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Identification of West Siberian *Quedius* (Coleoptera, Staphylinidae) by COI barcodes calls for integrative taxonomy and curation of public DNA libraries

Valeria Krivosheeva[1], Maria Salnitska[1], Darya Semerikova[1], Angesom Abraham Gebremeskel[1], Anastasiya Ivanova[1], Alexey Solodovnikov[2]

1 *X-BIO Institute, University of Tyumen, 6 Volodarskogo Str, Tyumen, 625003, Russia*

2 *Natural History Museum of Denmark at the University of Copenhagen, Universitetsparken 15, Copenhagen, 2100, Denmark*

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Corresponding author: Valeria Krivosheeva (krivosheeva.valery@gmail.com, v.a.krivosheeva@utmn.ru)

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Abstract

Using West Siberian *Quedius*, we tested a widespread claim that DNA barcoding facilitates and accelerates taxonomic identification of arthropods. Our results indicate that even though neither BOLD nor GenBank had any barcodes from specimens of *Quedius* collected in West Siberia, these libraries were useful for the identification of our newly barcoded specimens from that region. However, correct identification was possible only after critical reciprocal evaluation of multiple conflicting data sources. Only six of 11–13 putative species could be confidently and easily identified to species level using the BOLD ID Engine or GenBank BLAST alone; all other cases required additional examination. Nevertheless, barcoding helped identify female singletons or teneral individuals that could not be identified morphologically and revealed that our own morphology-based species identification is prone to errors. Very subtle morphological differences between species may be revealed by DNA barcoding (e.g., *Q. boops*, *Q. boopoides*), and dubious morphology-based species concepts can be tested and potentially improved (e.g., specific limits of *Q. molochinus*, *Q. fellmani*, and *Q. nitipennis*). Finally, the use of barcoding helped record *Q. balticus* and *Q. pseudolimbatus* in West Siberia for the first time. The benefits of barcoding are valid only when reference barcodes in public libraries are correctly identified and kept up to date with changing taxonomy. We argue that more extensive use of barcoding in revisionary taxonomy will lead to faster-growing and better-curated DNA barcode libraries.

Key Words

Biodiversity, BOLD, BLAST, species, insects

Introduction

Rove beetles (Staphylinidae) are a very diverse family of insects, the largest after weevils (Curculionidae). They account for ca. 67,000 described species worldwide, with many more yet to be discovered. Staphylinids have a high ecological importance in all terrestrial biomes. However, their taxonomic identification is challenging, and therefore, rove beetles are insufficiently or poorly known everywhere except certain parts of Europe and North America (Betz et al. 2018; Newton 2022). Recently, multiple claims have been made that DNA barcoding may facilitate specimen identification, especially for poorly known organisms and faunas (Pentinsaari et al. 2019; Brunke et al. 2020; Grant et al. 2024), a highly relevant and promising statement for the study of rove beetles.

West Siberia is a geographic area where rove beetles are abundant, but their fauna is poorly known due to the large and inaccessible terrain. This is a big region of Eurasia, covering almost 3 million km^2 and extending for 2,500 km from north to south and for 1,900 km from west to east. West Siberia is located between the Ural Mountains, which separate Europe from Asia, and the Yenisei River. The northern boundary is the Kara Sea, and the southern boundary is the South Siberian Mountains and Kazakh Uplands. West Siberia has five natural zones spread through latitudes from north to south: tundra, forest-tundra, forest, forest-steppe, and steppe (Gvozdeckiy and Mihailov 1978). According to Krivosheeva et al. (2023), the rove beetle fauna of West Siberia includes 726 species but is insufficiently known, especially in the northern parts of the region. Krivosheeva et al. (2023) showed that even though there was not a single DNA barcode generated from a rove beetle specimen collected in West Siberia, the biggest barcode libraries, BOLD and GenBank, are promising for the identification of West Siberian rove beetles. Barcodes deposited in these libraries could be useful for identification due to the distribution of European or North American species already included in these databases in West Siberia.

Here we aim to explore the opportunities and limitations of the available DNA barcoding data using the West Siberian material of the rove beetle genus *Quedius* Stephens, 1829, from the subfamily Staphylininae as a model group. *Quedius* was chosen because it is a large and diverse group in West Siberia and the Palaearctic region as a whole (Salnitska and Solodovnikov 2019). It can be considered as a proxy for the entire family Staphylinidae (Brunke et al. 2020; Salnitska and Solodovnikov 2021; Bacal et al. 2024; Hu et al. 2024). Also, we have conducted enough taxonomic work on this genus to be able to evaluate the accuracy of the barcode-based identifications using various lines of evidence. According to Krivosheeva et al. (2023), 24 species of the genus *Quedius* have been hitherto recorded from West Siberia, which is used as a starting point in this paper. To test how publicly available barcodes may (or may not) be useful for the identification of *Quedius* material collected in West Siberia, we designed an experiment based on the three most common challenges encountered by entomologists investigating local fauna.

The first common challenge is the identification of a species that has one or more very similar congeners. For some rove beetle species, and especially *Quedius*, even the morphology of male genitalia, which normally is considered the most reliable species-specific character set, may be difficult to assess due to subtle differences among species. The separation of *Q. limbatus* (Heer 1839) from *Q. sublimbatus* Mäklin, 1853 in both sexes is an example of this challenge (Salnitska and Solodovnikov 2019). Comparing the barcode of a given specimen to the reference barcodes of one or more species that it is suspected to be should resolve the problem.

The second challenge is when a group of similar species can be separated from each other based only on the structure of the aedeagus. Females in these groups cannot be reliably identified without association with males and are frequently left unidentified and neglected in many studies, as seen with females of *Q. fuliginosus* (Gravenhorst 1802) and *Q. curtipennis* Bernhauer, 1908 in Hansen et al. (2022). Comparing the barcode of a female specimen to the reference barcodes of one or more species is considered to be a way to obtain a reliable identification.

The third challenge is where morphology alone, including genitalia, is insufficient for unambiguous identifications. Earlier studies have shown that such cryptic species can be delimited only using an integrative approach, or at least that not all their specimens can be identified without DNA barcodes. In *Quedius*, the separation of *Q. umbrinus* Erichson, 1839, from *Q. pseudoumbrinus* Lohse, 1958, was explored in detail (Salnitska and Solodovnikov 2021), while the separation of species in the *boops* group may be a similar but yet unexplored case (Salnitska and Solodovnikov 2019). Using DNA barcodes as an identification tool may be required to avoid misidentifications in these species complexes. Undefined species limits of this kind are the biggest challenge for a taxonomic revision, a local faunistic study, or other basic or applied research relying on correct species identifications.

This study aims to address whether DNA barcoding and available barcode libraries are able to overcome these challenges for taxonomic identifications of West Siberian *Quedius*.

Materials and methods

Species list for *Quedius* of West Siberia

A list of *Quedius* species known to occur in West Siberia was compiled from literature published before 2024 (Table 1). For this purpose, all occurrences of *Quedius* species in West Siberia were extracted from reliable references and then databased using the EarthCape Biodiversity Database Platform (Meyke 2019) software via Windows Client. In Table 1, we cite the catalogue of Salnitska and Solodovnikov (2019) only where they reference their own species records based on entomological collections; the published studies they cited are listed independently.

Experimental design

In total, we collected 49 specimens of *Quedius* from various regions of West Siberia, all of which were sorted into morphospecies and, where possible, identified to species level using the most recent morphology-based classification (Assing and Schülke 2012; Salnitska and Solodovnikov 2019; Hansen et al. 2022) (Figs 1, 2, Suppl. material 1).

We then DNA-barcoded a few selected representatives from each morphospecies—28 specimens in total (Table 2).

DNA barcodes were clustered into molecular taxonomic units and contrasted with our morphology-based species. Our DNA barcodes were compared with publicly available barcode libraries using GenBank BLAST and the BOLD ID Engine. By reciprocally assessing the congruence or conflicts between our morphology- and DNA-based identifications, we evaluate (1) the quality of the current, mainly morphology-based, species-level taxonomy of *Quedius* versus molecular-based species delimitation using the barcodes generated in this paper and from the BOLD and GenBank databases,

Table 1. List of *Quedius* species recorded in West Siberia according to the current literature.

Species	References
Quedius boopoides Münster, 1923	Bukhkalo et al. (2011, 2012), Schülke and Smetana (2015), Salnitska and Solodovnikov (2019)
Quedius boops (Gravenhorst, 1802)	Bukhkalo et al. (2011), Babenko and Nuzhnykh (2014), Schülke and Smetana (2015), Salnitska and Solodovnikov (2019)
Quedius brevis Erichson, 1840	Babenko (1982)
Quedius centrasiaticus Coiffait, 1969	Schülke and Smetana (2015)
Quedius dilatatus (Fabricius, 1787)	Bukhkalo et al. (2011, 2012), Schülke and Smetana (2015)
Quedius fellmani (Zetterstedt, 1838)	Olshwang (1992), Schülke and Smetana (2015), Salnitska and Solodovnikov (2019)
Quedius fulgidus (Fabricius, 1792)	Babenko (1982)
Quedius fuliginosus (Gravenhorst, 1802)	Babenko (1982), Bukhkalo et al. (2011, 2012), Babenko and Nuzhnykh (2014), Schülke and Smetana (2015), Hansen et al. (2022)
Quedius fulvicollis (Stephens, 1833)	Bukhkalo et al. (2011, 2012), Schülke and Smetana (2015)
Quedius jenisseensis (J. Sahlberg, 1880)	Bukhkalo et al. (2011, 2012), Schülke and Smetana (2015), Smetana and Shavrin (2018)
Quedius limbatus (Heer, 1839)	Bukhkalo et al. (2011, 2012), Salnitska and Solodovnikov (2019)
Quedius longicornis Kraatz, 1857	Bukhkalo et al. (2011, 2012), Schülke and Smetana (2015), Salnitska and Solodovnikov (2019)
Quedius mesomelinus (Marsham, 1802)	Schülke and Smetana (2015)
Quedius microps Gravenhorst, 1847	Zinchenko (2003), Pavlov (2005), Schülke and Smetana (2015)
Quedius molochinus (Gravenhorst, 1806)	Pavlov (2005), Bukhkalo et al. (2011, 2012), Filippov (2011), Schülke and Smetana (2015), Salnitska and Solodovnikov (2019), Hansen et al. (2022)
Quedius ochripennis (Ménétriés, 1832)	Pavlov (2005), Schülke and Smetana (2015)
Quedius paraboops Coiffait, 1975	Schülke and Smetana (2015)
Quedius picipes (Mannerheim, 1830)	Pavlov (2005), Schülke and Smetana (2015)
Quedius pseudoumbrinus Lohse, 1958	Salnitska and Solodovnikov (2021)
Quedius puncticollis (C.G.Thomson, 1867)	Zinchenko (2003), Bukhkalo et al. (2011, 2012); Schülke and Smetana (2015)
Quedius sublimbatus Mäklin, 1853	Schülke and Smetana (2015)
Quedius subunicolor Korge, 1961 (=*altaicus* Korge, 1962)	Schülke and Smetana (2015) (as *Q. altaicus*)
Quedius tenellus (Gravenhorst, 1806)	Babenko (1982), Schülke and Smetana (2015)
Quedius umbrinus Erichson, 1839	Salnitska and Solodovnikov (2019, 2021)

and (2) the quality of specimen identifications in the BOLD and GenBank DNA libraries that form the basis for the identity of the reference barcodes.

