (1955): 143, (1960a): 259, (1964): 168, (1966): 331, (1993): 50 (distribution); (1958): 363 (characters and biology); (1962a): 134 (characters); COIFFAIT (1961): 49, (1978): 193 (characters); LOHSE (1964): 211 (characters); HAVELKA (1964): 93 (distribution); HORION (1965): 274 (distribution); BORDONI (1976a): 94 (characters); ZERCHE (1977): 9 (distribution); TÓTH (1984): 119 (characters); LUCHT (1987): 109 (distribution); JANÁK (1992): 91 (distribution); HERMAN (2001): 50 (application to ICZN); TRONQUET (2006): 102 (distribution); MAZUR et al. (2007): 30 (distribution); MATELESHKO (2007): 184 (distribution); SCHATZ (2008): 388 (distribution); ZANETTI (2015): 96 (distribution).

Material examined. AUSTRIA: Golling, [47.59, 13.16], leg. Skalitzky (1 ♀ NMW); Kerschbaumeralm, [46.75, 12.76], 24.VII.-7.VIII.1948, leg. F. Schubert (1 ♀ NMW); Koralpe, [46.88, 14.99], leg. A. Otto (3 ♂♂ NMW); Lünensee, [47.05, 9.74], 14.VI.-3.VII.1952, leg. F. Schubert (1 ♀ NMW); Stuhleck, [47.56, 15.78], leg. Breit (1 ♀ NHMD); Stuhleck, Steiermark, [47.56, 15.78], leg. Wingelmüller (1 ♀ NMW); Tirol, [47.22,

11.51] (1 SDEI); Wechsel, [47.52, 15.91], leg. Scheerpeltz (3 ♀♀ NMW); Wolayersee, [46.61, 12.86], 3.-11.VIII.1949, leg. F. Schubert (2 ♂♂ 1 ♀ NHMD); Zillertal nr. Mayrhofen, [47.16, 11.87], 4.VIII.1914, leg. H. Wagner (1 SDEI); Wolayersee, [46.61, 12.86], 3.11.VIII.1949, leg. F. Schubert (2 ♀♀ NMW). CZECH REPUBLIC: Krkonoše [50.71, 15.66], leg. Obenberger (1 ♂ 2 ♀♀ NHMD); Spindelmühle [Špindlerův Mlýn], [50.73, 15.61], leg. Skalitzky (1 NHMD). GERMANY: Harz, Brocken, [51.79, 10.61], 9.V.1922, leg. Uhmann (1 ♂ SDEI); Hercyn mont. [Harz Mountains], [51.74, 10.63], 14.VI.1914, leg. Beckenkamp (3 ♀♀ SDEI); Thüringer Wald Oberhof, [50.71, 10.73], 8.IX.1951, leg. W. Liebmann (1 ♀ SDEI). ITALY: Gressory [Gressoney] la Trinite, [45.87, 7.82], 15.VII.1901, leg. Künnemann (1 SDEI); Malga Preghena Alta, Trento, 46.4148, 10.8922, 2100 m, under stones along stream with moss, 26.VIII.2019, leg. A. Zanetti (NHMD); Valle Brembana, Strada di Porcile, [46.06, 9.73], 1800-2000 m, 26.VI.1961, leg. V. Rosa (1 ♂ NMW). POLAND: Silesia [Bad] Flinsberg [Świeradów-Zdrój], [50.92, 15.31], leg. Kraatz (1 SDEI). SPAIN: Cantabria, Alto Campoo, W Reinosa, [43.03, -4.37], 4.VI.1991 2000m leg. Zerche (1 SDEI). SLOVAKIA: Ružomberok, [49.04, 19.23], VII.1952, leg. Přivora (1 ♂ NHMD); High Tatras, Mengušovská dolina, Vysoké Tatry, [49.16, 20.07], 1200 m, 17.V.1991, leg. J. Frisch (1 ♂ ZMHB); Tatra, Kráľova hoľa, [48.88, 20.13], 1300-1600 m, 12.VIII.1981, leg. Hieke (1 ♂ ZMHB). SWITZERLAND: Aarau, [47.38, 8.05], leg. Stierlin (1 SDEI).

Redescription. Measurements ♂♂ (n = 5): HW = 1.47–1.76 (1.58); HL = 1.31–1.44 (1.36); HL/HW 0.82–0.91 (0.86); PW = 1.96–2.33 (2.16); PL = 1.78–2.02 (1.91); PL/PW 0.86–0.92 (0.89); EW = 2.13–2.47 (2.32); EL = 2.18–2.47 (2.32); EL/EW 0.95–1.05 (1.00); EL/PL 1.15–1.26 (1.22); PW/HW 1.47–1.65 (1.58); forebody length 5.36–5.93 (5.58). ♀♀ (n = 5): HW = 1.58–1.67 (1.61); HL = 1.31–1.42 (1.37); HL/HW 0.79–0.89 (0.85); PW = 2.00–2.18 (2.08); PL = 1.82–1.89 (1.87); PL/PW 0.87–0.92 (0.90); EW = 2.22–2.40 (2.31); EL = 2.20–2.40 (2.31); EL/EW 0.96–1.01 (0.99); EL/PL 1.19–1.27 (1.23); PW/HW 1.45–1.57 (1.52); forebody length 5.36–5.69 (5.52).

Medium sized species; body black (Fig. 7E).

Head black, distinctly transverse, with eyes rather small (EyL/TL = 1.59–2.00 (1.82)); microsculpture of fine mesh, especially on frons, appears dull; no interocular punctures between anterior frontal punctures (cf. Fig. 6F); antennae dark brown to black, all antennomeres slightly elongate; palpi dark brown to black.

Thorax: pronotum black, slightly wider than long, clearly wider than head, with microsculpture of fine transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond first puncture of dorsal row; scutellum punctured and pubescent; elytra black, uniformly pubescent, as long as wide, clearly longer than pronotum; legs dark, outer face of tibia and tarsi often paler.

Abdomen black, tergites uniformly punctured, without clear iridescence.

Male. Aedeagus (Fig. 14A): paramere lanceolate with slight medial attenuation and extending into a slight expansion broadest below apex, apex extending into small blunt knob away from the median lobe, apex slightly asymmetric, reaching just beyond apex of median lobe, with sensory peg setae forming two rows fusing together towards apex; median lobe broad with gentle constriction to a point at apex, on parameral side with two small ridges continuing basad, positioned at level near basal level of peg setae band of the paramere; internal sac without C-sclerite.

Differential diagnosis. *Quedius unicolor* is very similar to other species with dark elytra from the *molochinus*-group – *Q. subunicolor*, *Q. sundukovi* and the dark form of *Q. molochinus*. It can be distinguished from *Q. subunicolor* by the dull frons due to meshed microsculpture (in *Q. subunicolor* the microsculpture consists of fine transverse waves or only slightly meshed). Also, the genitalia and the distributions are clearly different in the two species. It usually differs from the dark form of *Q. molochinus* in the darker appendages and the finer microsculpture in addition to a clearly different aedagus, which is without a C-sclerite in *Q. unicolor*, but with such in *Q. molochinus*. *Quedius unicolor* has non-overlapping distribution with *Quedius sundukovi* and can be clearly distinguished from the latter species by the presence of palisade fringe on tergite VII.

Quedius unicolor has historically been confused with *Q. subunicolor*. For details see comments about the latter species.

Comments. *Quedius unicolor* was originally described from Riesengebirge [Krkonosé] (KIESENWETTER & MÄRKEL 1847), a mountain range at the border between Poland and Czech Republic. It was later discovered in other mountainous area, including the Alps, the Carpathians, the Pyrenees, Picos de Europa, the Harz Mountains, and possibly extending into Sierra Nevada and even central Anatolia, although the latter records are not confirmed here (COIFFAIT 1961, ABACIGIL et. al 2009; Fig. 21). At these sites it seems to be restricted to a very specific habitat type, with most specimens being found under stones and in moss near mountain streams at higher elevations. COI barcodes of specimens from several sites, including the Austrian and Italian Alps, the Carpathians of Slovakia, and Picos de Europa in Spain displayed high genetic variability (Fig. 4), with the sites being grouped into three OTUs (the Carpathians, Picos de Europa, and the Alps) ranging from 3.5 % to 4.5 % divergence, with a 0.2% divergence between the Austrian and Italian Alps (Table 2). With such a high genetic divergence in the barcode region, we carefully checked for morphological differences. However, we found no obvious differences corresponding to the molecular clusters. Since the wings seem to be fully developed in this species, these genetic differences may be attributed to isolation by distance, the very specific habitat requirements of the species and its close association to a now fragmented habitat, which would limit gene flow among populations.

Bionomics. *Quedius unicolor* seems to be very habitat selective and is only found in alpine sites in sphagnum moss and under rocks near bogs, swamps and creeks (Fig. 2G). It is found at altitudes between 900 and 2300 m depending on the latitude of the locality, with higher elevations at more southern sites.

Distribution. *Quedius unicolor* is restricted to the montane and subalpine zone of Central and southern Europe (Fig. 21). Specifically, it is known from sites in the Carpathians, the Alps, the Pyrenees, Picos de Europa, the Sudetes, the Harz and the Ore mountain ranges. Due to its very specific habitat requirement, it may be under-collected and may actually be present in mountains further south. COIFFAIT

(1961) reported it from Sierra Nevada in Southern Spain, but this record may be in fact a misidentified *Q. hispanicus*. Another doubtful record of *Q. unicolor* comes from Koçere Stream in the Kazdağları Mountain of the North-western Anatolia by ABACIGIL et. al (2009), which is a location remote from the main range of this species.

Quedius vicinus (Ménétriés, 1832)

(Figs 1, 4, 8A, 13A, 20)

Staphylinus vicinus Ménétriés, 1832: 144 [Type locality: Lenkoran]

Quedius libanicus Coiffait, 1954: 160 [Type locality: Liban: grotte de Birket Aanjar]

References. FALDERMANN (1835): 129 (characters); HOCHHUTH (1862): 44 (distribution); COIFFAIT (1955): 427 (biology); (1961): 55, (1978): 195 (characters); JARRIGE (1971): 497 (distribution); KORGE (1971): 11 (characters); BOHÁČ (1988): 554 (characters); GUSAROV (1993): 73 (lectotype designation, synonymic notes); ASSING & WUNDERLE (2001): 37 (distribution); SALNITSKA & SOLODOVNIKOV (2018a): 131 (distribution); (2019): 51 (characters and distribution).

Type material examined. *Quedius vicinus*: LECTOTYPE ♀ [torso without head and thorax] (ZIN), designated by GUSAROV (1993) [not examined], labelled: “[golden square] / Lenkoran. / vicinus Menet. Lenkor.” (GUSAROV 1993).

Additional material examined. AFGHANISTAN: Obéh, [34.35, 63.23], 1680 m (1 ♂ NMW). CYPRUS: Episcopo, Limasol, [34.67, 32.88], 12.IV.1995, leg. Schmid (3 ♂♂ 5 ♀♀ NMW); Larnaca, [34.89, 33.63], salt lake, 10 m, 20.IV.1995, leg. W. Suppatschitsch (1 ♂ NMW). GEORGIA: Kumisi nr. Tbilisi, [41.61, 44.78], 20.VI.1988, leg. Wrase (1 ♂ cSch). IRAN: Darab to Estahban Rd., 20km NW Darab, 28.8525, 54.4093, 1300m, 16.IV.2006, leg. Serri & Frisch (1 ♀ SDEI); Sonqor, Kermanshah, [34.78, 47.59], 1800 m, 7.VII.1969, leg. Heinz (1 ♂ ZMHB); SE Sepidan, W Dalkhan, 30.2911, 52.0951, 2100m, 9.V.2007, leg. Frisch & Serri (2 ♂♂ SDEI). ISRAEL: Hazerim, [31.24, 34.71], 8.X.1988, leg. E. Orbach (1 ♂ NHMD); Kfar Ha Horesh, n. Nazareth, [32.70, 35.27], 500 m, 8.IV.1997, leg. Heinz (1 ♀ ZMHB) Lower Galilee, ca. 4 km W Tamra, 32.8633, 35.1715, loamy field edge, 25m 25.IV.2006 leg. D.W. Wrase (1 ♂ cSch); Wadi Musrara [Ayalon River], Petah Tiqwa, [32.09, 34.80], 5.XI.1932 (3 ♂♂ NMW). JORDAN: Wádi, Hisbán, NW Ma' dabá, 31.8286, 35.7945, 681 m, brook, slopes and field edges, under stones, 1.IV.2016, leg. Wrase & Laser (1 ♂ cSch). LEBANON: Beirut, [33.88, 35.50], leg. Kindern (1 ♀ SDEI). SYRIA: Zabadani, [33.72, 36.09], 15.IV.1978, leg. Heinz (1 ♀ ZMHB); Zainie, 45 km NE of Latakia, [35.78, 36.19], 4.V.1982, leg. M. Dvořák (1 ♀ MCZ). TURKEY: Antalya, Aksu, [36.88, 30.92], 13.IV.1977, leg. Korell (1 ♂ 1 ♀ ZMHB), Antalya, Alara Han, [36.69, 31.72], 300m, 1997, leg. H. Winkelmann (1 ♀ cSch); Antalya, 26 km W Alanya, nr. Incecum, [36.63, 31.74], 16.IV.-2.V.1954 leg. V. Brachat (1 ♂ cSch); Catalan, Adana, [37.20, 35.29], 18.IV.1985, leg. Barries (1 ♀ NMW); Karaman Stream, Antalya, [36.86, 30.61], IV.1962, leg. Schweiger (1 ♂ ZMHB); Mardin, [37.29, 40.72], 1300 m, 10.-15.V.1969, leg. Schubert (1 ♂ NMW); Muratpaşa, 20 km E Kirikhan, [36.47, 36.45], 20 m, 16.IV.1989, leg. Heinz (1 ♂ 1 ♀ ZMHB); E Pamucak, Selcuk, [37.96, 27.27], swamp, 28.III.1986, leg. Heinz (1 ♂ 1 ♀ ZMHB). TURKMENISTAN: Kopet Dag, 6 km NE Tschulni n. Firjuza, [37.98, 58.02], 18.IX.1976, leg. Hieke (5 ♂♂ ZMHB).

Redescription. Measurements ♂♂ (n = 5): HW = 1.64–1.80 (1.72); HL = 1.40–1.53 (1.48); HL/HW 0.83–0.87 (0.86); PW = 2.16–2.44 (2.30); PL = 2.02–2.20 (2.11); PL/PW 0.89–0.94 (0.92); EW = 2.20–2.47 (2.33); EL = 2.07–2.24 (2.16); EL/EW 0.91–0.94 (0.93); EL/PL 0.99–1.04 (1.02); PW/HW 1.52–1.60 (1.56); forebody length 5.49–5.96 (5.74). ♀♀ (n = 5): HW = 1.69–1.73 (1.72); HL = 1.38–1.49 (1.45); HL/HW 0.79–0.87 (0.84); PW = 2.22–2.42 (2.32); PL = 2.04–2.22 (2.12); PL/PW 0.91–0.92 (0.92); EW = 2.38–2.47 (2.44); EL = 2.18–2.36 (2.26); EL/EW 0.92–0.95 (0.93); EL/PL 1.01–1.11 (1.07); PW/

HW 1.52–1.66 (1.60); forebody length 5.73–6.07 (5.84).

Medium sized to large, robust species; body light to dark brown (Fig. 8A).

Head dark, distinctly transverse, with eyes rather small (EyL/TL = 1.45–1.82 (1.60)); microsculpture of transverse waves; no interocular punctures between anterior frontal punctures (cf. Fig. 6F); antennae and palpi pale yellowish-brown with base of antennomeres 1–3 clearly pale, all antennomeres clearly elongate.

Thorax: pronotum slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond first puncture of dorsal row; scutellum punctured and pubescent; elytra orange to yellowish-brown, uniformly pubescent, slightly wider than long, roughly of same length as pronotum; legs pale yellowish-brown with inner face of tibia and femur darkened.

Abdomen: tergites uniformly punctured, with slight iridescence.

Male. Aedeagus (Fig. 13A): paramere rather slender, with a slight apical expansion and extending into a blunt hook oriented away from median lobe, reaching just beyond apex of median lobe, with sensory peg setae forming two short broad rows fusing together towards apex; median lobe broadly constricting to a point at apex, on parameral side folded into two teeth almost meeting at middle, positioned at level near basal end of peg setae rows of paramere; internal sac without C-sclerite.

Differential diagnosis. *Quedius vicinus* stands out as a rather pale member of the *Q. molochinus*-group and is thus clearly recognizable from *Q. subunicolor*, *Q. unicolor*, *Q. sundukovi* and *Q. balticus*, in particular by having pale antennomeres 1–3. It is very similar to *Q. molochinus* and *Q. meridiocarpaticus*, but it is often paler than these, with elytra and appendages yellowish red compared to brownish red, and abdomen brown compared to dark brown. For confident identification genitalia should be checked as some individuals of *Q. molochinus* and *Q. meridiocarpaticus* can have similar external appearance. The aedeagus of *Q. vicinus* is distinguished from *Q. molochinus* and *Q. meridiocarpaticus* by the absence of a C-sclerite in the internal sac, and by the paramere with blunt apical hook oriented away from the median lobe (best seen in lateral view). *Quedius vicinus* is recognized from some similarly looking sympatric members of the subgenera *Microsaurus* and *Raphirus*, such as *Q. suramensis* – with which it has long been confused (see comments) – by the entire labrum and clearly parallel-sided abdomen.

Synonymic notes. GUSAROV (1993) designated a lectotype for *Q. vicinus* and clarified the identity of the species. Also he examined the female holotype of *Q. libanicus* Coiffait, 1954 described from ‘Lenkoran’ in Azerbaijan (see BOHÁČ (1988) for details about this locality) and synonymized it with *Q. vicinus*. Our data fully corroborate the synonymy of *Q. vicinus* and *Q. libanicus*.

The identity of *Q. vicinus* was confused for a long time since HOCHHUTH (1849) misidentified *Q. vicinus* as *Q. (Raphirus) suramensis* Eppelsheim, 1880. This led to

confusion of the two species from different subgenera of *Quedius*, clarified by GUSAROV (1993). Both species still remain confused in many collections although they are easily distinguished (see Differential diagnosis).

Bionomics. *Quedius vicinus* is mainly found near bodies of water like streams, rivers, lakes, etc., where it is collected in litter and under rocks. In an arid region, this maybe the only suitable microhabitats. It has also been found in caves (COIFFAIT 1955, as *Q. libanicus*), although this is most likely accidental, as nothing suggests that it is connected to these.

Distribution. *Quedius vicinus* is found from central southern Anatolia across eastern Transcaucasia and most of the northern part of the Middle East into southern Central Asia (Fig. 20). It extends into the Levant region including the island of Cyprus, but does not go into the Nile delta. It is unclear to what extent it occurs in Transcaucasia, where it may only penetrate into the eastern valleys along the west Caspian Sea coast. The species continues into Iran and Afghanistan, as well as to Middle Asia where it is only known from one locality in Kazakhstan (SALNITSKA & SOLODOVNIKOV 2018a).

Quedius pallipes-group

Diagnosis. Medium sized species with mostly brown, light brown to reddish elytra and appendages, rarely with darkened elytra. Eyes small, temples large, distance between temporal puncture and posterior margin of eye equals the diameter of the puncture; frons without additional setiferous punctures (Fig. 6F). Scutellum punctate and pubescent. Pronotum with punctures in posterior part of sublateral row. Palearctic origin.

Quedius hispanicus Bernhauer, 1898

(Figs 1, 2D, 3, 9A,B, 14C, 19)

Quedius hispanicus Bernhauer, 1898: 341 [Type locality: Cartagena und Cadix in Spanien] **stat. rev.**

Quedius cobosi Coiffait, 1964: 293 [Type locality: Espagne: Province de Almeria, Seron], **syn. nov.**

Quedius hammianus Sharp, 1911: 57 [Type locality: Anglia: Deal, Strood, Lymington, and Hayling Island], **syn. rev.**

Quedius rufulus Blümml, 1898: 216 [Type locality: Spanien, Granada], **syn. rev.**

Quedius secundus Last, 1952 [Type locality: Studland, Dorset; Mudeford, Hampshire; Chichester], **syn. rev.**

References. FAUVEL (1865): 16 (synonym of *Q. molochinus*); KRAATZ (1867): 414 (synonym of *Q. molochinus*); GANGLBAUER (1895): 403 (synonym of *Q. molochinus*); BERNHAUER (1900): 46 (distribution); PORTA (1907): 129 (synonym of *Q. molochinus*); GRIDELLI (1924): 81 (subspecies of *Q. molochinus*; characters); SCHEERPELTZ (1933): 1457 (synonym of *Q. picipennis*); MÉQUIGNON (1937): 3 (as *Q. molochinus pallipes*); KORGE (1960b): 69 (synonym of *Q. pallipes*); COIFFAIT (1961): 56 (characters and distribution); (1978): 196 (characters); HANSEN (1962): 319 (characters and distribution); SMETANA (1962a): 134 (characters); (1963): 39; (1970): 61 (distribution); LAST (1963): 45 (synonym of *Q. simplicifrons*); LOHSE (1964): 211 (characters and distribution); HORIZON (1965): 276 (distribution); BORDONI (1976a): 100 (synonym of *Q. pallipes*); POPE (1977): 31 (distribution); LUCHT (1987): 109 (distribution); LOHSE & LUCHT (1989): 172 (distribution); ISRAELSON (1990): 3 (distribution); BORGES (1990): Table II (distribution); WELCH (1993): 229 (ovariole number and ovary structure); OUTERELO et al. (1995): 80 (distribution; as *Q. pallipes*).

Type material examined. *Quedius cobosi*: PARATYPE: ♂ (MNHN), labelled: "PARATYPE [red label] / *Quedius cobosi* Coiff. H. COIFFAIT det. 1964 / Laujar Almeria -España A. Cobos coll."

Additional material examined. DENMARK: Lakolk, [55.14, 8.49], debris on beach, 1.XI.2013, leg. J. Pedersen & A. Brunke (1 ♂ NHMD); Skallingen, [55.50, 8.25], 17.X.1959, leg. F. Bangsholt (2 ♂♂ NHMD). GERMANY: Archsum, [Sylt], [54.87, 8.39], IX.1901 (1 SDEI); Insel Borkum, [53.58, 6.66], 12.VIII.1937, leg. Struse (2 ♀♀ 4 ♂♂ NMW); N Dagebüll, Nordfriesland, 54.7361, 8.7094, salt pasture among stones and clay on dam, 25.VIII.2017, leg. Wrase & Laser (1 ♂ cSch); Memmert, Juist, [53.64, 6.88], 13.VIII.1917, leg. Alfrum (1 SDEI). FRANCE: Bordeaux, St. Louis, [44.94, -0.52], 22.II.1964 leg. C. Jeanne (1 ♂ cBor); Camargue, Etang du Fangassier, [43.42, 4.63], 20.V.1994 salt marsh, leg. Schülke & Grünberg (1 ♂ cSch); Sainte Marie la Mer, [42.72, 3.03], 28.IV.1955, leg. J.T. Skovgaard (1 ♀ NHMD). PORTUGAL: Lissabon, [38.76, -8.87], leg. Von Heyden (1 ♂ 2 ♀♀ SDEI); Lusitania, Lissabon, [38.76, -8.87], IV.-V.1910, leg. A. Scharzmayr (1 ♂ 1 ♀ SDEI). AZORES: Faial. Baia da Areia das Fontes 1 km N of Praia do Norte, [38.61, -28.74], under stones, grassy ground, near rocky shore, 2.IV.1957, leg. Brinck and Dahl (5 ♀♀ MZLU); Faial, Caldeira, [38.58, -28.71], 10.IV.1957. leg. Brinck and Dahl (3 ♀♀ MZLU); Faial, Horta, Porto Pim., [38.52, -28.62], sandy ground, 7.IV.1957 leg. Brinck and Dahl (1 ♀ MZLU); Faial. Nasce Agua 3 km S of Cedros, [38.60, -28.68], ravine, under stones, 5.IV.1957, leg. Brinck and Dahl (1 ♂ MZLU); Faial, Praia do Almocharife, [38.55, -28.61], sandy grassy ground, under stones, 31.III.1957. leg. Brinck and Dahl (1 ♀ MZLU); São Miguel, Atlalhada, [37.74, -25.58], natural forest, 4.IX.1999, leg. H. Enghoff (2 ♀♀ NHMD). MADEIRA: Campanario, Fontes, [32.69, -17.01], 1200-1400m, 16.IX.2014, leg. Kleeberg (1 ♂ cSch); Funchal, [32.67, -16.91], 0-500 m, II.1966, leg. Palm (2 ♂♂ 3 ♀♀ MZLU); Pico do Castelo, [33.08, -16.33], 17.19.V.1977, leg. Palm (2 ♂♂ MZLU); Terreiro da Luta, [32.68, -16.91], 850 m, stream, 20.IV.1957, leg. Brinck and Dahl (1 ♂ MZLU). SPAIN: Alicante; Orihuela, [38.08, -0.94], 20.IV.1997, leg. Lauffer (2 MNCN); Altea, Rio Algar, Alicante, [38.61, -0.05], 27.II.1999, leg. Wrase (1 ♂ cSch); Aranjuez, Madrid, [40.02, -3.59], 520 m 3.-4.V.1988, leg. Feller (3 ♀♀ cSch); Arroyo de Journadiel, S Brozas, Cáceres, [39.56, -6.81], 325 m, 20.VI.1991, leg. Wrase (1 ♂ cSch); Ávila, Avila, [40.65, -4.68], leg. Sanz (3 MNCN); Badajoz: Aljucen, [39.04, -6.33], leg. Pacheco (1 MNCN); Boadilla del Monte, NW Madrid, [40.41, -3.88], 6.VII.1996, leg. D.Wrase (1 ♂ cSch); Cabo de Gata, SE Almeria, 36.7908, -2.2513, coastal area, 5.IV.2012, leg. T. Wolsch (1 ♀ cSch); Caboalles [de Abajo], [42.95, -6.37], leg. Paganetti (1 ♀ SDEI); Cádiz, [36.53, -6.22], 16.I.1894, leg. Navarro (2 MNCN); Cádiz, Algeciras, [36.16, -5.43], leg. Arias (1 MNCN); Cádiz, Vega del Barbate, Vejer de la Frontera, [36.25, -5.95], leg. De Quirós (1 MNCN); Cornudilla, [42.68, -3.42], 13.IX.1962, leg. J.T. Skovgaard (1 ♂ 1 ♀ NHMD); Cuenca, Uclés, [39.98, -2.86] (2 MNCN); Guipúzcoa, Arechavaleta, [43.03, -2.51], leg. Antoniol (1 MNCN); Guipuzcoa, Irun, Jaizubia, [43.34, -1.82], 10.V.2006, leg. Anichtchenko (1 ♂ 1 ♀ NHMD); Huelva, Cala, [37.97, -6.31], leg. C. Bolívar (1 MNCN); Jáen Mengibar, Rio Guadalquivir, [37.98, -3.79], 330m, 16.VI.1991, leg. Wrase (1 ♂ cSch); La Coruña, Coruña, [43.36, -8.4], leg. Ricol (2 MNCN); La Coruña, Villa Rutis, [43.28, -8.38], VII.1908, leg. Bolivar (2 MNCN); Laguna de Ruiz Sánchez, N Osuna, Sevilla, [37.41, -5.09], 26.V.1991, leg. Wrase (1 ♂ cSch); Los Guajares, Andalusien, 36.8174, -3.5546, quarry, 6.IV.2012, leg. T. Wolsch (1 ♂ cSch); Madrid, Escorial [40.57, -4.11] (1 MNCN); Madrid, Torrelaguna, [40.82, -3.53], leg. F. Beltran (1 MNCN); Madrid, Viñuelas [40.79, -3.34] (1 MNCN); Maranchon, Guadalajara, [41.04, -2.20], 24.XI.2005, leg. Anichchenko (1 ♂ NHMD); Murcia, Cartagena, [37.62, -0.99], leg. S. Gomez (1 MNCN); Palencia, [42.01, -4.52], leg. Paganetti (1 ♂ SDEI); Palmones, Cádiz, [36.17, -5.43], 29.V.1991, leg. Wrase (1 ♂ cSch); Quero, Toledo, [39.51, -3.24], 8.III.1999, saline, leg. D.W. Wrase (1 ♂ cSch); Serranía de Ronda, Málaga, [36.74, -5.17], 11.VI.1991, leg. Wrase (1 ♂ cSch); Sitges, [41.23, 1.84], 22.X.1922 leg. W.Liebmann (1 ♀ SDEI); Toledo, Nahalhermosa, [39.63, -4.47], 27.VII.2007 (1 ♂ NHMD); Tres Cantos, [40.60, -3.70], 29.-30.II.2000, leg. Anichtchenko (1 ♀ NHMD). MALLORCA: Palma, [39.56, 2.65], IV.1957, leg. T. Palm (1 ♀ MZLU); Rabassa, [39.54, 2.69], leg. Briet (3 ♂♂ 1 ♀ NMW); Valldecousa, [39.71, 2.62], 15.-20.IV.1957, leg. T. Palm (1 ♂ 3 ♀♀ MZLU). CANARY ISLANDS: GRAN CANARIA: Las Lagunetas, [28.01, -15.57], 22.XI.1988, leg. G. Gillerfors (1 ♀ MZLU). TENERIFE: Anaga Mountains, nr. Cruz del Carmen, [28.53, -16.27], 14.VI.1992, leg.

Hieke & Wendt (1 ♀ ZMHB); Cumbre Dorsal Esperanza-Forest, [28.38, -16.44], 1250m, 13.IV.1992, leg. Zerche (1 ♀ SDEI); Erjos env., [28.32, -16.81], 1100 m, 7.XII.2004, leg. Skoupý (1 ♀ cSch); Genovés, [28.36, -16.74], 400m, 9.VI.1989, leg. Felies (1 ♂ cSch); La Esperanza, [28.44, -16.37], 1200m, 18.VI.1992, leg. Hieke & Wendt (2 ♂♂ ZMHB); Orotava, valley Aguamansa, [28.36, -16.49], 1115m, 25.XII.1995, leg. Stüben & Bahr (1 ♀ SDEI); Nr. Orotava, [28.35, -16.51], 1400m, 19.VI.1992, leg. Hieke & Wendt (2 ♂♂ 1 ♀ ZMHB); Puerto de la Cruz env., [28.36, -16.52], 300m, 20.II.-5.III.2004, leg. E. Hajdaj (1 ♂ cSch); Tenó Alto, San Jerónimo, [28.34, -16.87], 800-900 m, 20.I.1999, leg. G. Zappi (2 ♂♂ 1 ♀ cBor). UNITED KINGDOM: ENGLAND: Chichester Harbour, [50.79, -0.96], 6.V.1947, leg. H. Last (2 ♂♂ NMW).

Redescription. Measurements ♂♂ (n = 6): HW = 1.62–1.76 (1.69); HL = 1.47–1.49 (1.48); HL/HW 0.86–0.92 (0.88); PW = 2.22–2.29 (2.25); PL = 2.07–2.22 (2.16); PL/PW 0.93–0.97 (0.96); EW = 2.27–2.49 (2.37); EL = 2.20–2.33 (2.26); EL/EW 0.92–1.00 (0.96); EL/PL 1.01–1.09 (1.05); PW/HW 1.49–1.56 (1.52); forebody length 5.76–6.02 (5.90). ♀♀ (n = 4): HW = 1.58–1.73 (1.66); HL = 1.38–1.53 (1.46); HL/HW 0.87–0.89 (0.88); PW = 1.96–2.27 (2.16); PL = 1.91–2.11 (2.05); PL/PW 0.93–0.98 (0.95); EW = 2.22–2.51 (2.42); EL = 2.11–2.42 (2.29); EL/EW 0.91–0.96 (0.95); EL/PL 1.08–1.15 (1.12); PW/HW 1.42–1.52 (1.48); forebody length 5.40–6.07 (5.80).

Medium to large sized species; body black to brown (Figs 9A,B).

Head black, distinctly transverse, eyes medium size (EyL/TL: 1.88–2.06 (1.94)), microsculpture of transverse waves, no interocular punctures between anterior frontal punctures; antennae pale.

Thorax: pronotum dark brown to brown, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row, sublateral row of pronotum with a cluster of one to three punctures situated slightly anterior of the anterior most puncture of the dorsal row; scutellum with fine setiferous punctures and with wavy to meshed microsculpture; elytra usually light brown to brown, occasionally black with paler suture and posterior margin, rarely completely black, relatively long, uniformly pubescent, quadrate or slightly wider than long, slightly longer than pronotum; legs pale, except inner face of tibia darkened.

Abdomen black to dark brown and slightly iridescent, tergites uniformly punctured, with slight iridescence.

Male. Aedeagus (Fig. 14C): paramere elongate, narrow, lanceolate with narrowly slightly asymmetrical apical portion exceeding apex of median lobe, with numerous sensory peg setae forming two lateral longitudinal groups connected subapically; median lobe with sides of apex folded into distinct tooth situated at proximal part of fold; internal sac with a pair of very long medial sclerites, and with a pair of globular sclerites.

Differential diagnosis. *Quedius hispanicus* can be distinguished from all species of the *Quedius* s. str. except *Q. pallipes*, by a cluster of 1–3 additional setiferous punctures in the posterior part of the sublateral row of the pronotum. They are very rarely missing on both sides of the pronotum in *Q. hispanicus*. It can be distinguished from *Q. pallipes* only by male genitalia characters: by a slightly narrower and, in medial section, more attenuate paramere; and by

a median lobe with sides of apex each folded into distinct tooth, tooth situated at base of the fold.

Synonymic notes on *Q. pallipes*, *Q. hispanicus*, *Q. simplicifrons*, *Q. cobosi*, and *Q. levasseuri*. LUCAS (1849) described *Quedius pallipes* from the coastal town of Philippeville [now Skikda], Algeria. FAIRMAIRE (1862) described *Quedius simplicifrons* as a very similar species from the French island of Corse. BERNHAUER (1898) described *Quedius hispanicus*, a species very similar to these, from the Spanish coastal towns of Cartagena and Cadiz. These three species have been mixed up, probably due to their very similar habitus, rendering their individual distributions unclear. COIFFAIT (1961) stated that *Q. pallipes* was restricted to North Africa and hypothesized that *Q. simplicifrons* – with *Q. hispanicus* as a junior synonym – could be a European subspecies of *Q. pallipes* without formally downgrading *Q. simplicifrons* to subspecific rank. Subsequently, some authors (HANSEN 1962, LOHSE 1964, HORION 1965, SMETANA 1970, BORDONI 1976, WELCH 1993) have treated *Q. hispanicus* as a valid species for Western European specimens, while others continued to consider it a synonym of *Q. simplicifrons* (POPE 1977, COIFFAIT 1978, CICERONI & ZANETTI 1995, SOLODOVNIKOV 2012). KORGE (1962b) mentioned specimens from Southern Italy and North Africa as conspecific with *Q. pallipes*. He also reported that these were collected at higher altitudes (up to just above 1000 m) very far from the coast. COIFFAIT (1964) further described two new species based mainly on genitalia differences of the males, *Quedius cobosi* Coiffait, 1964 from Seron in Spain, and *Quedius levasseuri* Coiffait, 1964 from Corse, both similar to *Q. pallipes* and *Q. simplicifrons*/*Q. hispanicus*. *Quedius cobosi* was characterised by the presence of numerous small setae on the edge of the paramere, while *Q. levasseuri* was described as having paler sutural and elytral posterior margins as well as a differently shaped aedeagus, compared to *Q. pallipes* and *Q. simplicifrons*. This history implies several species-group taxa of uncertain status, distribution and habitat preference that are similar to *Q. pallipes* and co-occur in the West Mediterranean. Studying a broad sample of specimens from that area, we found only two morphotypes, which differ only in the structure of the aedeagus. The first is found along the European Atlantic Coast, including Southern UK, Canaries, Madeira, Azores and inland in southern France and on the Iberian Peninsula (Figs 14C, 19). These areas include the type localities of *Q. hispanicus* and *Q. cobosi* (Fig. 19). The second is found in mainland Italy, on Corse and Sardinia, and in North Africa at both coastal and higher elevation sites (Figs 14D, 19). These areas include the type localities for *Q. pallipes*, *Q. simplicifrons*, and *Q. levasseuri*. There is no transition between the aedeagi of both types. The steep cliff shoreline between Nice, France and La Spezia, Italy may be unsuitable for these species and may represent a barrier for their dispersal. As the morphological difference between both types of genitalia is clear, and in agreement with the type localities, we here propose to use *Q. hispanicus* for the Iberian and Atlantic coast species

(type 1) and *Q. pallipes* for the Italian and North African species (type 2) (Figs 14, 19). *Quedius cobosi* syn. nov. is synonymized with *Q. hispanicus*.

However, barcodes from specimens across the entire distribution of both types 1 and 2 show very little variation, with no clear clustering corresponding to both genitalia types (Fig. 3). A rather uniform genetic barcode among specimens morphologically corresponding to both *Q. hispanicus* and *Q. pallipes* (only 0.5% divergence, Table 2) suggests that there may be some level of mitochondrial introgression between these species. External factors such as past or present infections by endosymbionts such as *Wolbachia* (e.g. KONDANDARAMAIAH et al. 2013) cannot be ruled out as an explanation either. This should be explored more thoroughly for example with the use of nuclear genes or genomics.

The original descriptions and distribution records of *Quedius hammius* Sharp, 1911 and *Quedius secundus* Last, 1952, both described from the UK, match the morphology and the ecological association with coastal sites of *Q. hispanicus*. *Quedius rufulus* Blümmel, 1898, described from Granada in Spain as having darker base of the antennae, most likely represents a variant of *Q. hispanicus*. All three species were hitherto in synonymy with *Q. simplicifrons*. Under the revised concept of the *Q. pallipes*-group, we synonymize them with *Q. hispanicus*.

Bionomics. *Quedius hispanicus* mainly occurs in saline habitats along the Atlantic coast, such as salt marshes and the banks of estuaries in flood debris. Further south in the Iberian Peninsula and southern France the species seems to be present inland in non-saline habitats. Inland it occurs in the debris along the banks of creeks and rivers. For example, AKH has collected it in the debris near streams and rivers in the Extremadura region (Fig. 2D) and also in the flood debris on a salt marsh near the coast in southern Denmark. Most records are from low elevations, except a few on Madeira and the Canary Islands, where *Q. hispanicus* is found up to 1400 m.

Distribution. *Quedius hispanicus* occurs along the Atlantic coast from southern Denmark to the Iberian Peninsula where it continues to the French Mediterranean coast, with one unverified report from the northwestern Italian coast (Fig. 19). In the Iberian Peninsula it occurs inland along most rivers and creeks. It also occurs on the Azores (Faial), Madeira (Madeira and Porto Santo), the Canaries (Tenerife and Gran Canaries) and Mallorca.

***Quedius pallipes* Lucas, 1849**

(Figs 1, 3, 9C, 14D, 19)

Quedius pallipes Lucas, 1849: 113 [Type locality: Algeria: environs de Philippeville]

Quedius leonhardi Bernhauer, 1914: 67 [Type locality: Gargano], **syn. rev.**

Quedius levasseuri Coiffait, 1964: 293 [Type locality: Corse, Porto-Vecchio], **syn. nov.**

Quedius sardous Gridelli, 1924: 81 [Type locality: Sardegna: Cagliari, Assemini, Decimo, Golfo Aranci, Gonnesa], **syn. rev.**

Quedius simplicifrons Fairmaire, 1862: 580 [Type locality: Corse], **syn. nov.**

References. FAUVEL (1869a): 487, (1869b): 151, (1902): 115 (distribution; synonym of *Q. molochinus*); PORTA (1907): 130 (distribution; synonym

of *Q. molochinus*); MÉQUIGNON (1937): 3 (distribution; subspecies of *Q. molochinus*); PAULIAN (1941): 268 (larval characters; variety of *Q. molochinus*); LAST (1952) (characters and distribution); KORGE (1960): 53 (characters); (1962b): 335, (1973): 275 (distribution); COIFFAIT (1961): 55 (characters); (1978): 196 (distribution); PALM (1963): 142 (characters); SCHEERPELTZ (1965): 407; (1965b): 511 (distribution); BORDONI (1974): 12; (1976): 100 (characters and distribution); 1976b: 102 (characters); CICERONI & ZANETTI (1995): 32 (distribution).

Type material examined. *Quedius leonhardi*: HOLOTYPE ♂ (FMNH), labelled: "Monte Gargano 6.25.5.1907 legit. M. Hill Coll. O. Leonhard / Leonhardi Brh. Typus unique / Chicago NHMus M. Bernhauer Collection / In euparal / D. Drugmand det., 1994 *Quedius* (S.str.) *molochinus* (Grav.) / FMNHINS 3982385 FIELD MUSEUM Pinned / PHOTOGRAPHED S. Ware 2020 Emu catalog".