Specimen acquisition and vouchering

Quedius specimens were collected during two summers between 17.07.2022 and 25.07.2023 in the Yamalo-Nenets and Khanty-Mansiysk autonomous regions and Kurgan and Tyumen provinces of West Siberia. They were collected using typical tools for collecting rove beetles, such as a sifter and Winkler eclectors (Salnitska et al. 2022). Collected material was stored in 96% ethanol at –20 °C. All specimens were given unique ID numbers and stored in the collection of the University of Tyumen (UTMN).

Tissue sampling and DNA extraction

For DNA extraction, one leg was detached from each specimen and placed in an Eppendorf tube with 96% ethanol. Extractions were carried out using the microcentrifuge columns method of the Extract DNA Blood & Cells kit (#BC111M) (Evrogen, Moscow, Russia). Every centrifugation was carried out at 13,000 rpm. A prepared mix of "Lysis Solution" and "Proteinase K" (100 µl and 10 µl, respectively, for each sample) was added to the Eppendorf tubes with tissues that were previously dried from alcohol residues. Legs were crushed with tips. Ten microliters of suspension "Gauss" was added to increase the yield of DNA. After 20 seconds of vortexing, samples were incubated in a thermoshaker for 24 hours at 56 °C. After that, 100 µl of 96% ethanol and 400 µl of "Binding Solution M" were added, and the contents of the tubes were thoroughly mixed after adding each reagent. The contents of the tubes (≈700 µl) were transferred to microcentrifuge columns and centrifuged for 30 seconds. Seven hundred microliters of "Wash Solution" was added to each column, the columns were centrifuged, and then this washing process was repeated with new collection tubes. Any remaining washing solution was removed by centrifugation for 1 minute. Columns were incubated with open lids at room temperature (5 min), then 30 µl of elution solution was applied to the center of the column and centrifuged for 30 seconds. The procedure was repeated with the same amount of eluate for a final volume of 60 µl. The DNA extract was transferred to a new Eppendorf tube and stored at –20 °C.

PCR

The reaction consisted of 4 µl of DNA extract (only 2 µl for *Quedius* s. str. due to their larger body size), 1 µl of each primer (LCO1490 and HCO3198 (Folmer et al. 1994)), 4 µl of Red Buffer (Encyclo Plus PCR kit, #PK101, Evrogen), 0.4 µl of dNTPs, 0.5 µl of Taq Polymerase, and 9.1 µl

Table 2. Molecular taxonomic units (MTUs) of the barcoded West Siberian *Quedius* specimens and their morphological, GenBank BLAST, and BOLD ID engine identifications. Confident identifications (i.e., those with > 99% sequence similarity in GenBank and BOLD) are shown in bold.

Voucher code	Molecular taxonomic unit (MTU)	Morphology-based ID	Molecular species by BLAST	Molecular species by ID Engine	Integrative ID
UTMN_ LISP_000257 ♀	MTU 1	*Quedius fuliginosus*	***Quedius fuliginosus*** (100%)	***Quedius fuliginosus*** (100%)	*Quedius fuliginosus*
UTMN_ LISP_000258 ♂	MTU 1	*Quedius fuliginosus*	***Quedius fuliginosus*** (99.69%)	***Quedius fuliginosus*** (99.69%)	*Quedius fuliginosus*
UTMN_ LISP_000285 ♂	MTU 1	*Quedius fuliginosus*	***Quedius fuliginosus*** (99.84%)	***Quedius fuliginosus*** (99.84%)	*Quedius fuliginosus*
UTMN_ LISP_000261 ♂	MTU 2	*Quedius boops*	***Quedius boops*** (99.54%)	***Quedius boops*** (99.66%)	*Quedius boops*
UTMN_ LISP_000259 ♂	MTU 3	*Quedius boops*	***Quedius boopoides*** (99.69%)	***Quedius boopoides*** (99.84%)	*Quedius boopoides*
UTMN_ LISP_000260 ♂	MTU 3	*Quedius boops*	***Quedius boopoides*** (99.69%)	***Quedius boopoides*** (99.84%)	*Quedius boopoides*
UTMN_ LISP_000274 ♂	MTU 3	*Quedius boops*	*Quedius boopoides* (97.97%)	***Quedius boopoides*** (99.44%)	*Quedius boopoides*
UTMN_ LISP_000275 ♀	MTU 3	*Quedius boops*	***Quedius boopoides*** (99.39%)	***Quedius boopoides*** (99.54%)	*Quedius boopoides*
UTMN_ LISP_000281 ♂	MTU 3	*Quedius boops*	***Quedius boopoides*** (99.54%)	***Quedius boopoides*** (99.82%)	*Quedius boopoides*
UTMN_ LISP_000292 ♀	MTU 3	*Quedius boops*	***Quedius boopoides*** (99.69%)	***Quedius boopoides*** (99.84%)	*Quedius boopoides*
UTMN_ LISP_000280 ♀	MTU 3	*Quedius boops gr.*	***Quedius boopoides*** (99.39%)	***Quedius boopoides*** (99.82%)	*Quedius boopoides*
UTMN_ LISP_000254 ♀	MTU 3	*Quedius fellmani*	***Quedius boopoides*** (99.69%)	***Quedius boopoides*** (99.84%)	*Quedius boopoides*
UTMN_ LISP_000271 ♀	MTU 3	*Quedius fellmani/boops*	*Quedius boopoides* (98.45%)	***Quedius boopoides*** (99.27%)	*Quedius boopoides*
UTMN_ LISP_000251 ♂	MTU 4	*Quedius subunicolor*	*Quedius molochinus* (94.50%)	*Quedius sp*. (94.77%)	*Quedius subunicolor*
UTMN_ LISP_000264 ♂	MTU 5	*Quedius balticus*	Staphylinidae sp. (93.64%)	*Quedius laticollis* (93.86%)	*Quedius balticus*
UTMN_ LISP_000263 ♂	MTU 6	*Quedius molochinus*	*Quedius molochinus* (94.44%)	*Quedius molochinus* (94.33%)	*Quedius molochinus* clade 1 in Gebremeskel et al. (2024)
UTMN_ LISP_000252 ♂	MTU 7	*Quedius molochinus*	*Quedius molochinus* (95.84%)	*Quedius molochinus* (95.96%)	*Quedius molochinus* clade 1 in Gebremeskel et al. (2024)
UTMN_ LISP_000262 ♂	MTU 8	*Quedius fellmani*	***Quedius nitipennis*** (99.54%)	***Quedius nitipennis*** (99.53%)	*Quedius fellmani*
UTMN_ LISP_000272 ♂	MTU 9	*Quedius fellmani*	*Quedius fellmani* (96.43%)	***Quedius fellmani*** (99.85%)	*Quedius fellmani*
UTMN_ LISP_000279 ♀	MTU 9	*Quedius fellmani*	*Quedius fellmani* (96.59%)	***Quedius fellmani*** (99.69%)	*Quedius fellmani*
UTMN_ LISP_000255 ♀	MTU 9	*Quedius fellmani/boops*	*Quedius fellmani* (96.30%)	***Quedius fellmani*** (99.84%)	*Quedius fellmani*
UTMN_ LISP_000273 ♂	MTU 10	*Quedius jenisseensis*	*Quedius* sp. (85.69%)	*Quedius brunnipennis* (85.00%)	*Quedius jenisseensis*
UTMN_ LISP_000253 ♀	MTU 11	*Quedius limbatus*	*Quedius sublimbatus* (98.00%)	*Quedius sublimbatus* (97.99%)	*Quedius sublimbatus*
UTMN_ LISP_000276 ♀	MTU 11	*Quedius* sp. 1	*Quedius sublimbatus* (97.68%)	*Quedius sublimbatus* (97.67%)	*Quedius sublimbatus*
UTMN_ LISP_000266 ♂	MTU 12	*Quedius limbatus*	***Quedius pseudolimbatus*** (99.54%)	***Quedius pseudolimbatus*** (99.69%)	*Quedius pseudolimbatus*
UTMN_ LISP_000287 ♀	MTU 12	*Quedius limbatus* (?)	***Quedius pseudolimbatus*** (99.54%)	***Quedius pseudolimbatus*** (99.69%)	*Quedius pseudolimbatus*
UTMN_ LISP_000256 ♂	MTU 13	*Quedius limbatus*	***Quedius limbatus*** (99.69%)	***Quedius limbatus*** (99.84%)	*Quedius limbatus*
UTMN_ LISP_000289 ♀	MTU 13	*Quedius limbatus*	***Quedius limbatus*** (99.85%)	***Quedius limbatus*** (100%)	*Quedius limbatus*