Additional material examined. **ALGERIA:** Alger [Algiers], [36.71, 3.07], 2.-10.V.1972, leg. M. Dvořák (1 ♂ MCZ); Bona [Annaba], [36.89, 7.76], leg. Meinert (1 ♀ NHMD); Mandoura, Boumerdes, [36.83, 3.66], 17.VI.1988, leg. Sama (1 ♂ cSch). **CHAD:** Tibesti, Distr. Emi, Miski, [20.18, 17.94], 29.X.1885 (1 ♂ NMW). **FRANCE: CORSE:** Ajaccio, [41.93, 8.73] (1 ♂ NHMD); Aleria, [42.11, 9.49], 1905, leg. O. Leonhard (1 ♂ 1 ♀ SDEI). **ITALY:** Aspromonte, Samo, [38.07, 16.05], 250m, 12.III.2000, leg. F. Angelini (1 ♀ NHMD); Barletta, [41.32, 16.27], 14.V.1962, leg. J.T. Skovgaard (4 ♂♂ 3 ♀♀ NHMD); Calaria, Locri, [38.25, 16.28], 3.V.1975, leg. R. Mourgua (1 ♀ cSch); Canale, [44.79, 7.99], leg. Paganetti (2 ♀♀ SDEI); Gargano, [41.71, 15.72], leg. L.S. Giovanni (1 ♀ NHMD); Lago S. Floriano, Toscana, [42.42, 11.35], 30.V.2002, leg. Bordoni (1 ♂ 1 ♀ cBor); Lido di Roma, [41.73, 12.28], 17.-18.VI.1939 Palm (1 ♀ MZLU); Monti Aurunci, Itri, [41.31, 13.49], 25.IX.1973, Leg. M. Zampetti (1 ♀ cBor); Portonaccio, Lazio, [42.02, 12.39], 9.IX.1932, leg. G. Sacca (6 ♀♀ cBor); Puglia, Riserva Naturale Le Cesine, [40.35, 18.33], 11.VI.1999 leg. F. Angelini (2 ♀♀ NHMD); Roseto Capo Spulico, [39.98, 16.61], 10.XII.2000, leg. F. Angelini (1 ♀ NHMD). **SARDINIA:** Assuni, [39.87, 8.94], leg. Krausse (1 ♀ SDEI); Cagliari, [39.21, 9.11], 29.I.1967, leg. S. Riese (3 ♀♀ cBor); Lago Omodeo, Oristano, [40.13, 8.92], 2.V.1979, leg. S. Riese (1 ♂ cBor); Oristano, [39.88, 8.58], 21.IV-7.V.1978, leg. S. Riese (1 ♂ 1 ♀ cBor); Ottana, [40.23, 9.04], 14.V.1976 (2 ♀♀ cBor); Sant'Antioco, [39.06, 8.45], IV.1984, leg. Bordoni (1 ♂ cBor); Sorgono, [40.02, 9.11], 1912 leg. Krausse (1 ♀ SDEI); Stagni Cobras, Oristano, [39.91, 8.49], 19.IV.1971, leg. Visua (1 ♀ cBor). **SICILY:** Catania, [37.51, 15.09], IV.1965, leg. Fello (1 ♂ cBor); Enna, [37.56, 14.28], 1.V.1990 leg. Roland (1 ♂ NHMD); Gibilmanna, [37.98, 14.01], 800m 23.IV.1981, leg. T. Palm (1 ♀ MZLU); Marausa, [37.95, 12.5], 8.III.1982, leg. Alique (1 ♂ cBor); Stracusa, [37.06, 15.28], 18.VII.1969, leg. Alraub (1 ♂ 4 ♀♀ cBor). **MOROCCO:** Al Hakkama, ca. 18 km SE Tanger, 35.6377, -5.6841, fields, fallow, pastures, 100m, 26.II.2004, leg. D.W. Wrase (1 ♀ cSch); Bouznika, [33.81, -7.14], 12.III.1974 (1 ♂ cBor) Douyiet, [34.04, -5.12], 8.IV.1974 (1 ♂ 1 ♀ cBor); Fouarat, Rabat, [34.25, -6.52], 1932, leg. A. Théry (1 ♂ NMW); 10 km N Mdiq, Tetouan, 35.7182, -5.3427, brackish wetland under plants in soil, 27.II.2004, leg. D.W. Wrase (1 ♂ cSch); Mohammedia, Oued Mellah, Chefchaouen, 33.71, -7.33, stony slopes and bushes, 4.II.2003, leg. D.W. Wrase (1 ♀ cSch); Rif Mts. El-Malha, 19 km SE Bab-Taza, Chefchaouen, 34.9801, -5.0791, stony fallen land, ca. 440 m, 29.II.2004, leg. D.W. Wrase (1 ♀ cSch); 2 km W Tetouan, [35.55, -5.45], 16.II.1999, leg. Wrase (1 ♀ cSch). **TUNISIA:** El Besbassia, 10 km SW Hammamet, Sousee, [36.35, 10.52], 28.XI-6.XII.1995, leg. D.W. Wrase (1 ♂ cSch); El Kantaoui, 12 km NW Sousee, [35.89, 10.58], 25.-30.XI.1992, leg. D.W. Wrase (1 ♂ cSch); Gabès, [33.88, 10.12], 30.V.-5.6.1969, leg. Palm (1 ♂ MZLU).

Redescription. Measurements ♂♂ (n = 4): HW = 1.64–1.73 (1.69); HL = 1.47–1.51 (1.48); HL/HW 0.86–0.89 (0.88); PW = 2.16–2.31 (2.22); PL = 2.04–2.22 (2.11); PL/PW 0.93–0.96 (0.95); EW = 2.33–2.51 (2.39); EL = 2.16–2.36 (2.23); EL/EW 0.97–1.10 (1.06); EL/PL 0.97–1.10 (1.06); PW/HW 1.47–1.55 (1.50); forebody length 5.69–6.00 (5.83). ♀♀ (n = 6): HW = 1.62–1.69 (1.67); HL = 1.36–1.47 (1.41); HL/HW 0.83–0.87 (0.84); PW = 2.13–2.27 (2.18); PL = 1.98–2.04 (2.03); PL/PW 0.90–0.96 (0.93); EW = 2.33–2.47 (2.41); EL = 2.13–2.29 (2.22);

EL/EW 0.90–0.94 (0.92); EL/PL 1.07–1.12 (1.10); PW/HW 1.45–1.62 (1.54); forebody length 5.49–5.73 (5.66).

Medium to large sized species; body black to light brown (Fig. 9C).

Head black, distinctly transverse, with eyes of medium size (EyL/TL: 1.76–2.20 (1.97)), microsculpture of transverse waves, no interocular setiferous punctures between anterior frontal punctures; antennae pale.

Thorax: pronotum paler dark brown to brown, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row, sublateral row of pronotum with a cluster of one to three punctures situated slightly anterior of the anterior most puncture of the dorsal row. Scutellum with fine setiferous punctures and with wavy to meshed microsculpture; elytra usually light brown to brown, occasionally with paler suture and posterior margin, rarely completely black, relatively long, uniformly pubescent, slightly wider than long, of equal length or slightly longer than pronotum; legs pale, except inner tibia surface which is darkened.

Abdomen black to dark brown and slightly iridescent, tergites uniformly punctured, with slight iridescence.

Male. Aedeagus (Fig. 14D): paramere elongate, narrow, lanceolate with narrowly slightly asymmetrical apical portion exceeding apex of median lobe, with numerous sensory peg setae forming two subapical, lateral longitudinal groups connected apically below apex; median lobe with sides of apex folded into distinct teeth situated at medial part of fold. Internal sac with a pair of distal, very long medial sclerites, and with a pair of globular proximal sclerites.

Differential diagnosis. *Quedius pallipes* is distinguished from other *Quedius* s. str., except *Q. hispanicus* by a cluster of 1–3 additional setiferous punctures in the posterior part of the sublateral row of pronotum, which are very rarely missing. It can only be distinguished from *Q. hispanicus* by male genitalia characters; paramere slightly wider and less attenuate in middle portion, median lobe with sides of apex each folded into distinct tooth, tooth situated at about midlength of fold.

Synonymic notes. See under *Quedius hispanicus*. Based on the type locality, we here propose to use the name *Q. pallipes* for the Italian and North African species with the aedeagus type 2 (Figs 14, 19). Our examination of hundreds of specimens of the *Q. pallipes*-group across its full distribution range showed that specimens from Corse – which matched the original description of *Q. simplicifrons* – were conspecific with *Q. pallipes*. Therefore, *Q. simplicifrons* Fairmaire, 1862, syn. nov. described from Corse, is here synonymized with *Quedius pallipes* Lucas, 1849.

Quedius sardous Gridelli, 1924 from Sardegna was originally described as a variety of *Q. picipennis* [now *Q. molochinus*]. Following COFFAIT (1961), *Q. sardous* was considered to be an infrasubspecific form of *Q. simplicifrons*. Here we move *Quedius sardous* Gridelli, 1924 syn. rev. to synonymy with *Quedius pallipes* Lucas, 1849.

The original description of *Quedius leonhardi* Bernhauer, 1914, a species described from Gargano in Italy and hitherto considered a synonym of *Q. molochinus*

(e.g., HERMAN 2001), matches *Q. pallipes*, except for the missing puncture in the sublateral row of pronotum, usually present in *Q. pallipes*. However, we have seen specimens of *Q. pallipes* (earlier named as *Q. pallipoides*, see below) with this puncture missing, while neither the described coloration of *Q. leonhardi* nor its distribution in central Italy match what we know about *Q. molochinus*. Thanks to S. Ware and M. Turcatel of the FMNH we were able to study images of the type of *Q. leonhardi* (see supplementary Fig. S4), which confirmed that *Q. leonhardi* fits the concept of *Q. pallipes*. Therefore, *Q. leonhardi* Bernhauer, 1914, syn. rev. is here moved from synonymy with *Q. molochinus* (Gravenhorst, 1806) to synonymy with *Q. pallipes* Lucas, 1849.

Based on the original description of COIFFAIT (1964), and additional data by BORDONI (1976) and COIFFAIT (1978), *Q. levasseuri*, Coiffait 1964, known only from the type series from Porto Vecchio on the island of Corse, we suggest that the male holotype have a teratological aedeagus. The shape of its aedeagus, not seen in any other specimen from this relatively well collected region, is the only unique trait of *Q. levasseuri*, because we observed its other presumably unique characters, the pitchy black elytra with narrow reddish margins, in both *Q. hispanicus* and *Q. pallipes*. Based on our hypothesis about the teratological aedeagus, we propose to synonymize *Q. levasseuri*, syn. nov. with *Q. pallipes*, which is also known from Corse.

Bionomics. *Quedius pallipes* is found at elevations from sea level to ca. 1000 m, in wet debris and under rocks, mainly near water sources. For example, based on examined specimen labels, it has been recorded in a brackish wetland under plants in soil, and on rocky slopes with bushes, both in interior Morocco. Based on records near coastal sites the species is most likely halotolerant.

Distribution. *Quedius pallipes* is distributed across northern Africa, the Italian Peninsula and the islands of Sicily, Sardinia and Corse (Fig. 19). In northern Africa it is found in Morocco, Algeria and Tunisia, mainly in the coastal regions of these countries, or near water sources inland. A single record from Tibesti in Northern Chad is doubtful, as it is based on an unclear label, which may refer to the small settlement of Miski in the Emi Koussi District. In the Italian Peninsula it is found everywhere except its northern mountainous parts.

Quedius molochinoides-group

Diagnosis. Species of medium to large size with two interocular punctures between anterior frontal punctures (Fig. 6G). Body dark, elytra and appendages variable in coloration, from completely dark to reddish-brown or light brown. Eyes medium sized, temples relatively large, with temporal puncture separated from posterior margin of eye by distance equivalent to diameter of this puncture. Scutellum punctate and pubescent. Restricted to the Nearctic Region.

Comments. The Nearctic *Q. molochinoides*-group currently includes five species of which four (*Q. molochinoides*, *Q.*

horni and *Q. lanei*, now also *Q. altanai*) are impossible to separate morphologically from each other without dissection of male genitalia. Only the northern *Q. labradorensis* can be confidently delimited within the group based on its larger size and pale basal three antennomeres. Our thorough examination of the entire group showed that *Q. horni* is most easily recognized based on the aedeagus. This species is now known from the Pacific Northwest, from Oregon to southern Alaska, including Vancouver Island and Haida Gwaii (most of ecoregion 7.1). Most specimens of this species were taken on coastal sites or inland near rivers and creeks to mid elevation in the Cascades and Mount Olympia, suggesting its close association with wet habitats. Presumably this species is somewhat halotolerant. When specimens of what was known as *Q. lanei*, were closely examined morphologically, we found two distinct morphotypes distinguished by differences in male genitalia. Species from the eastern foothills of the Cascades, the Sierra Nevada and the Blue Mountains (ecoregions 6.2.8, 6.2.9, 6.2.12) represent a morphotype with a broader paramere and median lobe, the latter being acuminate near apex (Figs 16D, 17). This includes specimens from the Sierra Nevada (Nevada and California), which were earlier assigned to *Q. molochinoides* (e.g., SMETANA 1971a). Specimens from the central and southern Rockies as well as western Sierra Madre (ecoregions 6.2.10, 6.2.13, 6.2.14, 6.2.15, 13.1.1) represent a different morphotype with a more slender paramere and median lobe, the latter being non-acuminate (Figs 16C, 17). COI sequences of both morphotypes showed that four specimens corresponding to the first morphotype from Lake Tahoe in Nevada, Lassen National Forest in California, Gearhart Mountains in Oregon, and Strawberry Range in Oregon, formed a group, separate from the fifth specimen corresponding to the second morphotype (Fig. 4). The central-southern Rockies morphotype was only represented by a single incomplete sequence (407 bp) from Red Mountain Pass in Colorado. This sequence was over 6% divergent from all *Q. lanei* sequences, but only 1.2% from *Q. molochinoides*-group 3 (see below), from which it is morphologically distinct (Table 2). Based on the discovered congruence between the morphological and molecular groups, as well their obvious allopatry (Fig. 21), we suggest that *Q. lanei* is a species restricted to the eastern foothills of the Cascades, Sierra Nevada and Blue Mountains, whereas a new species, *Q. altanai* sp. nov., is described for specimens from the central and southern Rockies, as well as western Sierra Madre (teal in Fig. 21). *Quedius molochinoides* showed genetic subclustering of COI barcodes into three distinct BINs (Table 2). One BIN (*Q. molochinoides*-group 1) was restricted to the Canadian national parks of Banff and Waterton (ecoregion 6.2.4), an area delimited by the Rocky Mountains Trench to the West, where it is replaced by another BIN (*Q. molochinoides*-group 2), and the Canadian Plains to the east, which lack *Q. molochinoides*. In the north, this group is replaced by *Q. molochinoides*-group 3 from Jasper National Park, indicating a divide between groups 1 and 3 around Snow Dome peak and the Arctic Divide. One potential split is the Athabasca River Valley, that may have acted as a

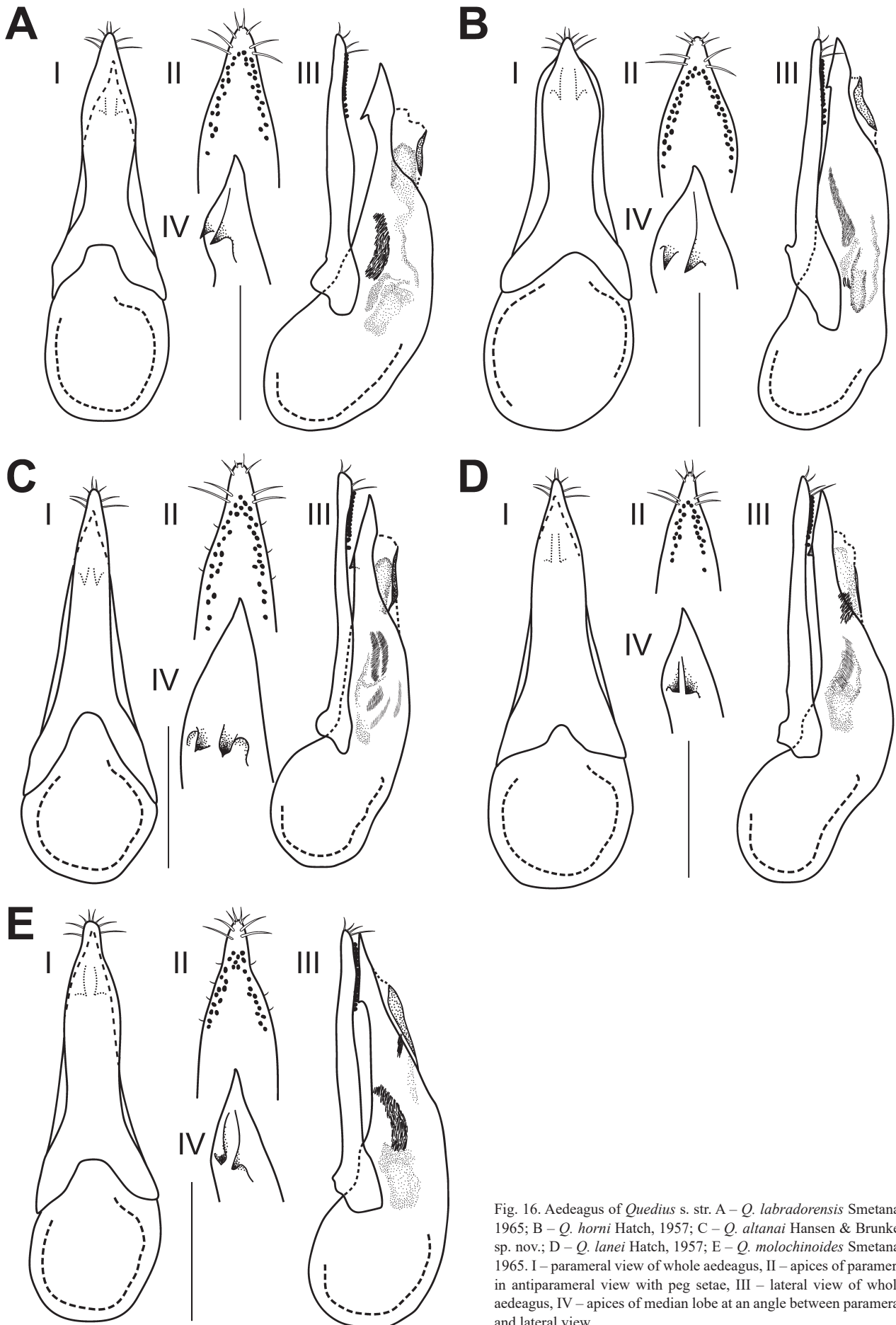


Fig. 16. Aedeagus of *Quedius* s. str. A – *Q. labradorensis* Smetana, 1965; B – *Q. horni* Hatch, 1957; C – *Q. altanai* Hansen & Brunke, sp. nov.; D – *Q. lanei* Hatch, 1957; E – *Q. molochinoides* Smetana, 1965. I – parameral view of whole aedeagus, II – apices of paramere in antiparameral view with peg setae, III – lateral view of whole aedeagus, IV – apices of median lobe at an angle between parameral and lateral view.

post-glacial distribution barrier combined with latitudinal climatic gradients. The extent of the distribution of group 1 southwards is still unknown, but it may very well extend into northern-central Montana and Idaho (Figs 4, 22). The *Q. molochionides*-group 2 is confined to the Canadian Rockies west of the Rocky Mountains Trench (ecoregion 6.2.3) and towards the North continuing to the Pacific Coast in Alaska, to the Kenai Peninsula northwards (ecoregion 6.1 and northern part of 7.1). The *Q. molochinoides*-group 3 is present from Becharof Peninsula in the west across the North American Taiga to glacial refugia of New England, Quebec and Newfoundland in the East (ecoregions 4, 5, and partly 6.1 and 7.1). Our results show that apparently these three molecular BINs within *Q. molochinoides* have distinctly allopatric distributions and thus potentially have limited gene flow among each other. However, since we have been unable to find morphological characters clearly separating them, for now we refrain from describing them as species. If future work shows that these are in fact distinct, then they may be described as separate species. Our results add further information to the complex diversification patterns found in the Canadian Rocky Mountains as illuminated through a series of studies on the Spruce Budworm complex (Lepidoptera: Tortricidae: *Choristoneura*) (LUMLEY & SPERLING 2010, 2011; BRUNET et al. 2017, DUPUIS et al. 2017). Similar to these studies, genome-wide sequencing may be needed to confidently resolve the population/species boundaries and distribution patterns in the *Q. molochinoides* group.

Quedius altanai Hansen & Brunke, sp. nov.

(Figs 1, 4, 10C, 16C, 17, 21)

Quedius lanei (misidentified): KORGE (1962b): 333 (characters, notes); SMETANA (1971a): 144 (characters and distribution); SMETANA (1971b): 1844 (collecting notes and distribution); SMETANA (1976a): 174 (distribution).

Type material. HOLOTYPE ♂ (CNC), labelled: "Cache Co., Logan Cn., 5300', Spring Hollow, 15.VII.1981, J.M. Campbell / sifting pile of squirrel midden / CNC 1017210 / Holotype *Quedius altanai* Hansen & Brunke, sp. Nov. des. A. Hansen & A. Brunke 2021". PARATYPES: USA: ARIZONA: Apache Co., Chuska Mountains, Wagonwheel Campground, [36.45, -109.17], 2500 m, pine and fir 25.-27.VIII.1977, leg. S. Peck (1 CNC); Chuska Mountains, Wagonwheel Campground, [36.45, -109.17], 2250 m, sifted from moss, 12.VII.1976, leg. J.M. Campbell (1 CNC). COLORADO: 6 mi S Molas Pass, [37.66, -107.7], 2895 m, 1.VIII.1973, leg. J.M. Campbell (2 CNC); Red Mountain Pass near Silverton, [37.89, -107.71], 3505 m, 28.VII.1973, leg. J.M. Campbell (1 CNC). IDAHO: Bloomington Lake Wasatch Mts, [42.14, -111.57], 2500 m, 8.VII.1952, leg. B. Malkin (1 ♂ FMNH); Boise County, Sawtooth Region, Bull Trout Lake, 3.2km SW Highway 21, [44.3, -115.25], 2130 m, 6.VI.1989, leg. A. Smetana (3 CNC); Custer County, Sawtooth Range Highway, 21 Banner Summit, [44.3, -115.23], 2190 m, 6.VI.1989, leg. A. Smetana (1 CNC); Custer County, Sawtooth Range, Stanley Lake, [44.24, -115.05], 1900 m, 8.VI.1989, leg. A. Smetana (5 CNC). NEW MEXICO: Otero, 19. Mi S of Cloudcroft, [32.69, -105.72], IV.22.1972, C.W. & L.B. O'Brien (1 ♂ CNC). UTAH: Ashley National Forest, 12 km S Manila, Deep Creek, 40.8550, -109.7297, 2340 m, sifting litter and mushrooms, 30.VI.2015, leg. M. Schülke (1 ♂ ZMHB); Cache County, Logan Canyon, Spring Hollow, [41.75, -111.71], 1615 m, sifting, pile of squirrel midden, 15.VII.1981, leg. J.M. Campbell (3 CNC, 2 NHMD); Cache County, Logan Canyon, Spring Hollow, [41.75, -111.71], 1615 m, 15.VII.1981, leg. J.M. Campbell (4 CNC); Cache County, Logan Canyon, 2km N Wood Camp, [41.75, -111.71], 1706 m, sifting, moss, 14.VII.1981, leg. J.M. Campbell (1 CNC); Lonesome Beaver, Henry Mountain, [38.1, -110.81],

25-26.VII.1968, leg. H.F. Howden (1 CNC); Mount Timpanegos, Wasatch Mountains, [40.39, -111.64], 5.VII.1935, leg. Van Dyke (2 CNC); Summit County, Bald Mount Pass, [40.68, -110.89], 3261 m, 11.VII.1981, leg. J.M. Campbell (2 CNC); Summit County, Whiskey Creek, Mile 39 Highway 150, Sulphur Campground, [40.79, -110.88], 2743 m, 11.VII.1981, leg. J.M. Campbell (2 CNC); Summit County, Wasatch National Forest, Beth Lake, [40.65, -110.96], 2895 m, 12.VII.1981, leg. J.M. Campbell (1 CNC). WYOMING: [Yellowstone] National Park, [44.63, -110.87], IV.1908, leg. Hubbard & Schwarz (1 CNC). Wyoming USA, 26.VI.1956, leg. E. Suenson (2 NHMD).

Description. Measurements ♂ (n = 1): HW = 1.67; HL = 1.49; HL/HW 0.89; PW = 2.20; PL = 2.07; PL/PW 0.94; EW = 2.24; EL = 2.13; EL/EW 0.95; EL/PL 1.03; PW/HW 1.48; forebody length 5.69. ♀♀ (n = 6): HW = 1.56–1.67 (1.60); HL = 1.20–1.42 (1.34); HL/HW 0.75–0.89 (0.84); PW = 1.96–2.24 (2.07); PL = 1.78–1.96 (1.86); PL/PW 0.87–0.95 (0.90); EW = 2.09–2.24 (2.18); EL = 1.96–2.16 (2.05); EL/EW 0.87–0.99 (0.94); EL/PL 1.04–1.14 (1.10); PW/HW 1.27–1.74 (1.51); forebody length 5.04–5.53 (5.25).

Medium sized species; body brown to black (Fig. 10C).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.61–2.07 (1.90)), microsculpture of transverse waves, with two interocular punctures between anterior frontal punctures (Fig. 6G); antennae and palpi dark with joints pale reddish, all antennomeres elongate, except the last and penultimate antennomere almost transverse.

Thorax: pronotum dark brown to black, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond first puncture of dorsal row; scutellum sparsely punctured and pubescent; elytra variable in coloration, from reddish brown, to almost yellowish pale, occasionally dark with lighter sutural margins, uniformly pubescent, with punctures clearly separated, slightly wider than long, slightly longer than pronotum; legs reddish brown with inner face of tibia and inner surface of femur darkened and tarsi paler.

Abdomen brown to black, tergites uniformly punctured, with clear iridescence.

Male. Aedeagus (Figs 16C, 17): Paramere lanceolate, rather slender, without clear basal attenuation, reaching apex of median lobe, with small sensory peg setae forming two irregular rows meeting in irregular cluster below apex; median lobe lanceolate, slender, continuously constricting towards pointed apex, on parameral side with two small teeth simply protruding outwards and slightly basad; internal sac with two larger oval and two smaller rounded internal sclerites.

Differential diagnosis. *Quedius altanai* can be distinguished from *Q. laticollis* and *Q. strenuus* by the presence of two additional setiferous punctures between the anterior frontal punctures. It can be distinguished from *Q. labradorensis* by the darker body and the clearly darkened basal three antennomeres. It can be distinguished from other members of the *molochinoides*-group (*Q. horni*, *Q. lanei* and *Q. molochinoides*) only by the male genitalia: by the slender paramere that is evenly narrowed from base to apex, and median lobe with an evenly narrowed apex and

two small subapical teeth pointing basad and often appearing as short carinae. However, the clearly allopatric distribution of *Q. altanai* with respect to all other species of the *molochinoides*-group makes such detailed examination for diagnostic purposes within the group largely unnecessary.

Bionomics. *Quedius altanai* prefers mountainous areas and occurs only at high elevations between 1600 and 3500 m. The habitat seems to be mainly moist debris, and under rocks in meadows or coniferous forests. Specimens from Red Mountain Pass were collected from under rocks near snowfields (SMETANA 1976) and those from Lincoln National Forest, New Mexico were found in a meadow-like biotope, amidst coniferous forest under a piece of wood at a small creek (SMETANA 1971). Other specimens have been reported from litter, moss, and squirrel middens mainly in coniferous forests.

Etymology. This species is dedicated to our great friend and colleague Aleš Smetana who has greatly advanced the study of the complex genus *Quedius* globally and who reviewed this paper. We are glad that Aleš saw it. Sadly, he recently passed away while this paper was still unpublished. We foresee large future taxonomic changes, when this huge genus will be split, inevitably following recent phylogenetic findings. So, this becomes a way to capture and eternalize his name within the core of the genus. The name is a combination the first part of the first name (*al-*) and the last part of the last name (*-tana*) given as a masculin eponym (*-i*).

Distribution. *Quedius altanai* is known from high elevation sites of the central and southern Rockies, as well as western Sierra Madre (Fig. 21). Its northernmost limit of the distribution is from middle Rockies, i.e. Central-Southern Idaho and Wyoming (ecoregion 6.2.10, 6.2.15). In the south it extends into the highest elevation sites of the Rockies (ecoregion 6.2.13 and 6.2.14) and interestingly into western Sierra Madre that often is represented by a different fauna (ecoregion 13.1.1). Westwards *Q. altanai* does not occur in the Cascades, Sierra Nevada or the Blue Mountains. There it is replaced by *Q. lanei*.

Quedius horni Hatch, 1957

(Figs 1, 4, 5, 10A, 16B, 17, 21)

Quedius horni Hatch, 1957: 216 [Type locality: Washington: Snohomish Co.: L. Ballinger]

References. KORGE (1962b): 333 (characters, notes); SMETANA (1965a): 39 (characters); (1971a): 146 (characters and distribution).

Material examined. CANADA: BRITISH COLUMBIA: 20 mi. E. Hope, Manning Pk., [49.18, -120.97], ex river debris, 21.VI.1968, leg. Campbell & Smetana (1 CNC); Tsawwassen, [49.01, -123.08], 19.V.1968, leg. Campbell & Smetana (1 CNC). HAIDA GWAIH: Queen Charlotte Island [Haida Gwaii], Skowkona Creek, 7.9km NW O. C. City, [53.33, -132.13], ex dung and carrion traps, 19-29.VII.1983, leg. J.M. Campbell (1 CNC); 7.9km NW Queen Charlotte City, [53.31, -132.14], dung trap, 19-29.VII.1983, leg. J.M. Campbell (1 CNC). VANCOUVER ISLAND: Mesachie Lake, Forest Experiment Station, [48.82, -124.13], 15-31.VII.1979, leg. I. Smith (2 CNC); Vancouver Island, [49.76, -125.46] (4 CNC). USA: ALASKA: Auke Bay, 16.2km N Juneau, [58.38, -134.65], sifting moss, 9.VI.1981, leg. Bright (1 CNC). OREGON: Blodgett, [44.59, -123.52], VI.1927, leg. Darlington (1 MCZ); Hood River County, 10 mi S Mount Hood at Clinger Springs, [45.4, -121.55], 1310 m, 8.VII.1978, leg. L. & N. Herman (1 CNC); Mt. Hood, South Side, [45.29, -121.7], 7.VI.1927, leg. Darlington (1 MCZ). WASHINGTON: Olympic National Park, Hoh Ranger

Station, [47.85, -123.93], 182 m, 13.V.1968, leg. Campbell & Smetana (1 CNC); Olympic National Park, 4-6 mi SE Soleduck Campground, [47.93, -123.77], 944 m, 15.VIII.1979, leg. J.M. & B.A. Campbell (1 CNC).

Redescription. Measurements ♂♂ (n = 4): HW = 1.64–1.69 (1.67); HL = 1.36–1.40 (1.39); HL/HW 0.82–0.84 (0.83); PW = 2.02–2.22 (2.13); PL = 1.82–2.00 (1.92); PL/PW 0.88–0.91 (0.90); EW = 2.11–2.31 (2.21); EL = 2.04–2.29 (2.11); EL/EW 0.88–1.01 (0.96); EL/PL 1.02–1.14 (1.10); PW/HW 1.44–1.59 (1.54); forebody length 5.24–5.69 (5.42). ♀♀ (n = 2): HW = 1.62–1.71 (1.67); HL = 1.36–1.42 (1.39); HL/HW 0.83–0.84 (0.83); PW = 2.02–2.16 (2.09); PL = 1.78–2.00 (1.89); PL/PW 0.88–0.93 (0.90); EW = 2.13–2.29 (2.21); EL = 2.04–2.16 (2.10); EL/EW 0.94–0.96 (0.95); EL/PL 1.08–1.15 (1.11); PW/HW 1.49–1.52 (1.50); forebody length 5.18–5.58 (5.38).

Medium sized, robust species; body black (Fig. 10A).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.76–2.06 (1.91)), microsculpture of transverse waves, with two interocular punctures between anterior frontal punctures (Fig. 6G); antennae and palpi pale reddish with most of antennomeres 1–3 clearly darkened; all antennomeres elongate, except apical antennomere almost transverse.

Thorax: pronotum black, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond first puncture of dorsal row; scutellum sparsely punctured and pubescent; elytra most often reddish brown, but occasionally fully darkened or dark with reddish sutural margins, uniformly pubescent, with punctures clearly separated, quadrate or slightly wider than long, slightly longer than pronotum; legs reddish brown with inner face of tibia and inner surface femur darkened and tarsi paler.

Abdomen black, tergites uniformly punctured, with clear iridescence.

Male. Aedeagus (Figs 16B, 17): paramere rather broad, with clear basal attenuation and pointed apex, reaching to apex of median lobe, with small sensory peg setae forming thin row in a semi-circle near edge of paramere, except at pointed apex; median lobe broad with sudden constriction to a point at apex, on parameral side with two fang-like subapical teeth basad; internal sac with elongate and broad sclerites.

Differential diagnosis. *Quedius horni* can be distinguished from *Q. laticollis* and *Q. strenuus* by the presence of two additional setiferous punctures between the anterior frontal punctures. It can be distinguished from *Q. labradorensis* by the darker body and the clearly darkened antennomeres 1–3. *Quedius horni* can be clearly distinguished from other members of the *molochinoides*-group (*Q. altanai*, *Q. lanei* and *Q. molochinoides*) only by the spoon-like shape of the paramere, which has a clear basal attenuation and broadening towards pointed apex, with its peg setae situated in a semi-circle near the edge of the of the paramere below its pointed apex. However, this species co-occurs with other species of the *molochinoides*-group only in Alaska, which makes such detailed examination for diagnostic purposes within the group less necessary anywhere else.

Bionomics. Little is known about the habitat requirements of *Q. horni*. It seems to prefer wet environments, as it has been collected in moist habitats from sea level to an elevation slightly above 1000 meters. Most specimens were collected in coastal sites or inland near rivers and creeks suggesting its close association with wet habitats near water bodies. For example, the species was found in river flood debris and on beaches under driftwood in British Columbia, in moss at Auke Bay, Alaska, in a dung trap on Haida Gwaii, and in forest litter around large firs at Mary's Peak, Oregon (SMETANA 1971a). Immature specimens were collected in late May at Tsawwassen, British Columbia and in early July on Mt. Hood, Oregon (SMETANA 1971a). Based on the records near coastal sites the species is most likely somewhat halotolerant.

Distribution. *Quedius horni* is now known from the Pacific Northwest, from Oregon to southern Alaska, including Vancouver Island and Haida Gwaii (most of ecoregion 7.1; Fig. 21). It can be found at coastal and riverine sites and to mid elevation of the Cascades and Mount Olympia. This revision, including barcoding, confirmed its first record from southern Alaska, and thus extended the species range significantly to the north. It is still uncertain how far south the species occurs, with the current southernmost record coming from central Oregon. Based on the extent of ecoregion 7.1, this may extend along the coast into California.

Quedius labradorensis Smetana, 1965

(Figs 1, 4, 10F, 16A, 17, 21)

Quedius labradorensis Smetana, 1965a: 37 [Type locality: Südost-Labrador: Forteau]

Quedius labradorensis insularis Smetana, 1971a: 140 [Type locality: Alaska: Anton Larsen Bay, Kodiak]. Preoccupied by *Quedius insularis* Bernhauer & Schubert, 1916; currently a junior synonym of *Philonthus umbratilis* (Gravenhorst, 1802).

Quedius labradorensis kodiakensis Smetana 1999: 79 (as a replacement name for *insularis* Smetana), **syn. nov.**

References. SMETANA (1964): 37, (1965a): 37, (1965b): 12 (distribution; misidentified as *Q. lanei* according to SMETANA 1971a: 138); (1971a): 138 (characters and distribution); (1973): 1428, (1976a): 172, (1978a): 826, (1981): 640 (distribution); DOWNIE & ARNETT (1996): 391 (characters and distribution); POHL et al. (2007): 299 (biology); WEBSTER et al. (2012): 315 (distribution).

Type material examined. *Quedius labradorensis*: HOLOTYPE ♂ (CNC), labelled: "SE Labrador Forteau N:o 285. 13-15.VII.51 Lindroth/Holotype *Quedius labradorensis* m. / 1963 Smetana det. / *Quedius labradorensis* m. 63 Smetana det. 19 / Holotype CNC No. 9473 *Quedius labradorensis* Smet.".

Quedius labradorensis insularis: HOLOTYPE ♂ (CNC), labelled: "Alaska, Anton Larsen Bay, Kodiak, 445, 24.VIII.1958, Lindroth / Holotype *Quedius labradorensis insularis* Smetana 1968 CNC No. 10866". PARATYPE: same collection data as holotype (1 ♀ CNC).

Additional material examined. CANADA: ALBERTA: George Lake, [53.95, -114.1], 10.IX.1966, leg. R. E. Leech (18 CNC); George Lake, [53.95, -114.1], 1.VI.1969, leg. H. Goulet (3 CNC); Wagner Natural Area, Edmonton 6km W, [53.57, -113.82], pan trap, 12-25.VI.1985, leg. Finnamore & Thormin (4 CNC). BRITISH COLUMBIA: 10 mi E of East Pine, [55.71, -120.97], 16.VI.1958, leg. Lindroth (1 CNC). MANITOBA: Onah, [49.81, -99.52], 20.VIII.1921, leg. N. Criddle (1 CNC); Riding Mountain National Park, [50.83, -100.20], pan traps, Bison enclosure, 4.VIII.1979, leg. D. B. Lyons (1 CNC); Riding Mountain National Park, Edward Creek at Highway 10, [50.92, -100.05], 17.IX.1979, leg. A. Smetana (1 CNC); Riding Mountain National Park, 1km SE Long Lake, [50.75, -100.32], 16.IX.1979, leg. A. Smetana (1 CNC).

NORTHWEST TERRITORIES: Highway 2 mi SE Fort Simpson, [61.82, -121.3], 23.VI-3.VII.1972, leg. A. Smetana (3 CNC). NOVA SCOTIA: Cape Breton Highland National Park, near Benjies Lake, [46.73, -60.8], 17.VI.1984, leg. A. Smetana (1 CNC); Cape Breton Highlands National Park, Fishing Cove Trail, [46.79, -60.87], 305 m, sifting, moss at seepage, 25.IX.1984, leg. J. M. Campbell & A. Davies (1 CNC); Cape Breton Highlands National Parks, Lone Shieling, [46.81, -60.73], pan trap, forest, 19-24.VII.1983, leg. L. Masner (7 CNC); Cape Breton Highland National Park, MacKenzie Mountain, [46.81, -60.81], pan trap, 2.VIII.1983, leg. D. E. & J. E. Bright (7 CNC); Cape Breton Highland National Park, North Mountain, [46.82, -60.65], fern bog, 11-19.VII.1983, leg. L. Masner (3 CNC); Cape Breton Highland National Park, Paquette Lake, [46.81, -60.44], pan trap, 1.VII.1983, leg. R. Vockeroth (1 CNC); Cape Breton Highlands National Park near Sammy's Barren, [46.81, -60.72], 440 m, sifting litter, Birch litter, 24.IX.1984, leg. J. M. Campbell & A. Davies (4 CNC); Cape Breton Highland National Park, [46.81, -60.76], 400 m, pan trap, forest, 11-13.VI.1983, leg. Y. Bousquet (1 CNC). ONTARIO: Cochrane, [49.14, -81.02], 22.VIII.1918, leg. H. Notman (1 CNC); Moosonee, [51.29, -80.71], 30.VI.1973, leg. J. M. Campbell & R. Parry (1 CNC); 22 mi S Pickle Lake, [51.15, -90.21], 20.VI.1973, leg. J. M. Campbell & R. Parry (1 CNC); 36 mi S Pickle Lane, [50.76, -90.28], 22.VI.1973, leg. J. M. Campbell & R. Parry (2 CNC); Thunder Bay, Mount McKay, [48.34, -89.28], 487 m, 15.VI.1973, leg. J.M. Campbell & R. Parry (3 CNC); Thunder Bay, Powell Lakes, 10km NE Lake Superior, [49.02, -82.98], forest FIT, 31.V.1980, leg. M Kaulbars (1 CNC). QUEBEC: Charlevoix-East, Ste-Mathilde, [47.68, -70.11], 28.VIII.1975, leg. J. F. Landry (2 CNC); Duparquet, [48.47, -79.17], 30.V.1936, leg. G. Stace Smith (2 CNC); Lac Duparquet, [48.49, -79.26], cedar fir forest, 4.-11.VIII.1996, leg. Paquin (5 CNC); Lac Cascapedia, Parc Gaspesie, [48.92, -66.32], 518 m, pan trap, 14.VII.1972, leg. J. M. & B. A. Campbell (1 CNC); Lac Pointe, [46.33, -72.7], 22.IX.1980, leg. C. Chantal (3 CNC); Longue-Pointe-de-Mingan, [50.28, -64.19], undergrowth vegetation, 16.VII.2008, leg. LeSage & Lussier (1 ♂ CNC); Montreal, [45.5, -73.62], 9.VI.1908, leg. E. J. Kiteley (2 CNC). ILE D'ANTICOSTI: Pte Sud-Ouest, [49.39, -63.59], 15.VII.1977, leg. J. F. Landry (1 CNC). SASKATCHEWAN: Flotten Lake, [54.62, -108.50], 6.-13.VI.1998, leg. T. Cobb (3m SMNH); Lac La Rouge, Stueck Island, [55.19, -105.01], 19.VII.1979, leg. E. J. Kiteley (1 CNC). USA: ALASKA: Denali State Park, Byers Lake Campground, [62.74, -150.11], 23.VI.1978, leg. Smetana & Becker (2 CNC); Denali NP, Wickersham Dorne, 63.348, -150.97749, 977m, alpine tundra, pitfall traps, 29.VI.2017, leg. A. Haberski et al. (3 UAM); Denali NP, Wickersham Dorne, 63.348, -150.97749, 977m, shrubs, pitfall traps, 23.-27.VII.2017, leg. A. Haberski et al. (19 UAM); Denali NP, Wickersham Dorne, 63.548, -150.97749, 811m, shrubs, pitfall traps, 3.-19.VII.2018, leg. D. Sikes et al. (4 UAM); Denali NP, Wonder Lake, 63.48822, -150.86237, 645m, spruce, pitfall traps, 7.-21.VI.2018, leg. D. Sikes et al. (1 UAM); Fairbanks Park, 64.7924, -148.1511, 440 m, S-facing hill, forest edge *Populus tremuloides*, pitfall traps, 17.-14.VII.2007, leg. B. Mortensen (1 UAM). KODIAK ISLAND: 30 mi S Kodiak, [57.54, -153.51], 23.VIII.1958, leg. G. E. Ball (1 CNC). MICHIGAN: Isle Royale, Daisy Farm, [48.09-88.60], 17.VIII.1965, leg. Bixler (1 ♂ FMNH). NEW HAMPSHIRE: Carter Notch, [44.26, -71.19], 6.VIII.1908, leg. F. Blanchard (1 CNC). NEW YORK: Indian Falls, Mount Marcy, [44.11, -73.92], 16.VI.1942, leg. H. Dietrich (1 CNC).

Redescription. Measurements ♂♂ (n = 3): HW = 1.76–1.87 (1.80); HL = 1.49–1.56 (1.52); HL/HW 0.83–0.85 (0.84); PW = 2.20–2.44 (2.28); PL = 2.07–2.29 (2.15); PL/PW 0.94–0.95(0.94); EW = 2.29–2.40 (2.35); EL = 1.93–2.18 (2.07); EL/EW 0.82–0.95 (0.88); EL/PL 0.91–1.04 (0.96); PW/HW 1.46–1.57 (1.50); forebody length 5.49–5.93 (5.73). ♀♀ (n = 2): HW = 1.89–1.93 (1.91); HL = 1.58–1.62 (1.60); HL/HW 0.84; PW = 2.33–2.38 (2.36); PL = 2.13–2.16 (2.14); PL/PW 0.90–0.92 (0.91); EW = 2.36–2.40 (2.38); EL = 2.09–2.13 (2.11); EL/EW 0.87–0.91 (0.89); EL/PL 0.98–0.99 (0.98); PW/HW 1.47–1.48 (1.47); forebody length 5.84–5.87 (5.86).

Large species; body brown to black (Fig. 10F).

Head black, transverse, with eyes medium sized (EyL/TL = 1.72–1.89 (1.82)), microsculpture of transverse waves, with two interocular punctures between anterior frontal punctures (Fig. 6G); antennae and palpi reddish with basal three antennomeres clearly pale, all antennomeres elongate.

Thorax: pronotum brown to black, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching almost to level of second puncture of dorsal row; scutellum sparsely punctured and pubescent; elytra most often pale orange to reddish brown, rarely fully darkened, clearly wider than long, of similar length as pronotum, with rather short uniform pubescence, with punctures clearly separated from each other; legs reddish with inner face of tibia darkened and tarsi paler.