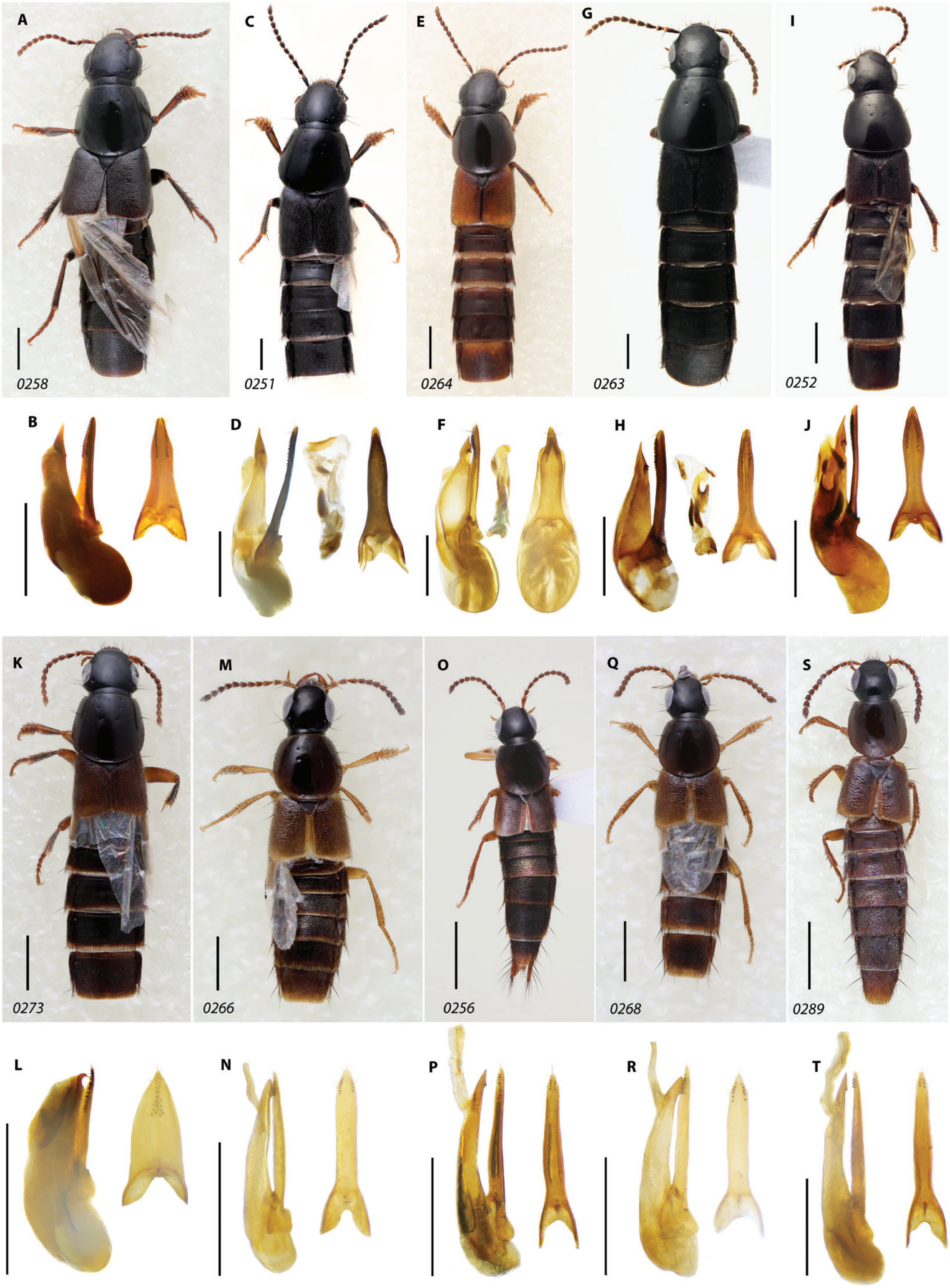

Figure 1. Habitus and aedeagi of voucher *Quedius* specimens from West Siberia barcoded in this study (all UTMN_LISP). **A, B.** 000258, male, congruently identified by morphology and barcoding as *Q. fuliginosus*; **C, D.** 000251, male, congruently identified by morphology and barcoding as *Q. subunicolor*; **E, F.** 000264, male, congruently revealed as a species by barcoding (MTU 5) and morphology, identified by morphology only as *Q. balticus* because of lacking reference barcodes in BOLD or GenBank; **G, H.** 000263, male, forming MTU 6, identified by BOLD and Genbank as *Q. molochinus* but with low similarity and identity and by morphology as *Q. molochinus*; **I, J.** 000252, male, forming MTU 7, identified by BOLD and Genbank as *Q. molochinus* but with low similarity and identity, by morphology as *Q. molochinus*; **K, L.** 000273, male, congruently revealed as a species by barcoding (MTU 10) and morphology, identified by morphology only as *Q. jenisseensis* because of lacking reference barcodes in BOLD or GenBank; **M, N.** 000266, male, initially identified by morphology as *Q. limbatus* but as *Q. pseudolimbatus* by BOLD and Genbank which is corroborated by our re-examination; **O, P.** 0000256, male, congruently identified by morphology and barcoding as *Q. limbatus*; **Q, R.** 000268, male, non-sequenced specimens that after re-examination was identified by morphology as *Q. pseudolimbatus*; **S, T.** 000289, female, congruently identified by morphology and barcoding as *Q. limbatus*. Scale bars: 1 mm (**A–L, M, O, Q, S**); 0.5 mm (**N, P, R, T**).

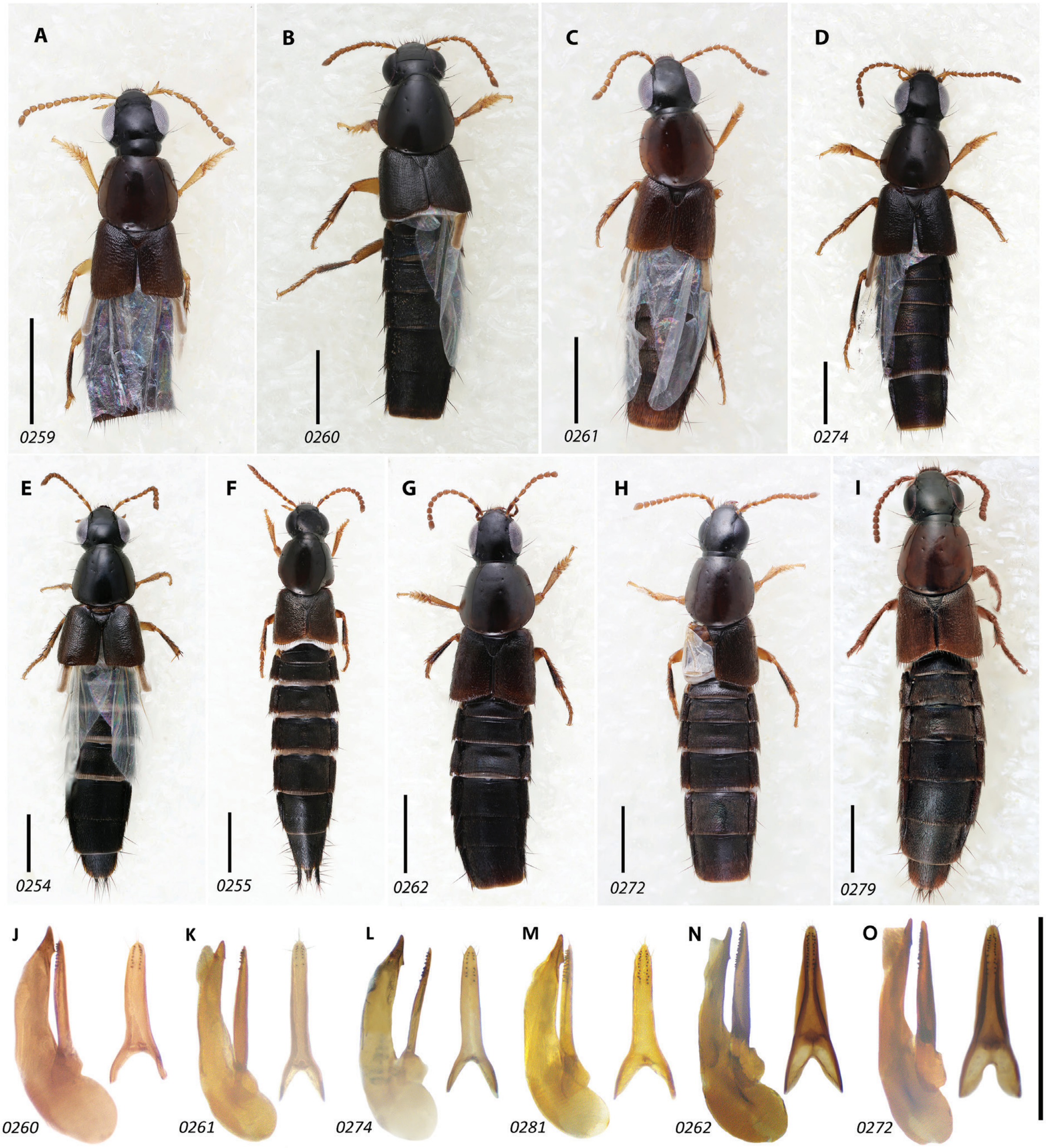

Figure 2. Habitus and aedeagi of voucher *Quedius* specimens from West Siberia barcoded in this study (all UTMN_LISP). **A.** 000259, male, identified by morphology as a *Q. boops* but as *Q. boopoides* by BOLD and BLAST; **B, J.** 000260, male, identified by morphology as a *Q. boops* but as *Q. boopoides* by BOLD and BLAST; **C, K.** 000261, male, forming MTU 2, congruently identified by morphology and barcoding as *Q. boops*; **D, L.** 000274, male, identified by morphology as a *Q. boops* but as *Q. boopoides* by BOLD and BLAST; **E.** 000254, female, identified by morphology as *Q. fellmani*, but as *Q. boopoides* by BOLD and BLAST, morphological reexamination showed that it does not belong to *Q. fellmani*; **F.** 000255, female, identified by morphology as either *Q. fellmani* or *Q. boops* but by BLAST and BOLD identified as *Q. fellmani*; **G, N.** 000262, male, identified by morphology as a *Q. fellmani* and forming MTU 8 separated from main *Q. fellmani* clade (MTU 9), BOLD and BLAST identified it as a *Q. nitipennis*; **H, O.** 000272, male, identified by morphology and barcoding as a *Q. fellmani*; **I.** 000279, female, identified by morphology and barcoding as a *Q. fellmani*; **M.** 000281, male, identified as a *Q. boops* by morphology and as a *Q. boopoides* by barcoding. Scale bars: 1 mm.