Addomen brown to black, tergites uniformly punctured, without clear iridescence.

Male. Aedeagus (Figs 16A, 17): paramere rather broad, with slight basal attenuation and extending into softly rounded apex, reaching to the apex of median lobe, with small sensory peg setae forming two broad irregular rows near the edge of the of the paramere, except at very apex which is slightly folded; median lobe continuously slimming toward pointed apex, on parameral side with two folded teeth which almost meet to form a cavity with a small slit towards apex; internal sac with elongate and internal sclerites.

Differential diagnosis. *Quedius labradorensis* can be distinguished from *Q. laticollis* and *Q. molochinus* by the presence of two additional setiferous punctures between the anterior frontal punctures. It can be distinguished from other members of the *molochinoides*-group (*Q. lanei*, *Q. molochinoides*, and *Q. horni*) by the larger body size and pale basal three antennomeres.

Synonymic notes. The subspecies *Q. l. kodiakensis* was described as a form restricted to Kodiak Island, which differs from the nominotypical subspecies by a slightly larger body and more spatulate paramere with larger peg setae (SMETANA 1971a). Generally, species of *Quedius* s. str. display some variation in body size and shape of the paramere. With more material available, the observed variation between the putative subspecies falls within the variation observed in the widely distributed nominal subspecies. Thus, we consider *Quedius l. kodiakensis* Smetana, 1999 syn. nov. a junior subjective synonym of *Quedius labradorensis* Smetana, 1965.

Bionomics. As a northern species, *Q. labradorensis* prefers wet boggy habitats with specimens collected in litter and moss of mixed forests, mainly poplar and birch, in Ontario (SMETANA 1971a), in deep moss in Saskatchewan (SMETANA 1990), fern bogs in Nova Scotia, margins of creeks on Kodiak Island (SMETANA 1971a), and shrubby alpine tundra in Alaska. SMETANA (1976a) reported this species from moss, mushrooms, and deciduous leaf litter (birch and poplar stands) near streams. In the Alberta foothills forests, *Q. labradorensis* is considered to be an open-ground specialist after forest logging, which only spread short distances into adjacent pristine forests, with numbers of this species also increased after logging (POHL et al. 2007).

In New Brunswick, most adults have been found from April to May in old-growth eastern white cedar swamps in moss usually near small streams, with the exception of one adult found under a patch of white-tailed deer dung, and one collected at a mercury-vapor light (WEBSTER et al. 2012). The species is found mainly at higher elevation (750–1500 m) in the southeastern part of its range and at lower elevations up to 800 m in the northern part of its range. Several specimens found in pan traps across Canada indicate that the species may be actively flying or hunting in the vegetation.

Distribution. *Quedius labradorensis* is a northern species distributed transcontinentally across boreal North America from Labrador and Newfoundland to Alaska where it extends to Kodiak Island (ecoregions 4, 5, and northern part of 6 and 7, Fig. 21). To the south it is found in some of the large remaining wetlands, as well as at higher elevation sites, e.g. in Northern Rockies and Cypress Hills in the West, and at Mount Washington and the MacIntyre Range in the East. The northernmost records from Fairbanks Park in Alaska, and Fort Simpson in the Northwest Territories suggest that the species extends throughout the boreal ecoregion of the continent.

Quedius lanei Hatch, 1957

(Fig. 1, 4, 5, 10B, 16D, 17, 21)

Quedius lanei Hatch, 1957: 216 [Type locality: Washington: Blue Mts.]

References. KORGE (1962b): 333 (characters and notes); SMETANA (1971a): 144 (characters and distribution); (1976a): 174 (distribution).

Material examined. USA: CALIFORNIA: Fresno County, Huntington Lake, [37.24, -119.18], 25.IV.1960, leg. L. G. Ingles (2 CNC); Lassen National Park, Summit Lake, [40.49, -121.42], 2042 m, 15.VII.1979, J. M. & B. A. Campbell (3 CNC). **NEVADA:** Lake Tahoe, Zephyr Cove, [39.01, -119.94], 1889 m, 9.XII.1986, leg. A. Smetana (1 CNC). **OREGON:** 16 mi NE Bly Deming Creek Road, [42.55, -120.76], 1828 m, 21.VII.1979, leg. J. M. Campbell & J. Schuh (3 CNC); Grant County, Strawberry Range, Strawberry Lake, [44.3, -118.68], 1920 m, 4.VI.1989, leg. A. Smetana (20 CNC); Klamath County, Gearhart Mountain, [42.51, -120.86], 2194 m, 24.VI.1974, leg. A. & D. Smetana (1 CNC); Klamath County, Mare's Egg Springs, 7.3 mi SW Fort Klamath, [42.66, -122.08], 25.VI.1974, leg. A. & D. Smetana (2 CNC); Union County, Blue Mountain Road 62, Jarboe Creek, [45.80, -117.85], 1200 m, 29.V.1989, leg. A. Smetana (1 CNC). **WASHINGTON:** Blue Mountain, [45.5, -118], 914 m, 29.VIII.1923, leg. M. C. Lane (1 CNC).

Redescription. Measurements ♂♂ (n = 3): HW = 1.56–1.78 (1.63); HL = 1.33–1.49 (1.39); HL/HW 0.84–0.87 (0.86); PW = 2.04–2.22 (2.11); PL = 1.80–2.00 (1.87); PL/PW 0.88–0.90 (0.89); EW = 2.16–2.29 (2.20); EL = 2.02–2.11 (2.06); EL/EW 0.92–0.95 (0.94); EL/PL 1.06–1.14 (1.10); PW/HW 1.49–1.53 (1.52); forebody length 5.18–5.60 (5.33). ♀♀ (n = 6): HW = 1.53–1.73 (1.64); HL = 1.27–1.40 (1.35); HL/HW 0.77–0.86 (0.82); PW = 1.96–2.29 (2.09); PL = 1.73–2.00 (1.85); PL/PW 0.87–0.91 (0.89); EW = 2.00–2.44 (2.18); EL = 1.93–2.29 (2.07); EL/EW 0.92–1.02 (0.95); EL/PL 1.09–1.18 (1.12); PW/HW 1.46–1.63 (1.55); forebody length 4.98–5.69 (5.27).

Medium sized species; body dark brown to black (Fig. 10B).

Head black, distinctly transverse with eyes medium sized (EyL/TL = 1.81–2.14 (1.99)), microsculpture of transverse waves, with two interocular punctures

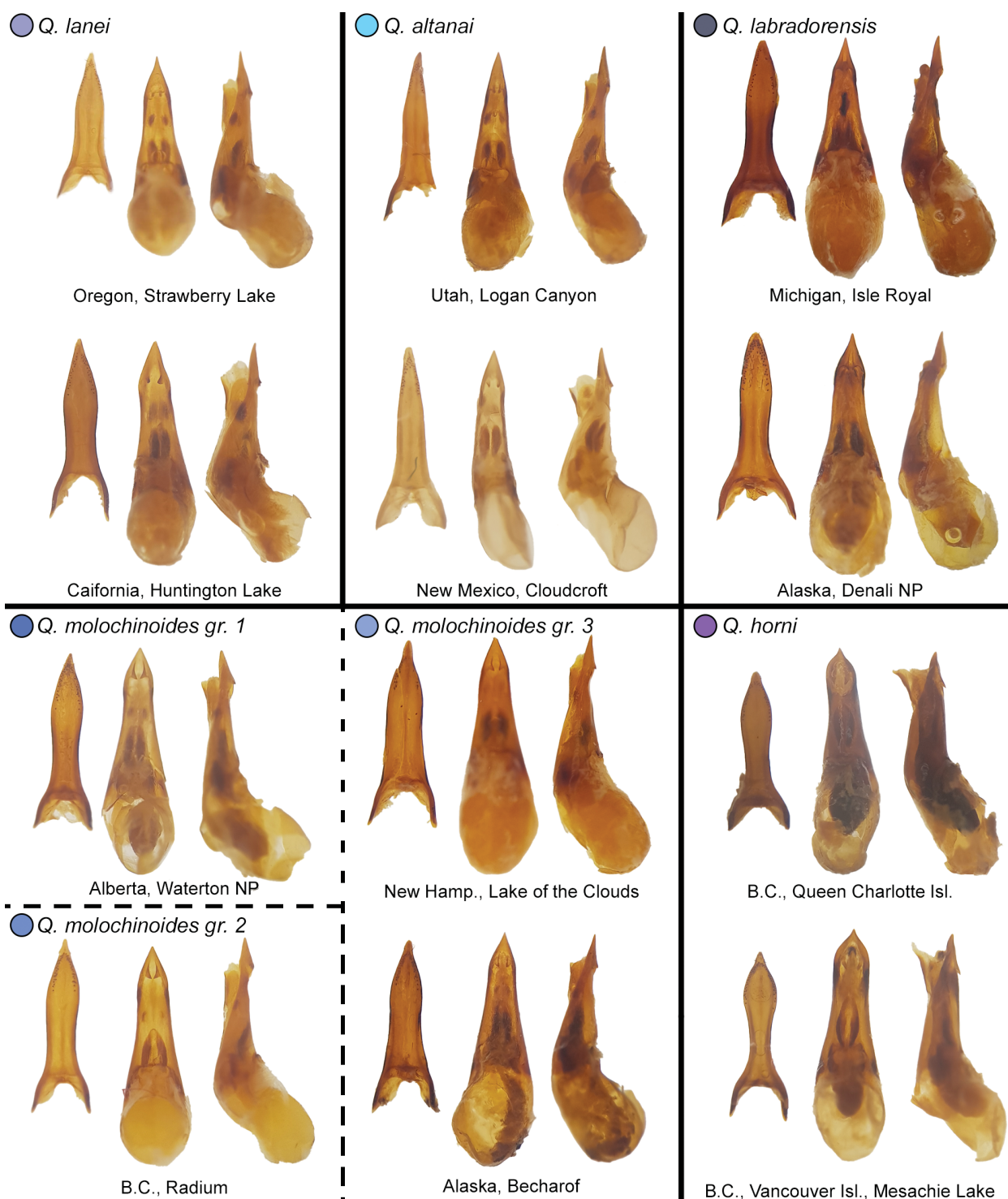


Fig. 17. Variation in genitalic morphology of species from *Quedius molochinoides*-group. From left to right for each specimen, first paramere then median lobe (parameral view) and lastly median lobe (lateral view) are given. For each specimen locality is noted underneath.

between anterior frontal punctures (Fig. 6G); antennae and palpi dark with joints pale reddish, all antennomeres elongate, except last and penultimate antennomere almost transverse.

Thorax: pronotum black, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond level of first puncture of dorsal row; scutellum

sparsely punctured and pubescent; elytra variable in coloration, from all black or reddish brown to occasionally dark with reddish sutural margins, uniformly pubescent, punctures clearly separated, quadrate or slightly wider than long, slightly longer than pronotum; legs reddish brown with inner face of tibia and inner surface of femur darkened and tarsi paler.

Abdomen dark brown to black, tergites uniformly punctured, with clear iridescence.

Male. Aedeagus (Figs 16D, 17): paramere lanceolate, rather broad, without clear basal attenuation, extending to apex of median lobe, with small sensory peg setae forming two irregular rows meeting in an irregular cluster below apex; median lobe lanceolate, broad, with sides slightly constricting until abrupt constriction near pointed apex, on parameral side with two blunt teeth simply protruding inward and slightly basad; internal sac with two larger oval and two smaller rounder sclerites.

Differential diagnosis. *Quedius lanei* can be distinguished from *Q. laticollis* and *Q. strenuus* by the presence of two additional setiferous punctures between the anterior frontal punctures. It can be distinguished from *Q. labradorensis* by the darker body and the clearly darkened basal three antennomeres. It can be distinguished from other members of the *molochinoides*-group (*Q. altanai*, *Q. horni*, and *Q. molochinoides*) only by the male genitalia, specifically by the paramere, which is parallel-sided to constricted at base, and the broad median lobe with a constricted apex and two blunt teeth pointing in and downwards. However, *Q. lanei* does not seem to co-occur with any other species of the *molochinoides*-group, this fact reducing the need of genitalia investigation in all cases.

Comments. A series of specimens in SMETANA (1971) including one Hatch paratype from Fish Lake in Summerland, British Columbia ascribed to *Q. lanei* was found to belong to *Q. molochinoides*. *Quedius lanei* does not occur in Canada. Paratypes of *Q. lanei* from Idaho were found to belong to *Q. altanai* and have thus been moved to this species.

Bionomics. *Quedius lanei* prefers mountainous areas and occurs only at high elevations with records from roughly 1000 m in the northern part of its range to up to 2200 m in the southern part. Little is known about the preferred habitat of the species, but based on the examined records it seems to be found mainly in wet debris near creeks or mountain lakes. For example, the Oregon specimens from Klamath County were collected by sifting wet moss and deciduous leaf litter (willow) at the edges of fast-running creeks or by sifting wet debris on the bottom of a dried-out pond in a coniferous forest (SMETANA 1976).

Distribution. *Quedius lanei* is currently known from high elevation sites on the eastern slopes and foothills of Cascades, the Sierra Nevada and the Blue Mountains (ecoregions 6.2.8, 6.2.9 and 6.2.12, Fig. 21). It is found from southeastern Washington through Oregon to much of eastern California and limited areas of western Nevada. In the north it does not seem to extend into the northern part of the Cascades, although based on the ecoregions it may be present quite far north on the eastern slopes. To the northwest it is replaced by *Q. horni*. *Quedius lanei* was formerly considered to also include specimens from central and southern Rockies, but we here show that these belong to a different species *Q. altanai* described as new herein.

Quedius molochinoides Smetana, 1965

(Figs 1, 4, 5, 10D,E, 16E, 17, 21, 22)

Quedius molochinoides Smetana, 1965a: 35 [Type locality: Newfoundland: Ha-Ha Bay]

Quedius molochinoides miquelonensis Smetana, 1965a: 36 [Type locality: Miquelon], **syn. nov.**

References. SMETANA (1971): 141 (characters and distribution); (1976): 174, (1978): 826, (1981): 640 (distribution); DOWNIE & ARNETT (1996): 391 (characters and distribution).

Type material examined. *Quedius molochinoides*: HOLOTYPE: ♂ (CNC), labelled: "NW Newfoundland Ha-Ha Bay N:o 103. 18.VII.49 Lindroth / Holotypus *Quedius molochinoides* m. / *Quedius molochinoides* m. 63 Smetana det. 19 / Holotype CNC No. 9474 *Quedius molochinoides* s. s. Smet. / CNC". PARATYPE (labelled as allotype): same collection data as holotype (1 ♀ CNC).

Quedius molochinoides miquelonensis: HOLOTYPE: ♂ (CNC), labelled: "Miquelon N:o 353 8-10.VIII.51 Lindroth / Holotypus". PARATYPE (labelled as allotype): "Quedius molochinoides miquelonensis m. / 1963 Smetana det. / *Quedius molochinoides miquelonensis* m. Smetana det. 1963/ Allotype CNC No. 9475 *Quedius molochinoides miquelonensis* Smet." (1 ♀ CNC).

Additional material examined. CANADA: ALBERTA: Castle river valley, SW corner of township, [49.49, -114.22], along the road, under rocks etc., 23.V.1990, leg. B.F. & J.L. Carr (1 CNC); Cirrus Mountain, Banff National Park, [52.16, -116.97], 1676 m, 16.VI.1968, leg. Campbell & Smetana (1 CNC); Crow's Nest Pass, Rocky Mount, [49.59, -114.53] (1 CNC); Kananaskis Forest Experiment Station, [51, -115.1], 1.VIII.1971, leg. J. M. & B. A. Campbell (1 CNC); Mile S Seebe, [51.09, -115.06], 26.VII.1968, leg. A. G. Raske (1 CNC); Tp. 5 Rge.3 W.5 Mer, [49.39, -114.34], leg. 23.VI.1994, leg. B. F. & J. L. Carr (1 CNC); Waterton, [49.05, -113.9], 10.VII.1930, leg. Washur (1 CNC); Waterton Lks. Nat. Pk., Cameron Lk., 49.0833, -113.9164, 12.VI.1973, leg. J. Redner & C. Starr (1 CNC); Waterton Lakes National Park, picnic area on Cameron Creek near Cameron Lake, [49.05, -113.98], 1630 m, pitfall trap, 7-11.VI.1980, leg. I. M. Smith (5 CNC); Waterton Lake National Park, Cameron Lake, [49, -114.04], berlese trap, grassy tussock, seepage area, 7.VI.1980, leg. I. M. Smith (1 CNC); Waterton Lake National Park, Crandell Lake Trail, [49.06, -113.94], berlese trap, Alder litter, 13.VI.1980, leg. I. M. Smith (1 CNC); Waterton Lakes National Parks, Lower Waterton Lake, 49.09, -113.85, 1370 m, ex moss, 26.VI.1980, leg. J. M. Campbell (7 CNC); Waterton Lakes National Park, Cameron Lake, [49, -114.04], pitfall trap, wet meadow, 8.VI.1980, leg. I. M. Smith (14 CNC); Waterton Lakes National Park, Cameron Creek picnic ground, [49.04, -113.98], pitfall trap, edge meadow, 17-28.VI.1980, leg. I. M. Smith (2 CNC); Waterton Lakes National Park, Maskinonge Lake, [49.1, -113.83], 1310 m, sifting litter, Populus litter, 14.VI.1980, leg. J. M. Campbell (1 CNC); Waterton Lakes National Park, near Highway 6, 4.4 km SE Junction Highway 5, [49.08, -113.79], pitfall trap, edge of beaver pond, 12-19.VI.1980, leg. I. M. Smith (2 CNC); Waterton Lakes National Park, Crypt Lake, [49, -113.84], 1981 m, under rocks, 22.VI.1980, leg. J. M. Campbell (1 CNC); Waterton Lakes National Park, near Lower Rowe Lake, [49.05, -114.05], berlese trap, moss from spring seepage area, 18.VI.1980, leg. I. M. Smith (4 CNC); Waterton Lakes National Park, Lookout Butte Picnic Site, [49.72, -113.56], flight interception trap, 9-14.VI.1980, leg. J. M. Campbell (1 CNC); Waterton Lakes National Park, Km 9 Chief Mountain Highway, [48.91, -113.43], 1371 m, flight interception trap, 7.VII.1980, leg. H. J. Teskey (38 CNC); Waterton Lakes National Park, near Highway 6 4.4 km SE Junction Highway 5, [49.08, -113.79], pitfall trap, in meadow by beaver pond, 7-11.VI.1980, leg. I. M. Smith (3 CNC); Waterton Lake National Park, Rowe Lakes Trail, [49.05, -114.06], 1828 m, under bark, 12.VI.1980, leg. J. M. Campbell (2 CNC); Waterton NP, Rowe Creek, 49.0833, -113.9164, 1664 m, 2.VIII.1976, leg. J. M. Campbell (1 CNC). BRITISH COLUMBIA: Amiskwi River, Yoho National Park, [51.38, -116.55], 7.VIII.1971, J. M. & B. A. Campbell (1 CNC); Bowron Lake, [53.23, -121.37], 15.X.1953, leg. G. S. Smith (1 ♂ CNC); Creston, [49.09, -116.51], 29.VII.1956, leg. G. S. Smith, (1 CNC); 8 mi W Creston, [49.09, -116.72], ex river debris, 10.VI.1968, leg. Campbell & Smetana, (1 CNC); 21 mi W Creston, [49.09, -117.04], ex river debris, 9.VI.1968, leg. Campbell & Smetana (1 CNC); Fish Lake, Summerland, [49.84, -115.44], 27.X.1931, leg. A. N. Gartell (2 CNC); Highway 37, 30km S Dease Lake, [58.43, -129.99], 2.VII.1987, leg. L. Carr (2 CNC); Highway 37A, Bear Glacier, [56.09, -129.66], 6-7.VII.1987, leg. Larson & Carr (1 CNC); Kootenay National Park near Dog Lake, [50.78, -115.92], 24.V.1981, leg. I. Askevold (1 CNC); Mt. Revelstoke, [51.09, -118.04], 1737 m, under rocks in swamp, 1.VII.1952, leg. G. J. Spencer (1 CNC); Mount Revelstoke, [51.09, -118.04], 10.VII.1952, leg. G. J. Spencer (1 CNC); Radium, [50.62, -116.07], 26.IV.1994, leg. B.F. & J. L. Carr (1