(11.1 µl for *Quedius* s. str.) of sterile distilled water. Previously, a positive DNA template and distilled water (ddH2O) were used as positive and negative controls, respectively.

The following PCR cycling conditions were used: initial denaturation for 3 minutes at 94 °C; 35 cycles of 30 seconds at 94 °C, annealing at 53 °C for 30 seconds, and extension at 72 °C for 30 seconds; followed by a final extension at 72 °C for 5 minutes (Hebert et al. 2003; Schomann and Solodovnikov 2017). PCR products were visualized in a 1% agarose gel by electrophoresis.

DNA cleaning and sequencing

Post-PCR products were cleaned using the Cleanup S-Cap kit (#BC041L, Evrogen, Moscow, Russia) following the manufacturer's instructions (https://evrogen.ru/kit-user-manuals/BC041.pdf). Forward and reverse Sanger sequencing of target genes was performed by the Evrogen company (Moscow, Russia).

Phylogenetic and species delimitation analysis to reveal DNA barcode-based species clusters

Sequence alignments were carried out in MEGA XI (Tamura et al. 2021) using the ClustalW algorithm (Kumar et al. 2018) with the default settings. Genetic distances were calculated using the uncorrected p-distances test (Fitch and Margoliash 1967) via MEGA XI. Tables with calculated p-distances are shown in Suppl. material 2. Best-fit models were computed with jModelTest2 (2.1.6) (Darriba and Posada 2014) via CIPRES (https://www.phylo.org) (Miller et al. 2010). Bayesian Inference analysis (BI) was performed in MrBayes (3.2.7a) (Ronquist et al. 2012) via CIPRES. The COI barcode of *Philonthus politus* (Linnaeus, 1758) (GenBank ID: MZ610437.1; BOLD ID: COLFH008-14) was used as an outgroup. 1.5 million generations for two independent runs with four chains each were performed, sampling every 5000 generations and discarding 25% as burn-in. Convergence was verified by manually checking the stationary distribution plot of the log-likelihood values during run generations, the average standard deviation of split frequencies for values lower than 0.01, the potential scale reduction factor (PSRF), and estimated sample size (ESS) in the STDOUT output file from CIPRES. Phylogenetic trees were visualized by TreeViewer 2.2.0 (Bianchini and Sánchez-Baracaldo 2024) and edited in Adobe Illustrator 28.1 (https://www.adobe.com/products/illustrator.html). Species delimitation analyses were performed using ASAP (Assemble Species by Automatic Partitioning) via iTaxoTools (Puillandre, Brouillet and Achaz 2021; Vences et al. 2021) and by PTP via The Exelixis Lab web server (Zhang et al. 2013; https://cme.h-its.org/exelixis/). ASAP was used with the p-distance method and all other default settings. The PTP method was calculated for a rooted tree with an outgroup, using 100,000 MCMC generations and a 0.1 burn-in.

BOLD ID Engine and GenBank BLAST

Species identification by DNA barcodes was performed in BOLD ID Engine (https://www.boldsystems.org/index.php/IDS_OpenIdEngine) and GenBank BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). In BOLD ID Engine, we used the "Animal Identification" section and searched through the "All Barcode Records" and "Species Level Barcode Records" options. A GenBank BLAST search was run through the "Core nucleotide database" with default settings. GenBank BLAST and BOLD ID Engine play a significant role in species identification using molecular data. Both tools search for the best matches to the uploaded sequence but take different approaches.

BLAST performs a search through an extensive database ("Core nucleotide database" by default) that contains various types of nucleotide sequences (Korf et al. 2003; Benson et al. 2012). It does not provide any particular identification of the species but instead returns specimens that match the blasted sequence the best. BLAST has three interdependent metrics that can be used to evaluate how plausible a match is. Identity (%) displays how many nucleotides are in the same positions in the alignment. The max score is a score of the alignment where penalties are used for gaps and substitutions, so the higher it is, the more plausible a species identification is. E-value represents the number of different alignments with scores equal to or greater than a given alignment and is preferably approximately or equal to zero (Fassler and Cooper 2011).

BOLD is designed for species identification by evaluating sequences in its barcode database for the degree of convergence with the uploaded sequence. A species identification for an uploaded sequence is provided if the query sequence shows a match with convergence greater than 99%. Otherwise, BOLD does not give a particular identification but shows the barcodes with the best match (Ratnasingham and Hebert 2007). For the evaluation of the match, BOLD has only one metric, similarity (%), that accounts for the number of nucleotides matching in the alignment and penalties for gaps and substitutions (Petsko and Ringe 2004; Ratnasingham and Hebert 2007).

Since we cannot obtain exact species identifications for all our sequences from West Siberian *Quedius*, in this paper we refer to the best matches via BLAST and BOLD ID Engine searches as "species identifications" and compare them via identity (%) (BLAST) and similarity (%) (BOLD) metrics. For BLAST, although best-matching sequences are also selected by the lowest E-value and highest max score, only the identity (%) is reported in the Results.

Morphological examination and illustration

Beetle specimens were examined with Zeiss SteREO Discovery V8 and Nexcope NSZ 608T dissecting microscopes. Genitalia were dissected from specimens stored in alcohol in plastic cryovials and placed in the same vials, separated from the specimen by a small cotton ball.

Habitus photographs were taken using a Canon EOS 5D Mark III digital camera with a Canon MP-E 65 mm F2.8 1–5 × macrolens (Canon Inc.) mounted on a Cognisys Stackshot 3X macrorail connected to a controller. Photos of the aedeagi were taken using a BUCSF-1200C digital color camera attached to a Nexcope NSZ-405 scope. All images were stacked and combined using Helicon Focus 7.6.4 Pro (Helicon Soft Ltd. 2000). The illustrations were cleaned and edited in Adobe Photoshop 2020.

Results

Quedius of West Siberia

According to current literature (Salnitska and Solodovnikov 2019), 24 species of *Quedius* are reported to occur in West Siberia (Table 1). Using external and genital characters, we sorted our newly collected 49 specimens into 11–13 morphospecies, most of which were identified to species level (Suppl. material 1). Three species (*Q. balticus* Korge, 1960, *Q. jenisseensis* (J. Sahlberg, 1880), and *Q. subunicolor* Korge, 1961) were represented by single males whose identification was straightforward based on external morphology and the shape of the aedeagi. Notably, *Q. balticus* was not previously recorded in West Siberia. *Q. molochinus* was represented by two males confidently identified based on external characters and aedeagi. Other species (*Q. boops* (Gravenhorst, 1802), *Q. fellmani* (Zetterstedt, 1838), *Q. fuliginosus*, and *Q. limbatus*) were represented by three or more specimens, including at least one male to verify identification with male genitalia. *Q. boops* was represented by the largest number of specimens (15) and localities (11). Two females were identified as *Q. boops* based on their similarity to males found in nearby localities. Finally, six females could not be identified precisely: two could be either *Q. fellmani* or *Q. boops*, one is a species from the *Q. boops* group, and three may be *Q. limbatus* but with some uncertainty.

Our molecular taxonomic units and their correspondence to morphospecies

We obtained COI barcodes for 28 out of 49 newly collected *Quedius* specimens (Table 2). These 28 barcodes represented all 11–13 morphospecies, including tentatively identified females. Our Bayesian Inference (BI) phylogenetic and p-distance analyses of these barcodes revealed seven clades and three branches corresponding to 13 separate molecular taxonomic units (MTUs) (Fig. 3). MTU 1 contains three specimens morphologically identified as *Q. fuliginosus*. MTU 2 comprises one male specimen identified as *Q. boops*. MTU 3 includes six specimens of both sexes morphologically identified as *Q. boops*, one female identified as *Q. fellmani*, one female morphologically assignable to either *Q. fellmani* or *Q. boops*, and one female identified as a species from the *Q. boops* group. MTU 4 is represented by a male specimen identified as *Q. subunicolor*. MTU 5 contains one male identified as *Q. balticus*. MTUs 6 and 7 each include one male identified as *Q. molochinus*. MTU 8 comprises one male identified as *Q. fellmani*, which is sister to MTU 9 containing two specimens (male and female) identified as *Q. fellmani* and one female assignable to either *Q. fellmani* or *Q. boops*. The male specimen of *Q. jenisseensis* forms a separate MTU 10, sister to a clade comprising MTUs 11, 12, and 13. MTU 11 contains two females: one identified as *Q. limbatus* and one teneral specimen morphologically unidentifiable. MTU 12 includes two *Q. limbatus* specimens, one of which is a female with less certain identification. MTU 13 comprises two males identified as *Q. limbatus*.

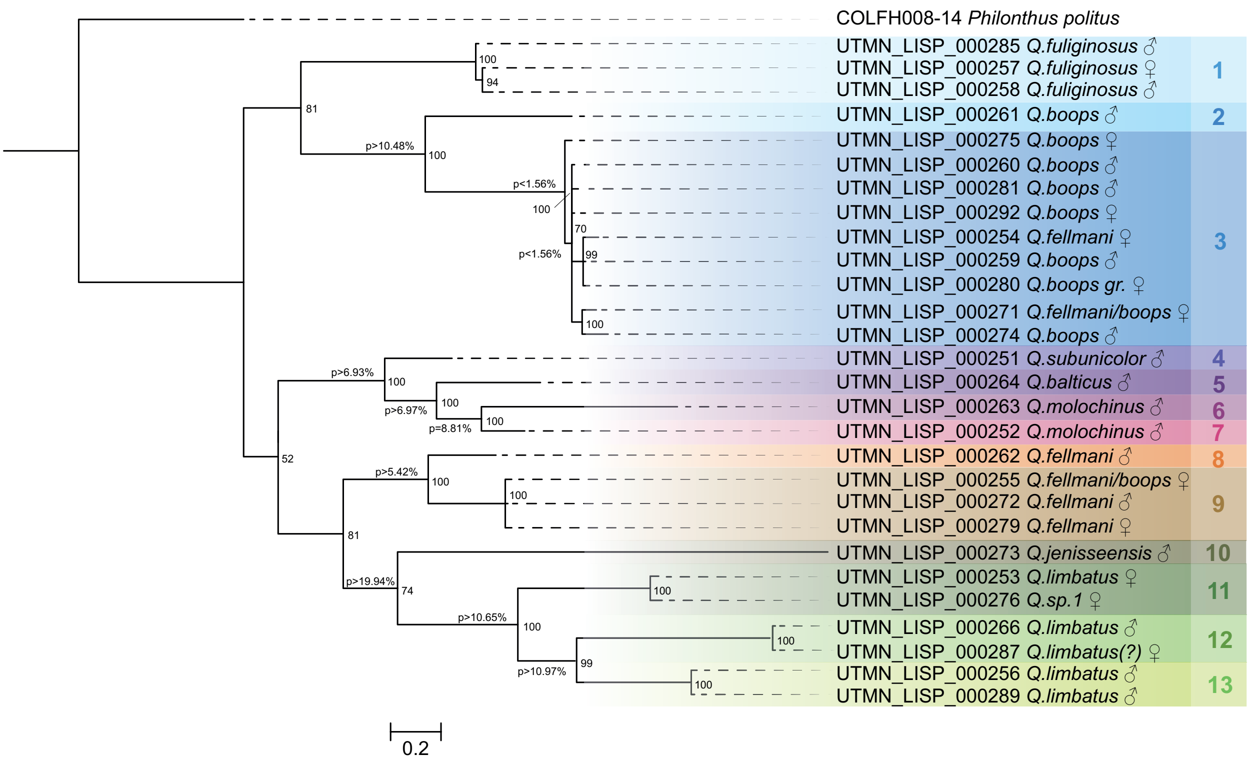

Figure 3. Molecular taxonomic units (MTUs) of West Siberian *Quedius* revealed via Bayesian inference phylogenetic analysis of their DNA barcodes and measuring pairwise molecular distances (P-distances) among all specimens. Colors and numbers refer to separate MTUs. Posterior probabilities and P-distances (>1) are provided at respective nodes.

Identification of molecular taxonomic units in BOLD and GenBank

The barcode-based MTUs described above were identified by the BOLD ID Engine or GenBank BLAST, as summarized in Table 2.

Assessment of molecular taxonomic units and their identifications with an expanded pool of data

Comparing our MTUs (Fig. 3) with morphology-based identifications reveals that only specimens identified as *Q. balticus*, *Q. subunicolor*, *Q. fuliginosus*, and *Q. jenisseensis* formed congruent MTU clades or branches. Conflicts between molecular and morphological identifications were detected in all other cases.

Attempts to identify MTUs via BOLD or GenBank were unambiguous only for *Q. fuliginosus*. For *Q. balticus* and *Q. jenisseensis*, COI barcodes were absent from both libraries, and the best available matches had low metric support. To further explore these molecular–morphological conflicts, we constructed three datasets (*Quedius* s. str., *Q. boops-fellmani-boopoides-nitipennis* complex, and *Q. limbatus* complex), combining our barcodes with all relevant sequences from BOLD and GenBank for detailed phylogenetic analyses. BI results are presented in Figs 4, 5, 6 and are discussed below.

Quedius subunicolor (Fig. 4)

A closer examination of BOLD data for *Q. subunicolor* revealed two specimens, COLFF286-13 and FBCOD1064-11, assigned to different species BINs. The barcode "*Q. subunicolor* FBCOD1064-11" likely represents a different species, *Q. unicolor*, as the specimen was collected in Carinthia, Austria—within the known distribution of *Q. unicolor* but outside that of *Q. subunicolor* (Hansen et al. 2022). This misidentification probably resulted from a lack of expert examination. Our test phylogenetic dataset confirms that FBCOD1064-11 clusters with a reliably identified *Q. unicolor* specimen (QUEDC012-19) from Hansen et al. (2022) (Fig. 4), with a low genetic distance (0.15%). The second BOLD barcode, "*Q. subunicolor* COLFF286-13," is 249 base pairs shorter than our barcode but otherwise identical. Another *Q. subunicolor* barcode, QUED22-0026 (collected in Sweden, Arvidsjaur, and confidently identified by Aslak Kappel Hansen, unpublished data), clusters in the *Q. subunicolor* clade of our dataset with 0% intraspecific distance. This supports the correct identification of COLFF286-13 from Finland in BOLD, consistent with the known distribution of *Q. subunicolor* (Hansen et al. 2022). The failure of the BOLD ID Engine to match our West Siberian specimen to COLFF286-13 is presumably due to sensitivity to barcode length.

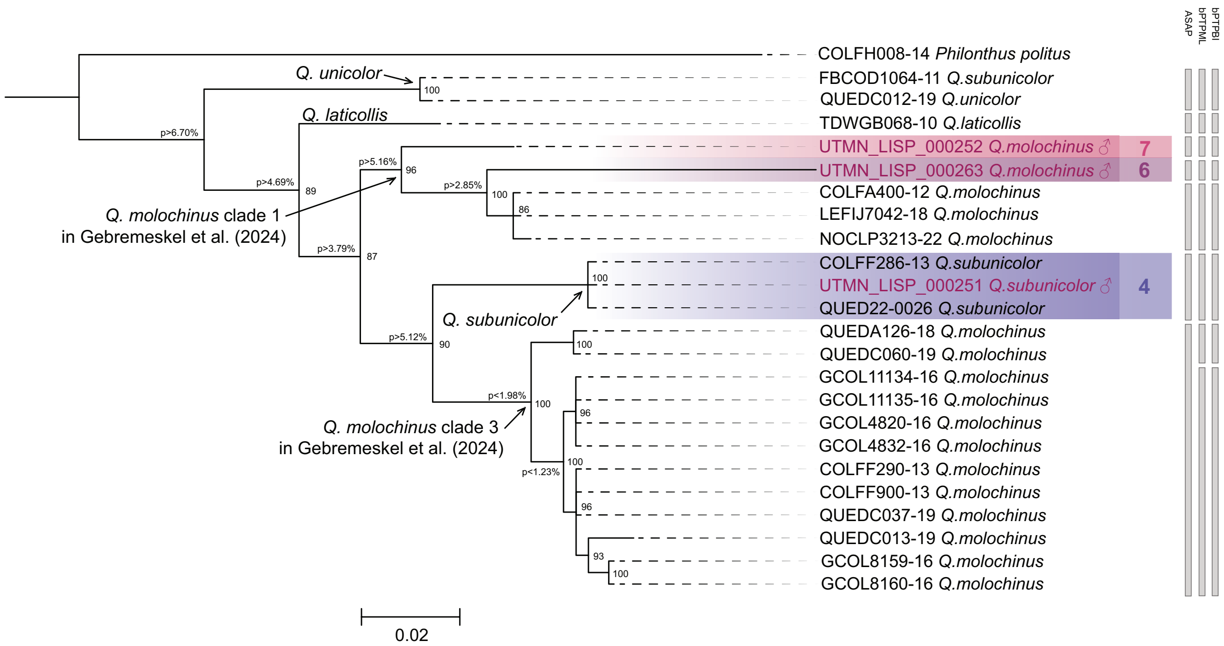

Figure 4. DNA barcode-based identification of West Siberian specimens of *Quedius* s. str. using barcodes from BOLD and GenBank, performed via Bayesian inference phylogenetic analysis and measuring pairwise molecular distances (P-distances) among all specimens. Terminals of West Siberian specimens (all UTMN_LISP) are marked with red font. Identifications of West Siberian terminals are our own and based on specimen morphology. Identifications of other terminals (from BOLD or GenBank) are from those databases. Clade and branch colors, as well as their numbering, refer to respective molecular taxonomic units (MTUs) in Fig. 3. Posterior probabilities and P-distances (>1) are provided at respective nodes. Presumed correct identifications of species are indicated at their respective nodes or branches with bold font. Grey vertical bars indicate species delimitation analyses, including ASAP (Assemble Species by Automatic Partitioning), bPTPML, and bPTPBI (Bayesian implementations of the Poisson Tree Process model based on the Maximum Likelihood tree and Bayesian tree, respectively).