CNC); Sinclair Creek, Kootenay National Park, [50.63, -116.06], 1828 m, 12.VI.1968, leg. Campbell & Smetana (1 CNC); Summerland, [49.6, -119.67], 27.X.1931, leg. A. N. Gartell (1 CNC); Trinity Valley, [50.4, -118.91], under old log, 16.IX.1943, leg. H. B. Leech, (1 CNC); Vernon, [50.31, -119.28], under stone, 18.IX.1939, leg. H. Leech (1 CNC); Vernon, Deep Lake, [50.79, -120.34], rotten log, hibernating, 10.IV.1989, leg. H. Leech, (1 CNC); Vernon, Monashee Mountains, [50.27, -119.27], 1371 m, under stone, 14.X.1934, leg. H. Leech (1 CNC). **ONTARIO:** 12 mi NE Moosonee, [51.44, -80.45], 1.VII.1973, leg. R. Parry & J. M. Campbell (1 CNC); Gregoire Mills, [49.29, -81.95], 22.VI.1973, leg. J. Redner & C. Starr (1 CNC). **YUKON:** Mile 11 Canol River, [61.98, -132.45], 1219 m, 22.VIII.1962, leg. P. J. Skitsko (1 CNC); Slim's River km 1705 Alaska Highway, [61.01, -138.51], ex marsh, 7.VII.1981, leg. Bright (1 CNC). **QUEBEC:** Lac Mitis, 48.30, -67.80, 9.-12.VII.1993, leg. Hébert & Jobin (1 LFC); Parc Gaspesie (Gaspé-O), Mont Logan, [48.89, -66.64], 1040 m, Spruce forest clearing with moss and ericaceae, pitfall traps, 2.-14.VII.1993, leg. F. Landry (1 CNC). **USA: ALASKA:** Becharof NWR, Island Arm East, 57.76107, -155.98752, S facing slope, *Salix*, fern, & cow parsnips, pitfall traps, 29.VI.-5.VII.2007, leg. Savage (4 UAM); Chichagof Island, 57.98256, -135.21811, 970 m, *Dryas*, *Salix*, *Cladonia portentosa*, ground search, 15.VII.2013, leg. Ridling (1 UAM); Chichagof Island, 57.98708, -135.20357, 702 m, *Nephrophyllidium crista-galli*, *Geranium erianthum*, *Artemisia arctica*, pitfall traps, 14.-15.VII.2013, leg. Ridling (7 UAM); S Chilkat Peninsula, 58.42520, -135.15205, 687 m, subalpine, *Vaccinium*, *Cornus*, pitfall traps, 11.-12.VII.2010, leg. D. Sikes (1 ♀ UAM); Haines, Flower Mountain, 59.39353, -136.31129, alpine *Sanguisorba*, *Carex*, pitfall traps, 15.-16.VII.2010, leg. D. Sikes (3 UAM); Hope, Kenai Peninsula, [60.89, -149.65], 27.VII.1951, leg. W. J. Brown (1 CNC); Kenai Mountain Creek Above Tern Lake Campground, [60.53, -149.53], 274 m, 13.VI.1978, leg. Smetana & Becker (1 CNC); Kenai Mountain, 2 mi S Moose Pass, [60.44, -149.37], 182 m, 30.V.1978, leg. Smetana & Becker (1 CNC); Kenai Mountain, 22 mi N Seward, [60.44, -149.45], 152 m, 27.V.1978, leg. Smetana & Becker (2 CNC); Lituya Bay, Cenotaph Island, [58.64, -137.57], 182 m, 22 Pitfalls in Alder Woods, 25.-26.V.1977, D. Mann, (1 CNC); Moose Pass, Kenai Peninsula, [60.49, -149.42], 16.VI.1951, leg. W. J. Brown (2 CNC); Mount Hawthorne, 58.23652, -134.23904, 748m, subalpine meadow, low ridge top, baited pitfall traps, 22.-23.VII.2013, leg. Ridling (4 UAM); Palmer, 61.60, -149.10, pasture, muskox dung, 1.VIII.1988, leg. Pilny (1 DEBU); Seward [60.12, -149.39], 14.V.1951, leg. W. J. Brown (2 CNC); Skagway, 59.50, -135.10, moist pasture, cow & horse dung, 15.VII.1988, leg. Pilny (1 DEBU); Valdez, [61.14, -146.35], on snow, 29.IV.1972, leg. Dick (1 UAM); Valdez, 61.1167, -146.2667, *Picea* & *Populus* forest, under wood and stones, wet vegetated gravel, 10.VIII.1988, leg. Pilny (2 DEBU). **IDAHO:** Moscow, [46.80, -116.85], 14.IV.1916, leg. A. C. Burrill (1 CNC). **NEW HAMPSHIRE:** Mount Washington, [44.27, -71.31], 1874, leg. Blanchard (4 MCZ); White Mountains, Peabody River, [44.39, -71.15], 1828 m, 12.VII.1925, leg. Quirsfeld (1 CNC). **NEW YORK:** Indian Falls, Mount Marcy, [44.11, -73.92], 2.IX.1942, leg. H. Dietrich (1 ♂ CNC); Lake Tear, Mount Marcy, Essex County, [44.11, -73.93], 27.VII.1922, leg. H. Notman (1 CNC).

Redescription. Measurements ♂♂ (n = 2): HW = 1.56–1.71 (1.63); HL = 1.36–1.44 (1.40); HL/HW 0.84–0.87 (0.86); PW = 2.00–2.22 (2.11); PL = 1.91–2.00 (1.96); PL/PW 0.90–0.96 (0.93); EW = 2.02–2.36 (2.19); EL = 1.84–2.29 (2.07); EL/EW 0.91–0.97 (0.94); EL/PL 0.97–1.14 (1.05); PW/HW 1.48–1.54 (1.51); forebody length 5.11–5.73 (5.42). ♀♀ (n = 5): HW = 1.69–1.89 (1.77); HL = 1.38–1.56 (1.45); HL/HW 0.81–0.83 (0.82); PW = 2.20–2.38 (2.26); PL = 2.00–2.13 (2.07); PL/PW 0.89–0.93 (0.92); EW = 2.22–2.49 (2.36); EL = 2.09–2.22 (2.18); EL/EW 0.88–0.96 (0.93); EL/PL 1.02–1.11 (1.06); PW/HW 1.52–1.63 (1.55); forebody length 5.53–5.87 (5.70).

Medium sized species; body dark brown to black (Figs 10D,E).

Head black, distinctly transverse with eyes medium sized (EyL/TL = 1.76–1.94 (1.87)), microsculpture of transverse waves, with two interocular punctures between

anterior frontal punctures (Fig. 6G); antennae and palpi dark with joints reddish pale, all antennomeres elongate, except last and penultimate antennomere almost transverse.

Thorax: pronotum dark brown to black, slightly wider than long, clearly wider than head, with microsculpture of transverse waves, three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond level of first puncture of dorsal row; scutellum sparsely punctured and pubescent; elytra variable in coloration, from all black to reddish brown, occasionally dark with reddish sutural margins, uniformly pubescent, with punctures clearly separated, slightly wider than long, same length to slightly longer than pronotum; legs reddish brown with inner face of tibia and inner femur darkened and tarsi paler.

Abdomen dark brown to black, tergites uniformly punctured, with clear iridescence.

Male. Aedeagus (Figs 16E, 17): paramere lanceolate, rather broad, parallel-sided or with slight basal attenuation, reaching apex of median lobe, with small sensory peg setae in two irregular rows meeting below apex to form a slightly pointed 'arrowhead' shape; median lobe lanceolate broad, sides slightly constricting until abrupt constriction near pointed apex, on parameral side with two large pointed teeth folded from lateral margin to form almost closed cavity; internal sac with two larger oval and two smaller rounder sclerites.

Differential diagnosis. *Quedius molochinoides* can be distinguished from *Q. laticollis* and *Q. strenuus* by the presence of two additional setiferous punctures between the anterior frontal punctures. It can be distinguished from *Q. labradorensis* by the darker body including the clearly darkened basal three antennomeres. It can be distinguished from other members of the *molochinoides*-group (*Q. altanai*, *Q. horni*, and *Q. lanei*) only by the male genitalia, specifically by the broad median lobe with two large, flattened pointed teeth strongly folded to form an almost closed cavity. *Quedius molochinoides* can also be accidentally confused with *Q. brunnipennis* Mannerheim, 1843 from the subgenus *Raphirus*, but will easily be recognized by the entire labrum and by more parallel-sided abdomen.

Synonymic notes. The subspecies *Q. m. miquelonensis* was described from the islands of St. Pierre and Miquelon as a slightly broader and larger form with the male sixth sternite wider and more sharply triangular (SMETANA 1971a) compared to the nominal subspecies. Generally, species within *Quedius* s. str. display notable intraspecific variation in body size. With the new material examined here the observed variation between the two subspecies falls within the limits of the variation observed within the widely distributed nominal subspecies. Thus, we consider *Quedius molochinoides miquelonensis* Smetana, 1965 syn. nov. a junior subjective synonym of *Quedius molochinoides* Smetana, 1965.

Comments. One of the paratypes of *Q. lanei* from Fishlake in Summerland of British Columbia, Canada was found to belong to *Q. molochinoides*. Specimens from the Okanagan area (Summerland, Copper Mountain and Vernon) are slightly different from the nominal species of

Q. molochinoides and others of *Q. molochinoides*-group 3, specifically their genitalia being more slender. Images of the genitalia for two of these are provided in the supplementary material (Fig. S5). We are hesitant to describe them as a new species as we are lacking genetic barcodes as evidence for this. That said they may very well represent yet another species new for science.

Bionomics. *Quedius molochinoides* prefers meadows or open forests where it has mainly been collected in litter, grass tussock or under rocks from low elevations up to 2000 m. Specimens from Newfoundland were found on more or less open ground with rich vegetation or in leaf litter under bushes near river edges (SMETANA 1971a), in British Columbia some specimens were collected in river flood-debris and by sifting wet debris and fallen leaves under bushes at mountain creeks, other specimens were found under rocks near snow in Kootenay National Park (SMETANA 1971a). In Alaska the species was collected using pitfall traps in subalpine meadows and shrublands. Immature specimens were collected in July in Alberta and Idaho and from July to September on Mt. Washington in New Hampshire (SMETANA 1971a).

Distribution. *Quedius molochinoides* is a northern species distributed transcontinentally across boreal North America from Labrador and Newfoundland to Alaska (ecoregions 4, 5, 6.1 and partly 6.2 and 7.1, Fig. 21). To the south it is found at higher elevation sites, e.g. in the northern Rockies in the west (north part of ecoregion 6.2) and Mount Washington and Mount Marcy in the East (ecoregion 5.3). The northernmost records are from Valdez in Alaska and Churchill in Manitoba, suggesting that the species extends throughout the boreal ecoregion of the continent. There is a single record from Moscow Mountains in Central Idaho, which represents the southernmost record in the Rockies (ecoregion 6.2.3). COI barcoding showed that *Q. molochinoides* forms three distinct clusters (Figs 4, 5)). *Quedius molochinoides*-group 1 is known from the Canadian national parks of Banff and Waterton Lakes and is delimited by the Rocky Mountains Trench to the west and the Canadian plains to the East (part ecoregion 6.2.4, Fig. 22). *Quedius molochinoides*-group 2 is found in the Canadian Rockies, west of the Rocky Mountains trench and towards the north continuing to the Pacific Coast in Alaska all the way to the Kenai Peninsula northwards (ecoregion 6.2.1, 6.2.2, 6.2.3 and partly 6.1 and 7.1). *Quedius molochinoides*-group 3 is present from the Becharof Peninsula of Alaska in the west across the North American boreal region to glacial refugia of New England, Quebec and Newfoundland in the east (ecoregions 4, 5, and partly 6.1 and 7.1).

Quedius laticollis-group

Diagnosis. Species of medium size with variable coloration of elytra and appendages, from completely dark to brown, reddish, or yellowish pale. Eyes smaller, temples larger, with temporal puncture separated from posterior margin of eye by distance equal to diameter of this puncture. Frons without interocular punctures (Fig. 6F). Scutellum punctate and setose. Pronotum without puncture(s) in the posterior part of the sublateral row. Restricted to the Nearctic Region.

Quedius laticollis (Gravenhorst, 1802)

(Figs 1, 4, 9D,E, 14E, 22)

Quedius laticollis (Gravenhorst, 1802): 173 [Type locality: Baltimore]
Quedius neomolochinus Korge, 1962b: 333 [Type locality: Washington, D.C.]

References. ERICHSON (1840): 536 (characters); MANNERHEIM (1843): 233 (characters); GRAVENHORST (1847): 227 (characters); KRAATZ (1857): 501 (characters); GANGLBAUER (1895): 403 (characters); FAUVEL (1902): 115 (characters); PORTA (1907): 129 (characters); GRIDELLI (1924): 81 (characters); SCHEERPELTZ (1933): 1457 (characters); MÉQUIGNON (1937): 3 (characters); SMETANA (1958): 364, (1965a): 39 (characters); (1971a): 136 (characters and distribution); (1973): 1427 (lectotype designation, synonymy); (1978a): 826, (1981): 640, (1990): 98 (distribution), DOWNIE & ARNETT (1996): 391 (characters and distribution), GOLDEN & CRIST (2000): 532 (biology), TISHECHKIN & CLINE (2008): 335 (biology).

Material examined. CANADA: ONTARIO: Manitoulin I., Kip Fleming Tract, 8 km SW Gore Bay, 45.8702, -82.5418, under stones oak savannah/alvar, 27.V.2010, leg. S. M. Paiero. (1 DEBU); Pinery Prov. Pk., 43.30, -81.83, oak savannah, ex. Leaf litter, reared from larva, 17.IV.2010, leg. A. Brunke (1 DEBU); Rondeau Provincial Park, Spicebush Trail, [42.30, -81.85], mushroom and litter, 4.VI.1985, leg. J. M. Campbell & A. Davies (3 CNC). QUEBEC: Levis, [46.73, -71.24], 25.VI.1979, leg. C. Chantal (1 CNC). USA: ALABAMA: Auburn, [32.59, -84.47], 8.IV.1978, leg. E. J. Kiteley (1 CNC); Ophelika, [32.65, -85.38], 23.I.1974, leg. E. J. Kiteley (1 CNC). ARKANSAS: Franklin County, Shores Lake, Ozark National Forest [35.63, -93.95], 20.V.1986, leg. J. M. Campbell (2 CNC); Logan County, Cove Lake, 9 mi SE Paris, [35.23, -93.63], ex debris at edge of lake, 25.V.1986, leg. J. M. Campbell (2 CNC); Logan County, 1km E Lookout Mount. Magazine, [35.16, -93.94], sifting litter, leaf litter along edge of stream, 23.V.1986, leg. J. M. Campbell (2 CNC); Logan County, Mount. Magazine, Lookout, [35.16, -93.64], sifting litter, deciduous leaf litter, 26.V.1986, J. M. Campbell (1 CNC); Mobile, [30.69, -88.06], 22.VI.1919 (1 MCZ); Newton County, Buffalo National Reserve, Steel Creek, [36.03, -93.33], treading clumps of Carex, 17.V.1986, leg. J. M. Campbell (2 CNC); Pulaski County, Pinnacle Mountain State Park, Base Trail, [34.84, -92.49], ex flood debris on river, 11.V.1986, leg. J. M. Campbell (1 CNC); Searcy County, Ozark National Forest, Forest Service Road 1205, Richland Creek, [35.77, -95.99], sifting litter, leaf litter along edge of stream, 15.V.1986, leg. J. M. Campbell (2 CNC); Stone County, Blanchard Springs State Park, [35.96, -92.17], 182 m, 18.V.1973, leg. D. H. Kavanaugh & H. Goulet (2 CNC). FLORIDA: Alacha Co., Gainesville, [29.63, -82.33], leaf litter & rotten logs, 5.V.1981, leg. Watrous (1 FMNH); Fort Walton Beach, [30.41, -86.61], 21.III.1975, leg. E. J. Kiteley (1 CNC); Leon Co., Tallahassee, [30.43, -84.29], mixed hardwood, 19.XI.1976, leg. Marshall & Justice (2 ♂♂ 3 ♀♀ FMNH); St. Augustine, [29.89, -81.31], leg. Liebeck (1 CNC); Suwanee Co., 15 mi SW Live Oak Hwy. 51., [30.11, -83.17], pine and hardwood litter, 24.III.1977, leg. O'Brien (1 ♂ FMNH); Volusia Co., 2 mi S Enterprise, [28.85, -81.30], leaf litter, 23.VIII.1965, leg. Suter (1 ♂ FMNH). ILLINOIS: Union County, Pine Hills near McCann Springs, [37.58, -89.43], 6.V.1976, leg. A Smetana, (4 CNC); Union County, 5 mi NE Reynoldsville, [37.40, -89.28], 9.V.1976, leg. A Smetana (1 CNC); St Clair County, [38.46, -89.95], 6.X.1901, leg. G. W. Bock (1 CNC); Willow Springs, [41.72, -87.86], 16.VIII.1923 (1 MCZ). LOUISIANA: Calcasieu Parish, Choupique Bayou, 7 mi N Hackberry, [30.13, -93.36], 16.IV.1976, leg. A. Smetana (27 CNC); Calcasieu Parish, 2 mi W Sulphur, [30.24, -93.45], 13.IV.1976, leg. A. Smetana (1 CNC); Corney Lake, [32.91, -92.74], 26.VI.1983, leg. B. F. & J. L. Carr (2 CNC). MARYLAND: Baltimore, [39.31, -76.61], 6.VII.1909, leg. F. E. Blaisdell (1 CNC); Baltimore, [39.28, -76.62] (1 MCZ). MASSACHUSETTS: Barnstable Co., Woods Hole, 41.5304, -70.6533, 30 m, near small pond, 30.IX.2010, leg. BIOBus (3 CMNH). MISSISSIPPI: Oktibeha County, Craig Springs, [33.31, -88.92], peripheral to cult. Cotton, pitfall trap, 10.X.1979, leg. G.L. Snodgrass (2 CNC). MISSOURI: Williamsville, [36.97, -90.54], deciduous duff, 12.VII.1955, leg. E. C. Becker (1 CNC). NEW JERSEY: Woodbury, [39.83, -75.15], VIII.1920, leg. H. A. Wenzel (1 CNC). NEW YORK: Inlet Valley, Ithaca, [42.44, -76.5], 18.X.1917, leg. H. Dietrich (1 CNC). NORTH CAROLINA: Ocracoke

Island, Ocracoke, [35.12, -75.93], 10.VIII.1972, leg. A. Smetana (2 CNC). **OKLAHOMA:** Latimer Co., [34.85, -95.25], IV.1994, leg. Stephen (5 TAMU). **PENNSYLVANIA:** Allegheny County, [40.46, -79.98], leg. E. A. Klages (1 CNC), Frankford, [40.01, -75.07], leg. H. W. Wenzel (1 CNC). **SOUTH CAROLINA:** Camden, [34.25, -80.60], 23.VI.1929, leg. Darlington (1 MCZ). **TEXAS:** Anderson Co., 15 mi SSE Palestine, 31.5667, -95.4667, pitfall traps, 1.-10.XI.1996, leg. Yantis (2 TAMU); Brazos Co., Koppe's Bridge, 5 mi SW College Station, [30.57, -96.33], leaf litter, hardwood forest, 15.I.1994, leg. Riley (1 TAMU); Columbus, [29.70, -96.54], VIII.1906, leg. C. V. Riley (1 CNC). Orange County, Bridge City, [30.02, -93.83], 18.IV.1976, leg. A. Smetana (33 CNC); Orange County, 3 mi NW Orange, [30.15, -93.81], 17.IV.1976, leg. A. Smetana (3 CNC); Sabine Co., Sabine Nat. Forest, 3.2 mi E Hemphill, [31.35, -93.79], pine litter, 29.VII.1975, leg. Ashe (1 TAMU); Trinity County, 2.5 mi NW Apple Springs, [31.24, -95.01], 23.IV.1976, leg. A. Smetana (1 CNC); Trinity County, 12 mi SW Lufkin, [31.20, -94.99], 22.IV.1976, leg. A. Smetana (3 CNC). **VIRGINIA:** Arlington Co., Roaches Run, [38.86, -77.04], 15.IV.2013, leg. J. R. Fisher (1 ♀ FMNH); Lee Co., Young-Fugate Cave, [36.79, -82.97], 25.VI.1963, leg. Holsinger (1 ♀ CMNH). **WEST VIRGINIA:** Glen Dale, [39.94, -80.75], grassy hillside, 29.VII.1973, leg. J. H. Redner (1 CNC).

Redescription. Measurements ♂♂ (n = 3): HW = 1.67–1.76 (1.70); HL = 1.33–1.40 (1.37); HL/HW 0.80–0.82 (0.80); PW = 2.20–2.24 (2.21); PL = 1.96–2.04 (1.99); PL/PW 0.89–0.91 (0.90); EW = 2.18–2.29 (2.24); EL = 1.93–2.07 (1.99); EL/EW 0.86–0.92 (0.89); EL/PL 0.99–1.01 (1.00); PW/HW 1.60–1.65 (1.62); forebody length 5.22–5.51 (5.36). ♀♀ (n = 4): HW = 1.60–1.84 (1.71); HL = 1.29–1.47 (1.38); HL/HW 0.80–0.83 (0.81); PW = 2.04–2.31 (2.19); PL = 1.89–2.22 (2.04); PL/PW 0.91–0.96 (0.93); EW = 2.09–2.44 (2.30); EL = 1.91–2.16 (2.03); EL/EW 0.86–0.91 (0.88); EL/PL 0.97–1.01 (1.00); PW/HW 1.57–1.60 (1.58); forebody length 5.09–5.84 (5.46).

Medium sized, robust species; body dark brown to black (Figs 9D,E).

Head black, distinctly transverse with eyes medium sized (EyL/TL = 1.61–1.88 (1.76)); microsculpture of transverse waves; no additional punctures between anterior frontal punctures (Fig. 6F); antennae and palpi reddish, all antennomeres elongate.

Thorax: pronotum dark brown to black, slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row with its posteriormost puncture reaching just beyond level of first puncture of dorsal row; scutellum punctured and pubescent; elytra most often dark brown more rarely fully darkened, uniformly pubescent, slightly wider than long, roughly same length as pronotum; legs reddish brown with inner face of tibia and inner femur darkened.

Abdomen dark brown to black, tergites uniformly punctured, without clear iridescence.

Male. Aedeagus (Fig. 14E): paramere rather broad lanceolate without clear medial attenuation, reaching just beyond apex of median lobe, with sensory peg setae forming a distinct triangular patch; median lobe broad with gentle constriction to a point at apex, on parameral side with two small teeth protruding slightly basad, positioned at level near lower level of peg setae patch of paramere.

Differential diagnosis. *Quedius laticollis* is very similar in North America to the introduced species *Q. molochinus*, from which it can be confidently distinguished through

examination of male genitalia. Other differences include slightly more stout antennae with less elongate, darker middle antennomeres in *Q. molochinus*. Also, the elytra in *Q. laticollis* have a finer and denser punctation and are most often brownish-red, yellowish, or dark in coloration, where it is either brick red or dark in *Q. molochinus*. *Quedius laticollis* is also similar to *Q. strenuus*, which replaces *Q. laticollis* in the Great Plains. However, all examined specimens of *Q. strenuus* are completely dark with pale appendages, contrary to the rarely fully darkened specimens of *Q. laticollis*. For confident separation of *Q. laticollis* and *Q. strenuus* the position of the peg setae of the paramere are diagnostic as they form two distinct rows in *Q. strenuus* and a triangular patch in *Q. laticollis*. *Quedius laticollis* cannot be confused with any other North American *Quedius* as they either have interocular punctures on frons or (from other subgenera) have clear medial incision of labrum and abdomen notably tapering apicad.

Synonymic notes. *Quedius neomolochinus* Korge, 1962 was originally described from Baltimore most likely without knowledge of Gravenhorst's description of *Q. laticollis*, which was at that time a synonym of *Q. molochinus*. KORGE (1962) also described a color variant (black with paler elytral suture and posterior margin) of *Q. neomolochinus* as *Q. marginatus* Korge, 1962 which is unavailable name according to the ICZN Article 45.6. *Quedius marginatus* was thought to be identical with *Q. neomolochinus* by SMETANA (1971a) when he revised the North American fauna of the tribe Quediini. Later SMETANA (1973) realized that *Q. laticollis* was identical to Korge's *Q. neomolochinus* and established the respective synonymy along with the lectotype designation for *Q. laticollis*. Our data fully corroborates such established concept of *Q. laticollis*.

Bionomics. *Quedius laticollis* is a rather common generalist found in a large variety of damp lowland habitats. Specimens have been reported from sphagnum in a tamarack swamp (SMETANA 1971a), from sifting damp leaves in a deciduous forest in Florida, from flood-debris along the edges of swamps and marshes, from tufts of swamp grass dumped into water in Louisiana and Texas (SMETANA 1978a), from forest floor litter (hardwood and pine) and from under rocks in Arkansas, and around cotton and soybean fields in Mississippi (SMETANA 1990). One of us (AJB) has collected this species under large boulders in spring in an open scrubby alvar habitat with few oak trees (Manitoulin, Island, Ontario, Canada). This habitat has poorly drained, thin soil on exposed bedrock. TISHECHKIN & CLINE (2008) recorded a single specimen from a pocket gopher burrow in Louisiana, most likely an accidental occurrence.

Distribution. *Quedius laticollis* is found in Eastern North America from the Atlantic Ocean to the Great Plains, where it is replaced by *Q. strenuus* (ecoregion 8, Fig. 22). In the south it extends to northern Florida and along the Gulf Coast, but not into the subtropical regions of Texas, Florida and Mexico. To the north it extends to the central and north part of Lake Huron (Manitoulin Island) and follows the Saint Lawrence Valley to Quebec City, as the northernmost record.

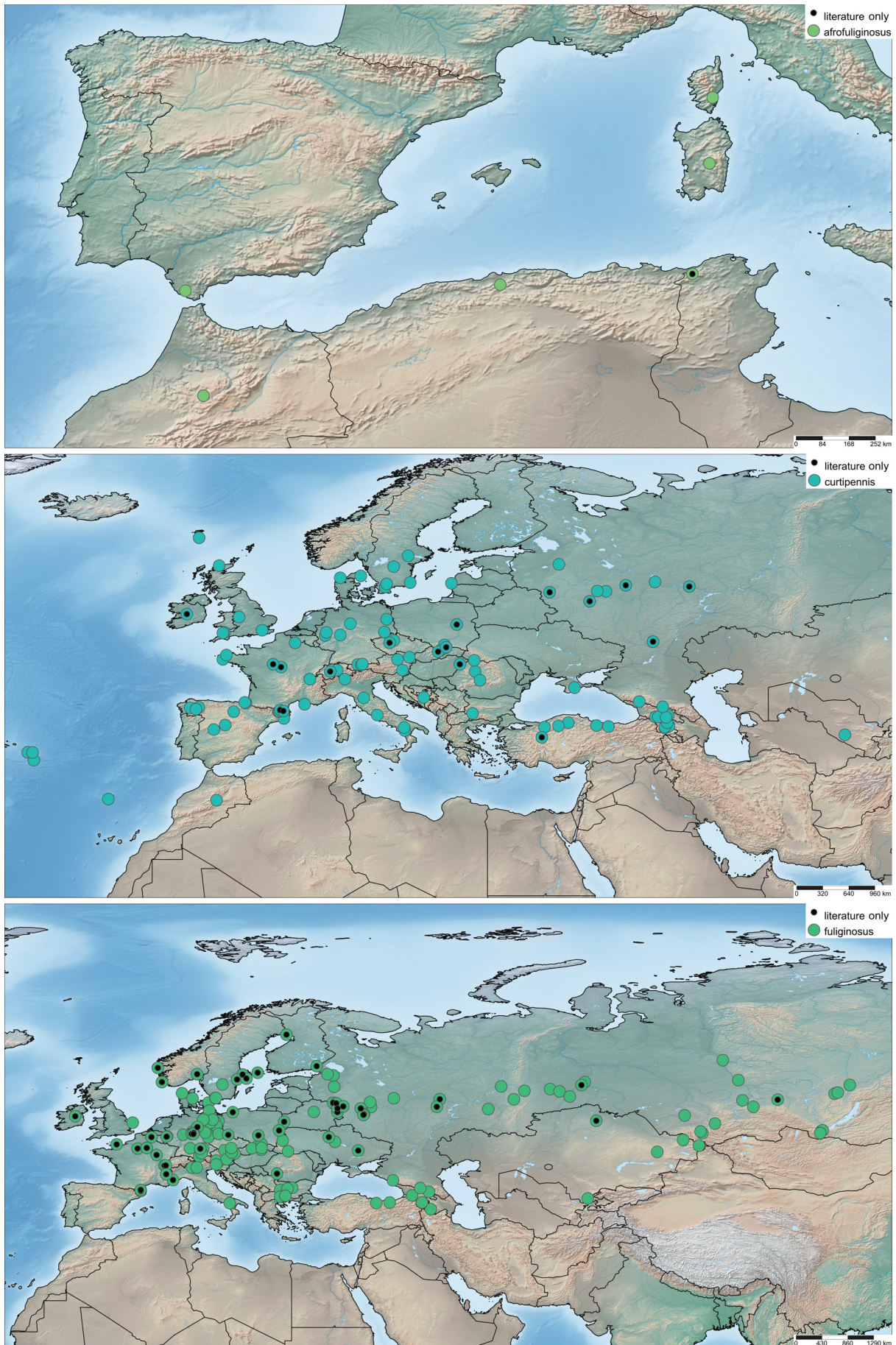


Fig. 18. Distribution of *Quedius afrofuliginosus* Gusarov, 1991 (top), *Q. curtipennis* Bernhauer, 1908 (middle) and *Q. fuliginosus* (Gravenhorst, 1802) (bottom).

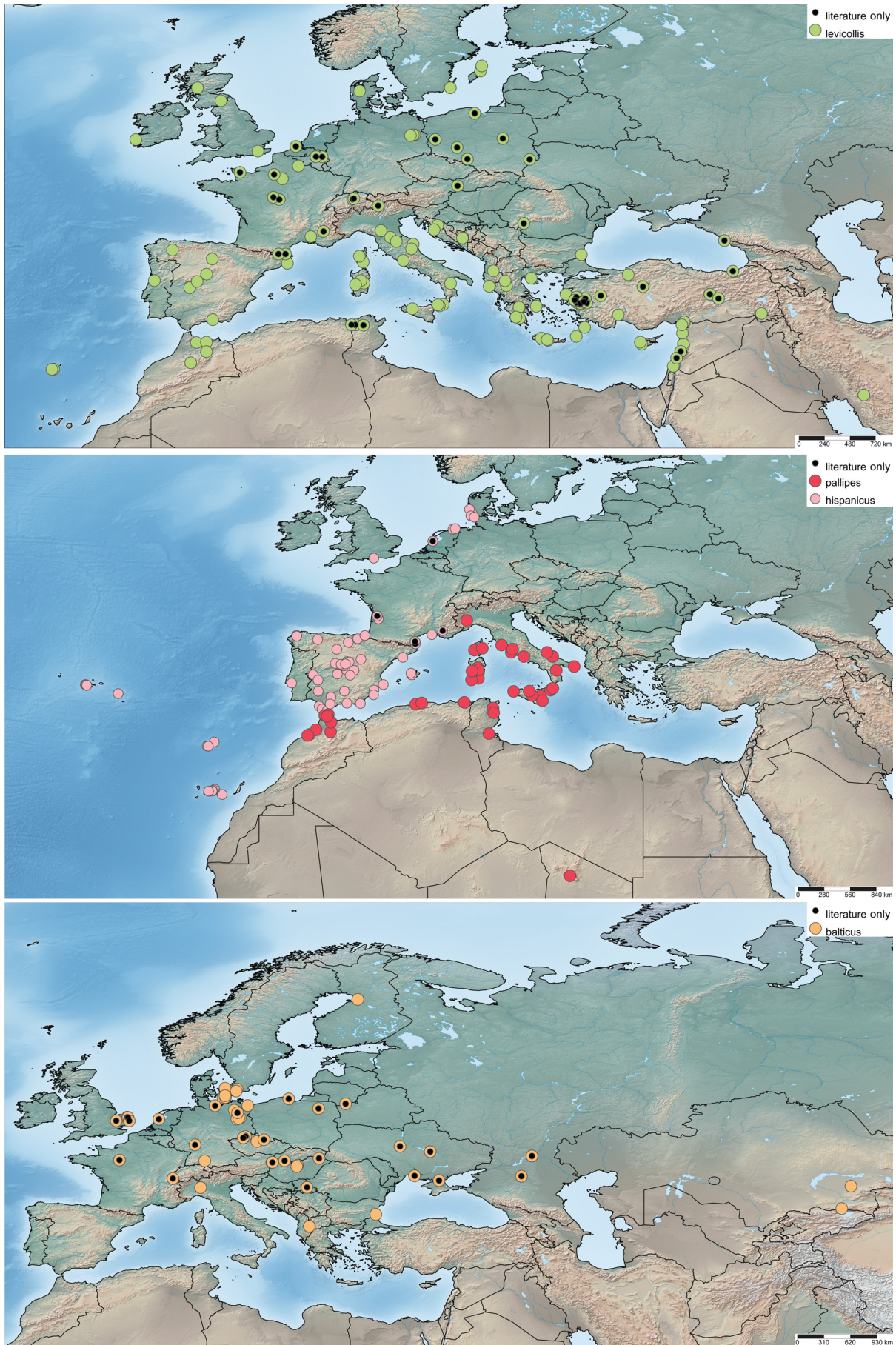


Fig. 19. Distribution of *Quedius levicollis* Brullé, 1832 (top), *Q. hispanicus* Bernhauer, 1898 and *Q. pallipes* Lucas, 1846 (middle), and *Q. balticus* Korge, 1960 (bottom).

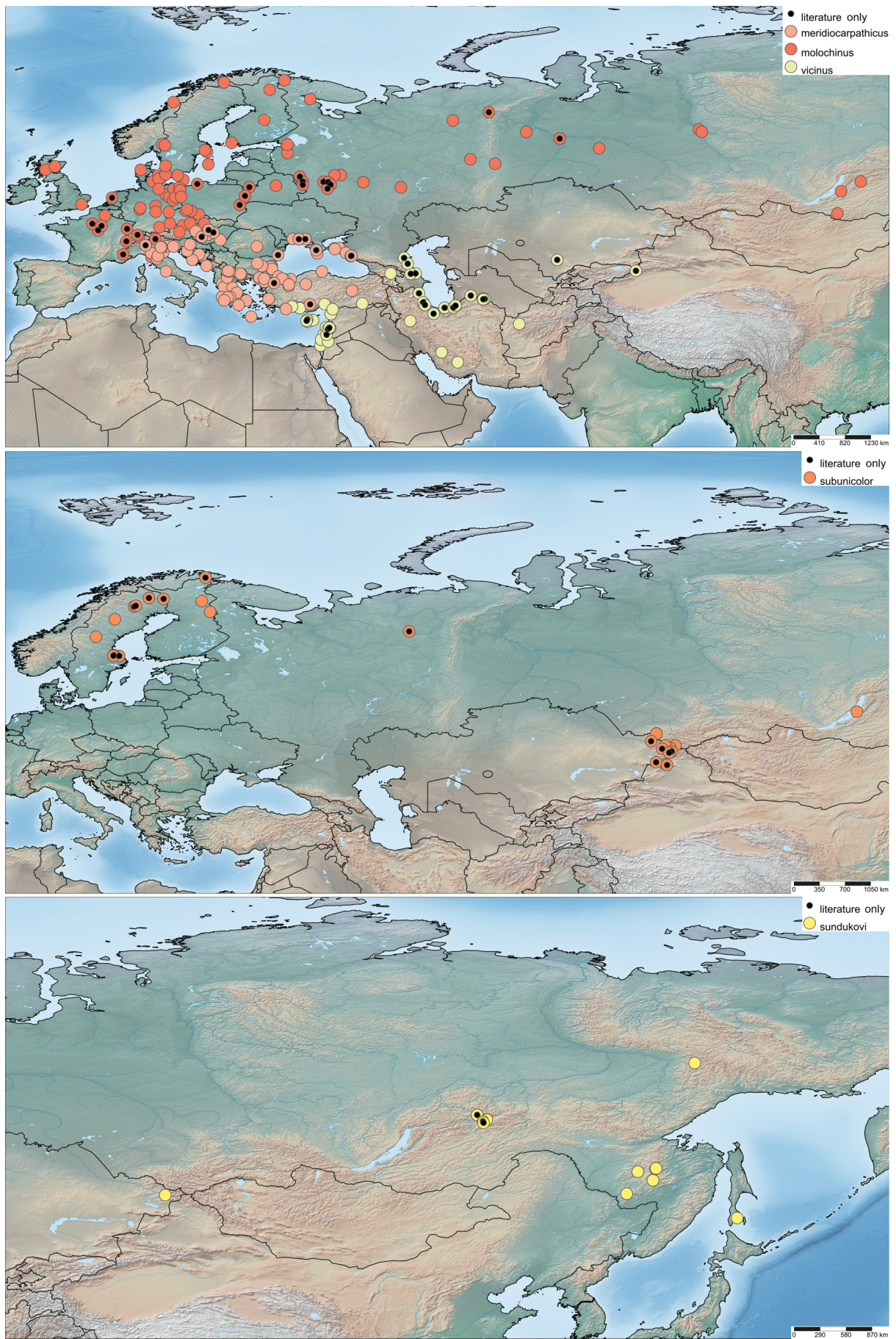


Fig. 20. Distribution of *Quedius molochinus* (Gravenhorst, 1806), *Q. meridiocarpaticus* Smetana, 1958, and *Q. vicinus* (Ménétriés, 1832) (top), *Q. subunicolor* Korge, 1961 (middle), and *Q. sundukovi* Smetana, 2003 (bottom).

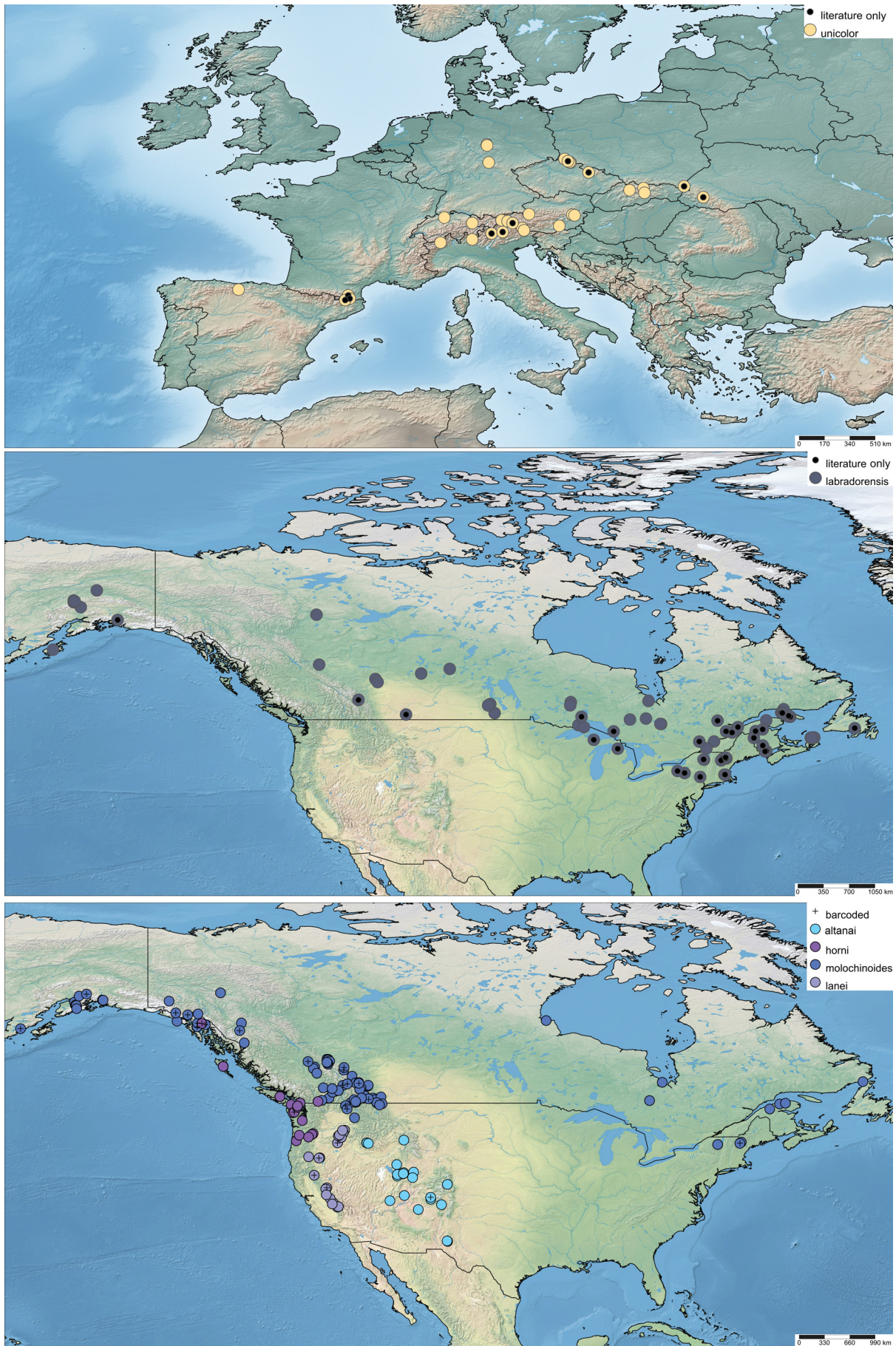


Fig. 21. Distribution of *Quedius unicolor* Kiesenwetter, 1847 (top), *Q. labradorensis* Smetana, 1965 (middle), *Quedius molochinoides*-group (bottom). Barcoded specimens are denoted with +.

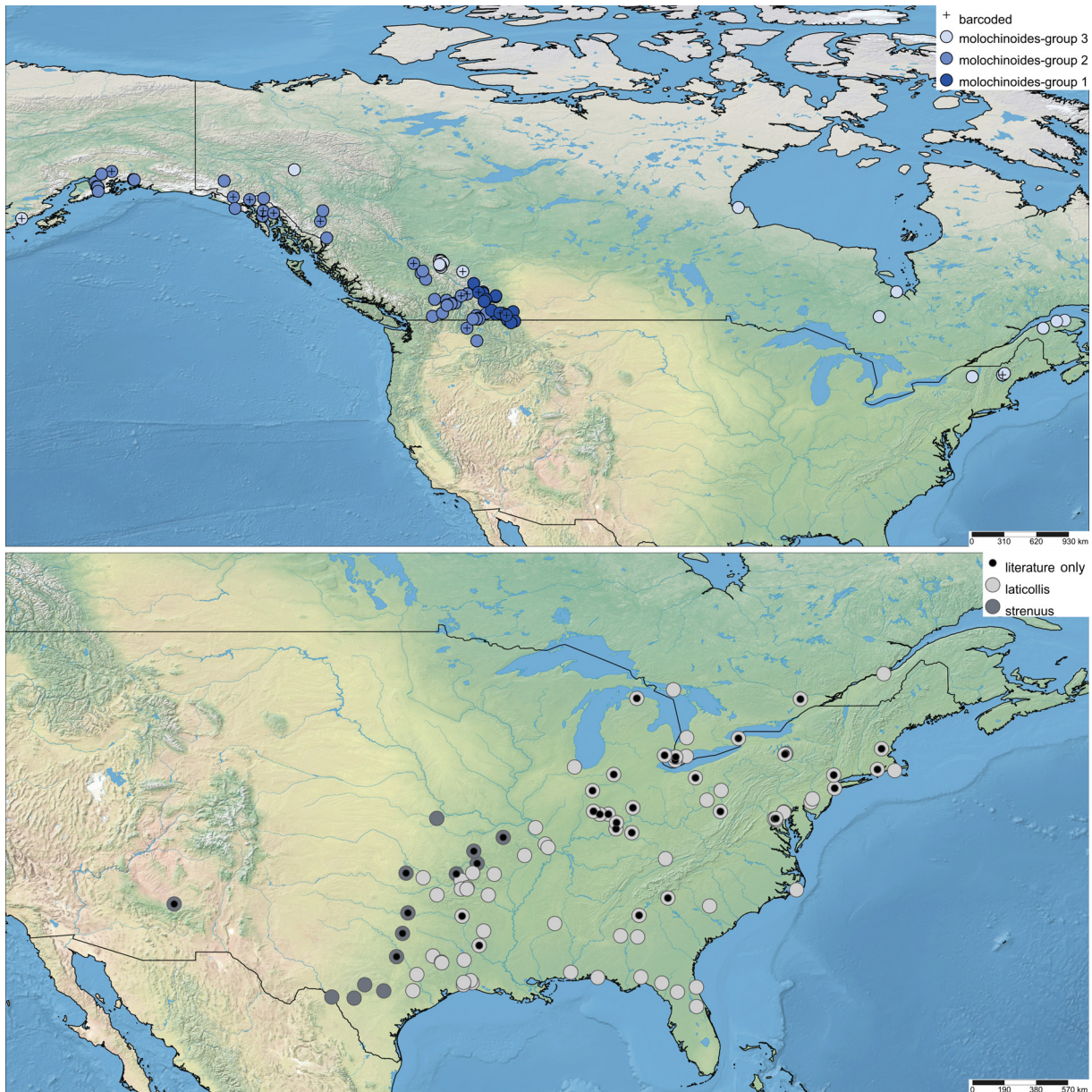


Fig. 22. Distribution of *Quedius molochinoides* Smetana, 1965 (top), and *Q. laticollis* (Gravenhorst, 1802) and *Q. strenuus* Casey, 1915 (bottom).