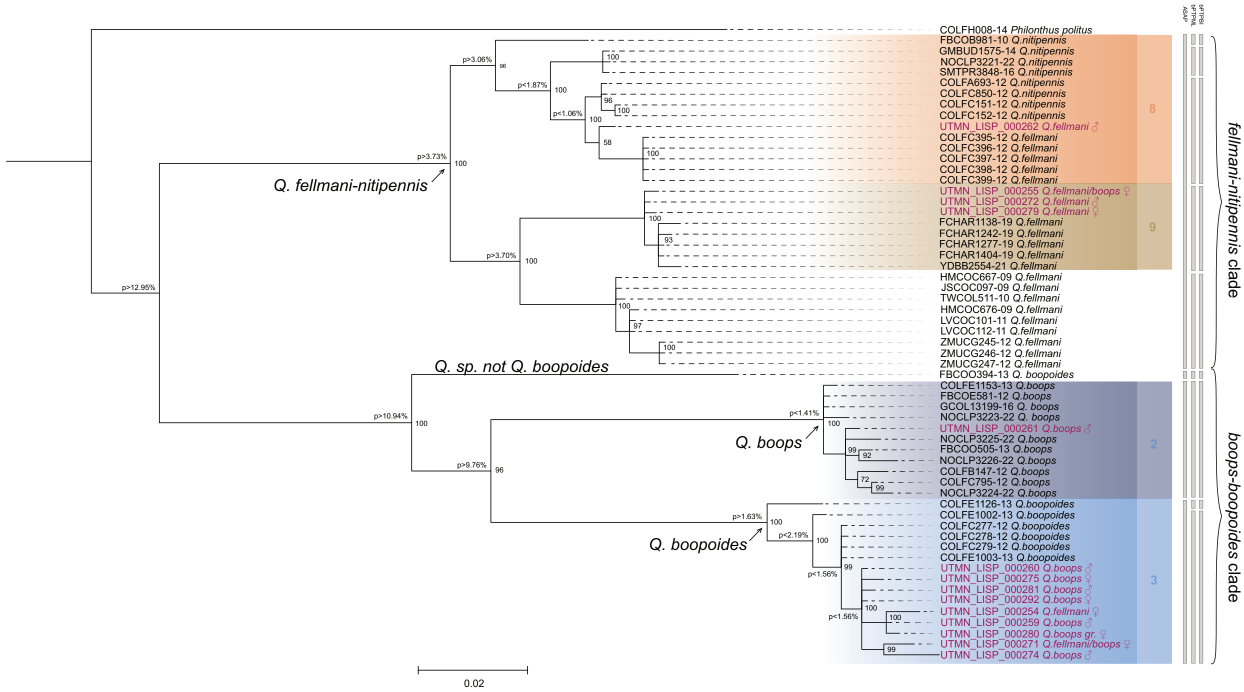

Figure 5. DNA barcode-based identification of West Siberian specimens of *Quedius* from the *Q. fellmani-nitipennis* and *Q. boops-boopoides* complexes using barcodes from BOLD and GenBank, performed via Bayesian inference phylogenetic analysis and measuring pairwise molecular distances (P-distances) among all specimens. Terminals of West Siberian specimens (all UTMN_LISP) are marked with red font. Identifications of West Siberian terminals are our own and based on specimen morphology. Identifications of other terminals (from BOLD or GenBank) are from those databases. Clade colors and their numbering refer to respective molecular taxonomic units (MTUs) in Fig. 3. Posterior probabilities and P-distances (>1) are provided at respective nodes. Presumed correct identifications of species are indicated at their respective nodes or branches with bold font. Grey vertical bars indicate species delimitation analyses, including ASAP (Assemble Species by Automatic Partitioning), bPTPML, and bPTPBI (Bayesian implementations of the Poisson Tree Process model based on the Maximum Likelihood tree and Bayesian tree, respectively).

In GenBank, *Q. molochinus* samples (GenBank: KU907087.1 = BOLD: GCOL11134-16; GenBank: KJ961909.1 = BOLD: COLFF900-13) were suggested by BLAST as the closest matches to our *UTMN 000251 Q. subunicolor* specimen, but with low identity scores insufficient for reliable species identification. This likely reflects the same issue described above, as GenBank contains the same two *Q. subunicolor* barcodes as BOLD. Correspondingly, the p-distance between the *Q. subunicolor* and *Q. molochinus* clades—including the referenced *Q. molochinus* samples—exceeds 5.12%.

Quedius molochinus complex (Fig. 4)

Our phylogenetic analysis places both specimens morphologically identified as *Q. molochinus* within a clade containing barcodes COLFA400-12 from Finland, LEFIJ7042-18 from Northwestern European Russia, and NOCLP3213-22 from Norway (Fig. 4), all identified as *Q. molochinus* in their source libraries. This clade, here referred to as "*Q. molochinus* clade 1" (following Gebremeskel et al. 2024), is sister to a larger clade composed of *Q. subunicolor* samples and other *Q. molochinus* specimens included in this analysis. However, specimens UTMN 000252 and UTMN 000263 show significant divergence within clade 1, with p-distances of over 5.16% and 2.85%, respectively. The remaining *Q. molochinus* samples form a second clade, designated as "*Q. molochinus* clade 3" (Gebremeskel et al. 2024), with an intraspecific p-distance below 1.98%. By contrast, the genetic distance between clade 1 and the combined clade of *Q. subunicolor* plus *Q. molochinus* clade 3 exceeds 3.79%. A single specimen of *Q. laticollis* (Gravenhorst, 1802) forms a distinct branch, diverging by more than 4.69% from the super-clade containing *Q. molochinus* clade 1, *Q. subunicolor*, and *Q. molochinus* clade 3. Species delimitation analyses partitioned the *Q. molochinus* specimens into four groups based on ASAP and five groups according to bPTP. These results suggest the presence of potential cryptic species within the widely distributed *Q. molochinus*, warranting further investigation, including examination of internal sac characters of the aedeagus, as also discussed in Gebremeskel et al. (2024).

Quedius fellmani and *Q. nitipennis* (Fig. 5)

Some specimens morphologically identified as *Q. fellmani* and *Q. boops* were assigned to *Q. nitipennis* (Stephens, 1833) or *Q. boopoides* Münster, 1923, based on their DNA barcodes. A combined phylogenetic analysis of barcodes

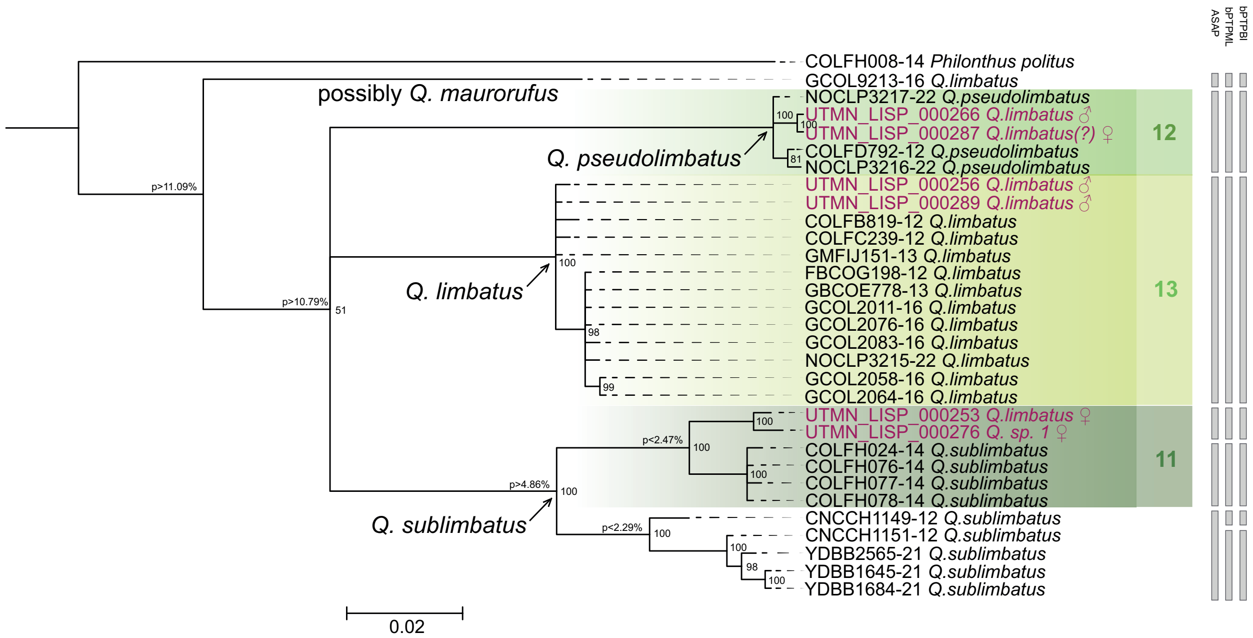

Figure 6. DNA barcode-based identification of West Siberian specimens from the *Quedius limbatus* complex, performed via Bayesian inference phylogenetic analysis and measuring pairwise molecular distances (P-distances) among all specimens. Terminals of West Siberian specimens (all UTMN_LISP) are marked with red font. Identifications of West Siberian terminals are our own and based on specimen morphology. Identifications of other terminals (from BOLD or GenBank) are from those databases. Clade colors and their numbering refer to respective molecular taxonomic units (MTUs) in Fig. 3. Posterior probabilities and P-distances (>1) are provided at respective nodes. Presumed correct identifications of species are indicated at their respective nodes or branches with bold font. Grey vertical bars indicate species delimitation analyses, including ASAP (Assemble Species by Automatic Partitioning), bPTPML, and bPTPBI (Bayesian implementations of the Poisson Tree Process model based on the Maximum Likelihood tree and Bayesian tree, respectively).

from this study and public DNA libraries revealed two large clades. One contains all publicly available barcodes identified as *Q. fellmani*, paraphyletic with respect to barcodes identified as *Q. nitipennis* (the *fellmani-nitipennis* clade), while the other includes all public barcodes identified as *Q. boops*, with a nested cluster of several barcodes identified as *Q. boopoides* (the *boops-boopoides* clade) (Fig. 5).

UTMN specimens 000262, 000272, and 000279 (morphologically identified as *Q. fellmani*) and female 000255 (tentatively identified as *Q. fellmani* or *Q. boops*) were placed within the *fellmani-nitipennis* clade. Females 000271 and 000280, identified with some uncertainty as *Q. fellmani* or *Q. boops* (000271) and as a member of the *boops* group (000280), clustered in the *boops-boopoides* clade. These placements largely agree with our morphology-based identifications, except for specimen 000254, which was placed in the *boops-boopoides* clade despite its initial morphological identification as *Q. fellmani*. Morphological re-examination (Fig. 2E) showed that 000254 has larger, more convex eyes and a more robust body than typical *Q. fellmani*, traits overlooked during initial identification. Similarly, re-examination of 000255 (Fig. 2F) confirmed its molecular-based assignment to *Q. fellmani*, showing smaller, less convex eyes and a slightly less robust body than *Q. boops* or *Q. boopoides.*

The paraphyly of *Q. nitipennis* with respect to *Q. fellmani* is a result revealed by DNA barcoding and is addressed in the Discussion below. The *fellmani–nitipennis* clade consists of two subclades with a p-distance between them greater than 3.73%. One subclade includes UTMN 000262 (MTU 8; *Q. fellmani*), BOLD-derived sequences from various Palaearctic localities, and specimen SMTPR3848-16 from Canada. The genetic distance among specimens in this subclade is less than 3.06%. Nearly half of the specimens in this clade are identified as *Q. nitipennis*, and the other half as *Q. fellmani*. According to the ASAP species delimitation analysis, all specimens in this clade form a single group, whereas bPTP splits them into five groups. In a personal communication, Adam Brunke suggested that the specimen from Canada represents an introduction of *Q. nitipennis* and that MTU 8 may also correspond to *Q. nitipennis*.

The second *fellmani–nitipennis* clade includes *Q. fellmani* samples that are subdivided into two subclades with a p-distance between them of more than 3.70% and internal p-distances of less than 0.63% and 0.82%, respectively. One subclade includes UTMN 000272, 000255, and 000279 (MTU 9), as well as the BOLD-derived *Q. fellmani* specimens from Canada (western localities—Nunavut and Yukon). The other subclade consists of BOLD-derived *Q. fellmani* from Canada (eastern localities—Manitoba) and Greenland. Notably, MTU 8 is from a western locality (124^{th} km on the road from Salekhard to Nadym), while all three specimens from MTU 9 are from two more eastern localities (Gaz-Sale town and the River Taz floodplain), separated by ca. 460 km from MTU 8. Morphological re-examination of UTMN 000262 (Fig. 2G and N), 000272 (Fig. 2H and O), 000279 (Fig. 2I), and 000255 (Fig. 2F) did not reveal any notable morphological differences between MTUs 8 and 9 either externally (compare Fig. 2G, I, F, H) or in the structure of the aedeagus (compare Fig. 2N, O). However, Adam Brunke mentioned in personal communication that he was able to find distinguishing characters between these clades; more material and data are needed for robust diagnoses of these putative species.

Quedius boops and *Q. boopoides*

Within the *boops–boopoides* clade (Fig. 5), specimen FBCOO394-13 (*Q. boopoides*) is sister to the rest of the clade, with a distance greater than 10.94%. This distance approaches the molecular divergence between the *fellmani–nitipennis* and *boops–boopoides* clades (12.95%). Based on the metadata in BOLD, the specimen was collected in Germany and identified by Frank Koehler. Presumably, FBCOO394-13 is misidentified and in fact represents neither *Q. boops* nor *Q. boopoides*. Although a habitus image is provided in BOLD, the quality is insufficient to verify the identification.

Specimen UTMN 000261 (MTU 2 in Fig. 3) and specimens 000254, 000259, 000260, 000271, 000274, 000275, 000280, and 000281 (MTU 3) formed two sister clades that are more than 9.76% p-distant from each other (Fig. 2). Based on the morphology of UTMN 000261 (Fig. 2C, K), where the subapical tooth of the aedeagus is weaker and located closer to the apex of the median lobe, the MTU 2 clade corresponds to *Q. boops* (Salnitska and Solodovnikov 2019). This hypothesis is also supported by the slightly narrower paramere and overall smaller aedeagus of this specimen, which also separate *Q. boops* from *Q. boopoides* (Assing and Schülke 2012). For UTMN 000260 (Fig. 2J), the subapical tooth of the aedeagus is stronger and located further from the apex of the median lobe, so the MTU 3 clade presumably corresponds to *Q. boopoides*. This hypothesis is supported by the basally slightly wider paramere and overall larger aedeagus of this specimen. Therefore, BOLD specimens COLFE1126-13, COLFE1002-13, COLFC277-12, COLFC278-12, COLFC279-12, and COLFE1003-13 in this clade are here considered correctly identified as *Q. boopoides*. Unfortunately, there is no high-resolution photo documentation of these vouchers in BOLD to verify this. Our ASAP species delimitation analysis divided the *boops–boopoides* clade into three groups: *Q. boops*, *Q. boopoides*, and the separate specimen *Q. boopoides* FBCOO394-13. Meanwhile, bPTP showed a similar pattern but further split the *Q. boopoides* group into two clades.

Molecular taxonomic units 11–13 (*Q. limbatus* complex)

In the test phylogenetic tree (Fig. 6), we obtained at least four molecular species with large (10.79%–11.09%) p-distances between them. The first species is represented by specimen GCOL9213-16 from Saxony-Anhalt, Germany, identified as *Q. limbatus*. Most likely, this specimen is misidentified in BOLD. It belongs to BIN ID ACG3571, which includes two specimens identified as *Q. scitus* (Gravenhorst, 1806) and one specimen identified as *Q. maurorufus* (Gravenhorst, 1806). An image of GCOL9213-16 is not provided in BOLD but is available, along with other metadata, from the Museum Koenig in Bonn (http://id.zfmk.de/collection_ZFMK/2519464/733080/89423). The image is of low quality but roughly matches *Q. maurorufus*, *Q. limbatus* (both species are externally similar), or another similar *Raphirus* Stephens, 1829 species. The *Q. scitus* specimen in the same BIN is clearly misidentified, as *Q. scitus* is a small brown *Microsaurus* Dejean, 1833 species—that is, from a different subgenus of *Quedius* that only superficially resembles *Q. maurorufus*. In fact, the photo of *Q. scitus* in BOLD (https://www.boldsystems.org/index.php/Public_RecordView?processid=FBCOO734-13), although of suboptimal quality, clearly shows that it is not a species of *Microsaurus* but a small *Raphirus*. *Q. maurorufus* introduced to Canada corresponds to BOLD BINs AAX9863 and ACZ1264, while the identity of ACG3571 remains unclear (Adam Brunke, personal communication).

The second molecular species is formed by three BOLD reference barcodes from Norway and Finland, identified as *Q. pseudolimbatus* A. Strand, 1938, and two UTMN specimens that we confidently (for male 000266) or tentatively (for female 000287) identified as *Q. limbatus* based on morphology, forming MTU 12. The species delimitation analysis placed all specimens from this clade into one group.

The third species clade, with unresolved sister group relationships, is formed by eleven BOLD reference barcodes from Norway, Germany, and Finland, all identified as *Q. limbatus*. UTMN 000256 and 000289 (West Siberian males forming MTU 13) were morphologically identified as *Q. limbatus* and grouped into this clade with a p-distance of less than 0.91% from the other barcodes. According to the species delimitation analysis, all these specimens formed one group.

Finally, the fourth species is formed by multiple reference barcodes from BOLD identified as *Q. sublimbatus*. It consists of two sister subclades with a molecular distance greater than 4.86% between them: one subclade includes four specimens from Finland, while the other contains five specimens from Canada. UTMN 000253 (morphologically identified as *Q. limbatus*) and 000276 (morphologically unidentified) formed MTU 11 and were placed in the subclade with specimens from Finland. The ASAP species delimitation analysis divided the specimens from this clade into three groups, one of which includes UTMN 000253 and 000276. bPTP identified four groups and, unlike ASAP, placed specimen CNCCH1149-12 from the second subclade into a separate group.

We re-examined UTMN 000266 (Fig. 1M, N), 000256 (Fig. 1O, P), and 000289 (Fig. 1S, T) and concluded that 000266 indeed fits the concept of *Q. pseudolimbatus* (Strand 1838; Salnitska and Solodovnikov 2019), while the latter two males fit the concept of *Q. limbatus*

(Assing and Schülke 2012; Salnitska and Solodovnikov 2019). In addition, re-examination of a non-sequenced "*Q. limbatus*" specimen, UTMN 000268 from West Siberia (Fig. 1Q, R), showed that its characters also match *Q. pseudolimbatus*. Both male specimens of *Q. pseudolimbatus* can be distinguished from West Siberian *Q. limbatus* material by their aedeagi as follows. In *Q. pseudolimbatus*, the apex of the median lobe is more obtuse because the subapical tooth extends to the apex and forms a carina, so that the apical portion of the median lobe in lateral view appears axe-shaped. The paramere (in ventral view) is broader and bears rows of 5–6 peg setae on its underside, each extending further basad. In *Q. limbatus*, the apex of the median lobe is sharp because the subapical tooth does not extend to the apical portion of the median lobe. The paramere (in ventral view) is narrower, with rows of 2–4 peg setae that extend only slightly basad. Compared to specimens of true *Q. limbatus*, the sequenced UTMN 000266 and 000287, as well as the non-sequenced 000268, appear more robust externally, with darker coloration of the pronotum and elytra and distinctly paler yellowish margins and appendages. This is congruent with molecular data suggesting that they are *Q. pseudolimbatus*.

Unfortunately, UTMN 000253 and 000276 (MTU 11), which were placed together with *Q. sublimbatus* reference barcodes (Fig. 6), are females. We were not able to find any morphological differences between them and UTMN *Q. limbatus* specimens 000256 and 000289 (MTU 13). The body size of UTMN specimen 000253 is larger, but this difference clearly falls within the known morphological variability of *Q. limbatus* (Assing and Schülke 2012; Salnitska and Solodovnikov 2019). *Q. sublimbatus* was described from North America (Mäklin 1853) and later recorded from Northern Europe and Northern Asia (Salnitska and Solodovnikov 2019). UTMN specimens 000253 and 000276 were collected from the Yamalo-Nenets Autonomous Region, which is consistent with the distribution of *Q. sublimbatus*.

New faunistic data for *Quedius* in West Siberia

As a result of this study, the following *Quedius* species previously recorded in West Siberia (Table 1) have been confirmed to occur in the region: *Q. boops*, *Q. boopoides*, *Q. jenisseensis*, *Q. fellmani*, *Q. fuliginosus*, *Q. molochinus*, *Q. limbatus*, *Q. sublimbatus*, and *Q. subunicolor*. For *Q. sublimbatus* and *Q. subunicolor*, our data represent the first precisely georeferenced records in the region, complementing earlier catalogue records from West Siberia (coded as WS) that lacked specific locality information (Schülke and Smetana 2015; for *Q. subunicolor*, the WS record is listed under *Q. altaicus*, a synonym of the former species according to Hansen et al. 2022). In addition, *Q. pseudolimbatus* and *Q. balticus* are reported from West Siberia for the first time. These findings are generally consistent with the known distributions of the respective species.