Quedius strenuus Casey, 1915

(Figs 1, 4, 9F, 14F, 22)

Quedius strenuus Casey, 1915: 401 [Type locality: Texas]

References. SMETANA (1971a): 132 (lectotype designation, characters and distribution); (1981): 638, (1990): 98 (distribution).

Type material examined. LECTOTYPE: ♀, designated by SMETANA (1971a) (USNM) [not examined], labelled: “Tex / Casey bequest 1925/ Type USNM 48279 / strenuus Csy”.

Additional material examined. USA: **KANSAS:** Lawrence, below bridge, Kansas River, [38.96, -95.26], under chunk of mud flat, 16.X.1936, leg. M. W. Sanderson (1 CNC). **TEXAS:** Braunfels, [29.69, -98.11], 13.VI.1927, leg. Darlington (1 MCZ); Del Rio, [29.36, -100.9], 8.VII.1938, leg. R. L. Sailer (3 CNC); Kerrville, [30.02, -99.13], 11.IV.1998, leg. Chamberlain (3 TAMU); Uvalde County, [29.30, -99.70], 26.V.1938, leg. J. H. Robinson (1 CNC).

Redescription. Measurements ♂♂ (n = 3): HW = 1.60–1.82 (1.73); HL = 1.33–1.51 (1.44); HL/HW 0.80–0.85 (0.83); PW = 2.20–2.47 (2.37); PL = 2.02–2.22 (2.14); PL/PW 0.89–0.92 (0.90); EW = 2.33–2.60 (2.50); EL

= 2.00–2.24 (2.16); EL/EW 0.85–0.88 (0.86); EL/PL 0.99–1.03 (1.01); PW/HW 1.63–1.67 (1.65); forebody length 5.36–5.96 (5.73). ♀♀ (n = 2): HW = 1.69–1.76 (1.72); HL = 1.44–1.47 (1.46); HL/HW 0.82–0.87 (0.85); PW = 2.33–2.44 (2.39); PL = 2.07–2.09 (2.08); PL/PW 0.85–0.89 (0.87); EW = 2.62–2.64 (2.63); EL = 2.18–2.29 (2.23); EL/EW 0.83–0.87 (0.85); EL/PL 1.05–1.10 (1.07); PW/HW 1.59–1.69 (1.64); forebody length 5.71–5.82 (5.77).

Medium sized, robust species; body black (Fig. 9F).

Head black, distinctly transverse, with eyes medium sized (EyL/TL = 1.76–2.00 (1.88)); microsculpture of transverse waves; no additional punctures between anterior frontal punctures (Fig. 6F); all antennomeres elongate, antennae and palpi reddish.

Thorax: pronotum black, slightly wider than long, wider than head, with microsculpture of transverse waves; three punctures in dorsal row and one to two in sublateral row

with its posteriormost puncture reaching just beyond first puncture of dorsal row; scutellum punctured and pubescent; elytra black, uniformly pubescent, slightly wider than long, roughly as long as pronotum; legs reddish brown with inner face of tibia and femur darkened.

Abdomen black, tergites uniformly punctured, with slight iridescence.

Male. Aedeagus (Fig. 14F): paramere rather broad lanceolate, slightly protruding beyond apex of median lobe, with sensory peg setae forming two distinct short and wide rows of multiple punctures; median lobe broad with gentle constriction towards pointed apex, on parameral side with two small hooked teeth protruding slightly basad, positioned at level near lower level of peg setae patch of the paramere.

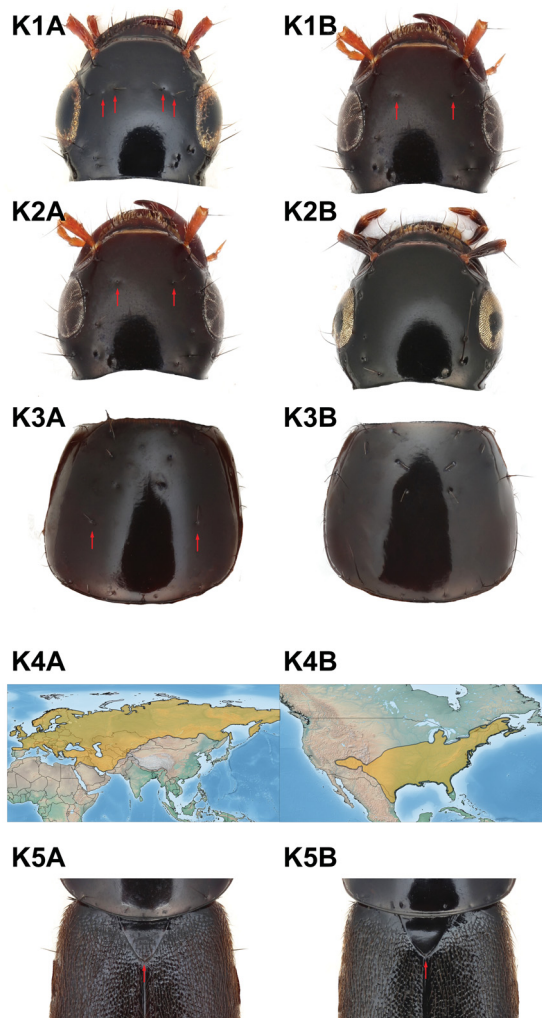
Differential diagnosis. *Quedius strenuus* is similar to *Q. laticollis* from which it normally differs by the completely dark body with pale appendages. For confident delimitation of both species from each other the position of the peg setae of the paramere can be used, which form two distinct rows in *Q. strenuus* and a triangular patch in *Q. laticollis*. Co-occurrence of the two species is unlikely since *Q. strenuus* replaces *Q. laticollis* to the west, in the forested areas of Great Plains of central-eastern and lowland areas of the southwestern United States. *Quedius strenuus* is also very similar to the introduced species *Q. molochinus*, which has not yet been found within the distribution range of *Q. strenuus*. Other differences include that, in *Q. molochinus*, the antennae are slightly stouter, less elongate, with darker middle antennomeres; as well as elytra are finer and more densely punctate, and either brick red or dark red (always dark in *Q. strenuus*). *Quedius strenuus* cannot be confused with other North American *Quedius* as they either have interocular punctures on frons or (those from other subgenera) have clear medial incision of labrum and abdomen notably tapering apicad.

Bionomics. Little is known about the bionomics of *Q. strenuus*. Based on current records, *Q. strenuus* is most likely restricted to lowland sites. As the region covered by its distribution is rather arid and most specimens were found near creeks, rivers, and lakes, it is likely to be strictly confined to moist microhabitats like wet flood or water-edge debris.

Distribution. *Quedius strenuus* is found across the Great Plains (ecoregion 9.4) and potentially a large part of lowland southwest United States (parts of ecoregion 10, Fig. 22). Only a few specimens, which we were not able to examine, were imprecisely recorded from lowland Southwest United State, from Arizona and Southern California. Of these, only a record from Lyman Lake in Apache County, Arizona (SMETANA 1981) is exact and fully reliable. Earlier SMETANA (1971a) mentioned subtle differences between these lowland specimens and ones from the Great Plains, but not clear enough to describe an additional species. The known range of *Q. strenuus* extends southwards almost to the border between USA and Mexico, northwards to Lawrence in Kansas. To the east *Q. strenuus* is replaced by *Q. laticollis*.

Key to species and species groups of *Quedius sensu stricto*

- 1 Presence of 4 or 6 additional setiferous punctures between anterior frontal punctures (Fig. K1A). Palearctic, two species introduced to the Nearctic. *Q. fuliginosus*-group 5
 - Presence of 2 or no additional setiferous punctures between anterior frontal punctures (Fig. K1B). 2
- 2 Presence of 2 additional setiferous punctures between anterior frontal punctures (Fig. K2A). Nearctic. *Q. molochinoides*-group 15
 - No additional setiferous punctures between anterior frontal punctures (Fig. K2B). 3
- 3 Additional 1 to 3 punctures in the posterior half of the sublateral row (Fig. K3A). W Palearctic. *Q. pallipes*-group 8
 - No additional puncture in the posterior half of the sublateral row (Fig. K3B). 4
- 4 Palearctic. *Q. molochinus*-group 9
 - Nearctic. *Q. laticollis*-group and *Q. molochinus* introduced from Palearctic. 19
- 5 Scutellum punctured and pubescent (Fig. K5A). W Palearctic, usually preferring warmer drier habitats. *Quedius levicollis* Brullé, 1832
 - Scutellum unpunctured and glabrous (Fig. K5B). 6



- 6 Head with 4 additional punctures between posterior frontal punctures, but without additional puncture between anterior and posterior frontal punctures (Fig. K6A). Median lobe without apical ridge. Palearctic. Introduced to multiple Nearctic localities. 7
- Presence of 4 additional punctures between posterior frontal punctures and one additional puncture on either side between anterior and posterior frontal punctures (Fig. K6B). Median lobe with apical ridge (Fig. 14A). Palearctic, known only from North Africa and the islands of Sardinia and Corse.
..... *Quedius afrofuliginosus* Gusarov, 1991
- 7 Basal three antennomeres at least slightly darkened. Eyes clearly protruding making the head seem more rectangular wider across (Fig. K7A). Apex of median lobe not laterally flattened (Fig. 14D). Palearctic. Introduced to E Canada. Prefers wetter humus rich habitats. Palearctic. Introduced to multiple Nearctic localities.
..... *Quedius fuliginosus* (Gravenhorst, 1802)
- Basal three antennomeres completely pale. Eyes not clearly protruding making the head seem round (Fig. K7B). Apex of median lobe laterally flattened (Fig. 14C). Palearctic. Introduced to multiple Nearctic localities. *Quedius curtipennis* Bernhauer, 1908
- 8 Sides of median lobe apex folded with distinct tooth situated at lower part (Fig. 15C). Western Europe along Atlantic Coast from Denmark to Iberia and inland in Southern France and Iberian Peninsula, also on the islands of Madeira, Azores, Canaries, and Balearic (Fig. K8A).
..... *Quedius hispanicus* Bernhauer, 1898
- Sides of median lobe apex folded with distinct tooth situated at medial part (Fig. 15D). North Africa, Italy and islands of Sardinia and Corse (Fig. K8B).
..... *Quedius pallipes* Lucas, 1846
- 9 Elytra shortened, distinctly shorter than pronotum (Fig. K9A), obviously brachypterous species without whitish apical seam on abdominal tergite VII (Fig. 11F). East Palearctic.
..... *Quedius sundukovi* Smetana, 2003
- Elytra normal, not shortened, about as long as pronotum (Fig. K9B), with whitish apical seam on abdominal tergite VII. 10
- 10 Basal three antennomeres at least slightly darkened (Fig. K10A). 11
- Basal three antennomeres pale (Fig. K10B). 13
- 11 Elytra most often reddish, very rarely darkened. Appendages only slightly darkened. Tibia, tarsi and apical antennomeres of antennae pale reddish brown (Figs K11A, 11E). Found near water bodies in Central-Eastern Europe and Middle Asia (Fig. 23). ..
..... *Quedius balticus* Korge, 1960
- Elytra always dark. Appendages darkened. Tarsi slightly paler brown to dark brown at most (Figs K11B, 10E–F). Found at higher elevations or latitudes (Figs 25, 27). 12
- 12 Head disc with fine isodiametric microsculpture (Fig. K12A). Without C-sclerite of the internal sac (Fig.

K6A



K6B



K7A



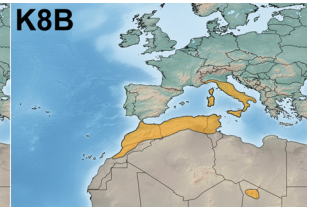
K7B



K8A



K8B



K9A



K9B



K10A



K10B



K11A



K11B



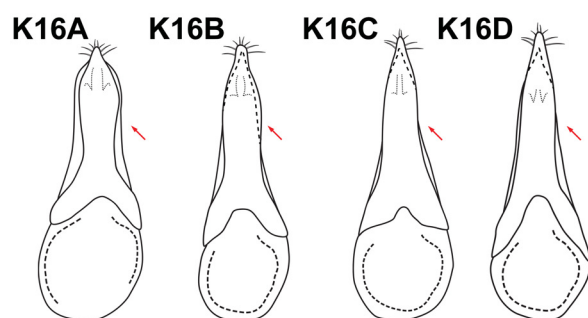
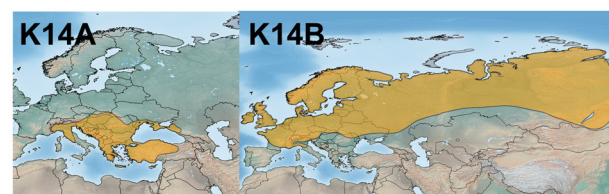
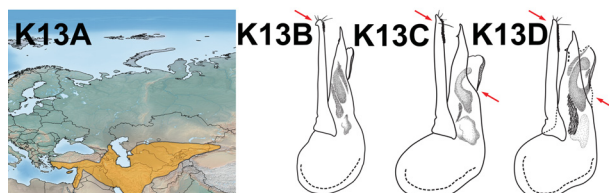
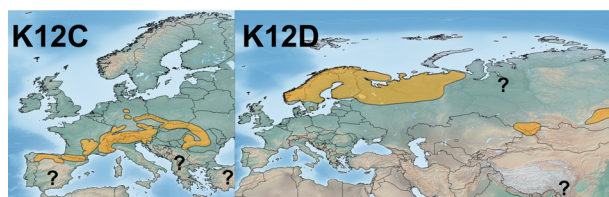
K12A



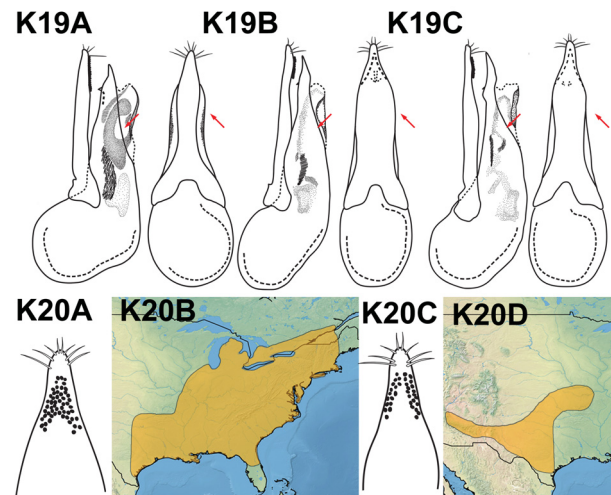
K12B



- 16A). Found at alpine sites of Central and Southern Europe (Fig. K12C).
 *Quedius unicolor* Kiesenwetter, 1847
- Head disc most often with microsculpture of fine transverse waves, rarely isodiametric (Fig. K12B). With clear C-sclerite of the internal sac (Fig. 15C). Found disjunct in boreal Scandinavia and Russia, as well as alpine in Altai Mountains and Transbaikalia (Fig. K12D). *Quedius subunicolor* Korge, 1961
- 13 Body brown. Elytra yellowish red. Apex of paramere pointing ventral, away from median lobe in form of a small blunt hook (Figs K13B, 15A). Central Anatolia, Middle East, Transcaucasus, Central Asia (Fig. K13A). *Quedius vicinus* (Ménétriés, 1832)
- Body most often black, or at most brownish. Elytra brick or brownish red. Apex of paramere straight, not pointing ventrad, away from median lobe (Figs K13C–D, 15D, 15F). Distribution more northern (Figs K14A–B)..... 14
- 14 C-shaped sclerite of internal sac without spine-like basal extension (Figs K13C, 15F). SE European distribution (Fig. K14A).
 *Quedius meridiocarpaticus* Smetana, 1958
- C-shaped sclerite of internal sac with spine-like basal extension (Figs K13D, 15D). N Palearctic distribution (Fig. K14B).
 *Quedius molochinus* (Gravenhorst, 1806)
- 15 Basal three antennomeres pale and antennae more elongate (antennomere 10 clearly longer than wide) (Fig. K15A). Elytra light to dark brown. Generally larger. Forebody length 5.49–5.93 (5.78) mm (Fig. 13F). Boreal North America (Fig. 28).
 *Quedius labradorensis* Smetana, 1965
- Basal three antennomeres darkened and antennae more robust (antennomere 10 more or less transverse) (Fig. K15B). Elytra black or reddish. Generally smaller. Forebody length 4.97–5.86 (5.39) mm. 16
- 16 Paramere with basal attenuation and broadening towards apex forming a spoon like shape, peg setae situated in a semi-circle along the edge of the paramere (Figs K16A, 8, 17B). Coastal to mid elevation from Oregon to Southern Alaska including Vancouver and Haida Gwaii.
 *Quedius horni* Hatch, 1957
- Paramere only with at most slight attenuation forming a lanceolate shape (Figs K16B–D). 17
- 17 Distributed across Boreal North America. South of the Northern Rocky Mountains (Fig. K17A). Teeth of median lobe clearly folded inwards (Figs K16B, 17E). *Quedius molochinoides* Smetana, 1965
- Central and Southern Rocky Mountains, Cascades, Blue Mountains and Sierra Nevada (Fig. K17B). Teeth of median lobe either protruding or not clearly formed (Figs K16C–D). 19
18. Found in the Cascades, Blue Mountains and Sierra Nevada (Fig. K18A). Paramere and median lobe clearly broader (Figs K16C, 17D).
 *Quedius lanei* Hatch, 1957



- Found in Central and Southern Rocky Mountains (Fig. K18B). Paramere and median lobe clearly more slender (Figs K16D, 17C). *Quedius altanai* sp. nov.
- 19 Paramere rather slender and clear C-sclerite of the internal sac (Figs K19A, 15D). Introduced in parts of Eastern North America, seems to be spreading. *Quedius molochinus* (Gravenhorst, 1806)
- Paramere rather broad and No C-sclerite of internal sac (Figs K19B–C). *Q. laticollis*-group 20
- 20 Peg setae of paramere forming a solid triangular field, usually with two wide and short extensions posteriorly (Figs K20A, 16E). E North America (Fig. K20B). *Quedius laticollis* (Gravenhorst, 1802)
- Peg setae of paramere arranged into two short longitudinal rows, which more or less diverge posteriorly (Figs K20C, 16F). Great American Plains (Fig. K20D). *Quedius strenuus* Casey, 1915



Prospects for future

This revision clarifies distributions for all species of a clear-cut monophyletic group in Quediini, which is an excellent model for exploring diversification of terrestrial invertebrates within the Holarctic biogeographic region. Some species of *Quedius* s. str. were included in the dated phylogenetic analysis by BRUNKE et al. (2017) who estimated the tribe Quediini to be around 46.6 My old (median value) and the split between the *Q. molochinus*- and *Q. pallipes*-groups of *Quedius* s. str. to occur around 6.6 Mya (median value). The biogeographical and ecological heterogeneity of the species groups within *Quedius* s. str. hints to possible extinctions and distribution shifts in the course of its evolution. For example, *Q. unicolor* is strictly associated with higher elevations in the European mountains and may have evolved as a more widely distributed lineage adapted to a colder climate that has now retracted to refugia in the European alpine zones. Others, like for example the *Q. pallipes*-group, have species strictly associated with coastal and riverine environments and may have originated once their common ancestor colonized these specialized niches during other climatic shifts, for example periods of aridization. The phylogenetic pattern of *Quedius* s. str. suggests that a single dispersal event from Eurasia to North America, most likely across Beringia resulted in the evolution and diversification of the *Q. laticollis*- and *Q. molochinoides*-groups in the Nearctic region. The highly debated timing and palaeoclimatic conditions of the landbridges that once connected Eurasia and North America (SANMARTÍN et al. 2001, SWANSON 2003, WEN et al. 2016, GRAHAM 2018, SCHÄR et al. 2018) can be addressed by a rigorous biogeographic study of *Quedius* s. str.

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Electronically archived data

Additional data (photos of types, list of all specimens examined, and list of data adopted from literature) is available at FigShare:
<https://doi.org/10.6084/m9.figshare.c.6307929.v1>

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