Discussion

For West Siberian species of the genus *Quedius*, only some were correctly identified using morphology, and the identity of only one species was unambiguously confirmed by DNA barcoding. This species was *Q. fuliginosus*, as its morphological identification did not pose any problems, and its congruent molecular identification showed a high score of similarity and identity with conspecific barcodes available in BLAST and BOLD. It was similarly straightforward to identify *Q. jenisseensis* and *Q. balticus* based on morphology alone, but we could not test our morphological identifications with molecular data due to the absence of reference barcodes for these two species. *Q. subunicolor* was easy to identify based on morphology alone, but its molecular identification was not smooth. Barcode FBCOD1064-11 was *Q. unicolor* misidentified as *Q. subunicolor*, and our 656 bp barcode of UTMN 000251 did not match the conspecific 407 bp barcode of COLFF286-13 in BOLD or GenBank. In all other cases, we faced more complex difficulties in species identification.

Our struggle to identify *Q. boops*, *Q. boopoides*, *Q. limbatus*, and *Q. pseudolimbatus* is a typical challenge for entomologists who must distinguish species with subtle morphological differences. Morphological differences between *Q. boops* and *Q. boopoides*, and between *Q. limbatus* and *Q. pseudolimbatus*, are confined to minute and hard-to-notice traits of the aedeagus. Uncertainty and confusion associated with the current morphological delimitation of *Q. boops* from *Q. boopoides* have been repeatedly discussed (Tottenham 1948; Assing and Schülke 2012; Salnitska and Solodovnikov 2019). In the *Q. boops* and *Q. boopoides* pair, barcoding revealed our own morphological misidentification for some West Siberian specimens. DNA-based correction of our misidentifications was possible because a sufficient number of correctly identified barcodes for both species are available in the barcode libraries. However, uncertainty and confusion associated with the morphological separation of both species have led to a number of incorrectly identified barcodes in these libraries, making barcode-based identification less straightforward. It requires a critical approach and, ideally, a revision of the voucher specimens, some of which may be wrongly identified, such as FBCOO394-13 ("*Q. boopoides*"). The largely sympatric distribution of members of the *Q. boops* complex (Salnitska and Solodovnikov 2019) increases the morphology-based misidentification rate within this complex.

In the *Q. limbatus* and *Q. pseudolimbatus* pair, barcoding was also very helpful in revealing our own morphological misidentifications through reference barcodes in the libraries. For example, we learned that we had completely overlooked *Q. pseudolimbatus* in our West Siberian material despite having collected males. Moreover, barcoding helped us discover a third species from this complex, *Q. sublimbatus*, represented in our material by females only. This corresponds to the second typical difficulty mentioned in the Introduction—when entomologists have singleton females of species that can be morphologically identified based on males only.

We also revealed an obviously misidentified "*Q. limbatus*" barcode (GCOL9213-16) in the libraries and noted that the overall metadata for other barcodes in this complex are insufficient for proper verification of species identifications (e.g., lacking or poor-quality images of voucher specimens, absence of genitalia photographs). However, our critical examination of the entire pool of our own and publicly available barcodes lends confidence that most barcode sequences for this complex in BOLD and GenBank are correctly identified. This conclusion aligns well with the known distributional data. *Q. pseudolimbatus* was described from northern Norway (Strand 1938) and later recorded from Sweden (Palm 1963). According to records in GBIF (https://www.gbif.org/ru/species/10933969), this species is common in both countries and also occurs in Finland. All three reference barcodes in BOLD that are conspecific with our verified male also originate from Northern Europe (Finland: Ostrobottnia Ultima; Norway: Hedmark, Trøndelag). *Q. sublimbatus* was described from North America (Mäklin 1853). This species is Holarctic and occurs in northern regions and in mountainous areas of more southern zones (Salnitska and Solodovnikov 2019). Notably, *Q. sublimbatus* was previously recorded from West Siberia (Table 1).

Testing our morphology-based identification of *Q. fellmani* through DNA barcoding illustrated the third typical difficulty—dealing with subtle morphological differences between closely related species when those differences are not clearly defined, possibly due to complex species limits that require an integrative approach. Our data suggest that *Q. fellmani* and *Q. nitipennis*, as currently defined based on morphology (e.g., Assing and Schülke 2012; Salnitska and Solodovnikov 2019), may not represent true evolutionary lineages. According to morphology, both of our West Siberian males appear conspecific—even after critical re-examination following barcoding. However, based on barcodes, they clearly represent distinct species, as one was identified as *Q. fellmani* and the other as *Q. nitipennis* using BOLD and GenBank tools. Moreover, our phylogenetic test with a larger dataset most likely shows *Q. nitipennis* to be paraphyletic with respect to *Q. fellmani*. It should be noted that the BOLD and GenBank-based identifications are impossible to verify due to insufficient voucher documentation.

Currently, *Q. fellmani* is characterized by a more obtuse apex of the median lobe compared to *Q. nitipennis*, gradually narrowing apicad; by a paramere that does not narrow in its middle portion; and by rows of peg setae converging apicad (Salnitska and Solodovnikov 2019). Interestingly, all our specimens belonging to the different molecular lineages, namely '*nitipennis*' or '*fellmani*,' exhibit aedeagal characters corresponding to *Q. fellmani* sensu Salnitska and Solodovnikov (2019). It is also believed that *Q. fellmani* is a widespread circumpolar arctoboreal species repeatedly recorded from Russia. In contrast, *Q. nitipennis* is characterized by a median lobe with a pointed apex, a paramere slightly narrowing in its middle part, and rows of peg setae underneath extending parallel or only slightly converging apicad (Salnitska and Solodovnikov 2019). *Q. nitipennis* is considered a West Palaearctic species, rarely recorded from the European parts of Russia and hitherto not recorded from West Siberia. However, these distributional data may be erroneous if based on misinterpreted species limits that are difficult to establish unambiguously from morphology alone. A similar case of discordance between morphological and molecular variability, which warrants further investigation, was revealed for *Q. molochinus* in our study, partially consistent with the findings reported by Gebremeskel et al. (2024). Finally, the morphology-based delimitation of *Q. fellmani* and *Q. nitipennis* illustrated by Salnitska and Solodovnikov (2019) stems primarily from European material and may require reevaluation in light of new, geographically broader data.

Conclusion

On one hand, DNA barcoding in our study proved to be a highly useful tool complementing, if not outperforming, traditional morphology-based identification. In several cases (e.g., the *Q. boops* and *Q. boopoides* pair, the *Q. limbatus* complex), barcoding corrected our misidentifications based on subtle morphological traits. Additionally, barcoding was the only method enabling identification of several singleton females. More importantly, it clearly highlighted situations where currently accepted, vague morphology-based species limits may not reflect true species lineages (e.g., the *Q. fellmani* and *Q. nitipennis* pair) or may conceal more complex polymorphism (e.g., *Q. molochinus*). These applications were possible due to the substantial reference barcode datasets accumulated over the years in BOLD and GenBank, the largest barcode libraries available.

On the other hand, DNA barcoding-based species identification was not straightforward for *Quedius*. Firstly, the DNA libraries facilitating such identification are far from complete. For some species (*Q. jenisseensis* and *Q. balticus*), barcodes were entirely absent from both databases. For several others, only a few barcodes were available, and some were of suboptimal quality (e.g., too short). The biggest problem, however, was the presence of numerous misidentified barcodes in the reference libraries. It was only through our critical, comparative, and reciprocal approach that we were able to detect these misidentifications and suggest correct species identities for many specimens. Any non-specialist user submitting a barcode to the BOLD ID Engine or GenBank BLAST would risk receiving an incorrect identification.

Expectedly, the majority of misidentified barcodes in BOLD and GenBank belong to species complexes with subtle morphology-based species boundaries, as their identification in these libraries often relies solely on morphological examination of voucher specimens—frequently by non-specialists. Correcting these misidentifications requires an integrative approach. However, this process is hindered by insufficient or missing voucher documentation and the complex communication chain needed to update metadata once errors are detected.

Given these challenges, we strongly encourage increased barcoding efforts for *Quedius*, rove beetles in general, and other similarly diverse and taxonomically challenging arthropod groups. Barcoding initiatives should be fully integrated into routine faunistic and taxonomic work conducted by specialists. Just as new, especially puzzling, specimens are routinely mounted and dissected during such work, they should also be regularly barcoded. This practice would enable the simultaneous collection of both morphological and molecular data from the outset, facilitating more robust species delimitation. Using morphological and molecular data pools together, in comparison with reference libraries, will lead to more precise species boundaries and, consequently, more accurate identification of individual specimens and barcode sequences. This integrative approach will also drive improvements in metadata submission standards and voucher specimen documentation in barcode libraries, creating a self-reinforcing cycle of enhancement. Better documentation—including high-quality habitus and aedeagus images—should become standard practice. Furthermore, wider adoption of integrative taxonomy and greater use of barcode libraries will foster continuous feedback from ongoing taxonomic research back to the libraries, resulting in corrected identifications for previously generated barcodes. This, in turn, will encourage the development of improved systems for updating and curating barcode metadata.

As a contribution toward this goal, we have uploaded our newly generated barcodes to BOLD, complete with detailed metadata such as high-resolution habitus and aedeagal images, exact localities, and specimen identifiers. We have also communicated with BOLD regarding misidentified *Quedius* barcodes in their reference database.

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Supplementary material 1

Occurences

Authors: Valeria Krivosheeva, Maria Salnitska, Darya Semerikova, Angesom Abraham Gebremeskel, Anastasiya Ivanova, Alexey Solodovnikov

Data type: xlsx

Explanation note: Description of data: material of *Quedius* collected in West Siberia for this study, barcoded and not, and identified here based on morphology before the molecular examination and all data after examination.

Link: https://doi.org/10.3897/dez.72.143622.suppl1

Supplementary material 2

P-distances

Authors: Valeria Krivosheeva, Maria Salnitska, Darya Semerikova, Angesom Abraham Gebremeskel, Anastasiya Ivanova, Alexey Solodovnikov

Data type: zip

Explanation note: Description of data: tables with calculated p-distances for the sequences used in our phylogenetic analysis.

Link: https://doi.org/10.3897/dez.72.143622.suppl2