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The limits of Quediini at last (Staphylinidae: Staphylininae): a rove beetle mega-radiation resolved by comprehensive sampling and anchored phylogenomics

ADAM J. BRUNKE1, ASLAK K. HANSEN2,3,4, MARIA SALNITSKA5,6, JANINA L. KYPKE2, ALEXANDER V. PREDEUS7, HERMES ESCALONA8, JULIE T. CHAPADOS1, JACKSON EYRES1, ROBIN RICHTER1, ALEŠ SMETANA1, ADAM ŠLIPIŃSKI8, ANDREAS ZWICK8, JIŘÍ HÁJEK9, RICHARD A. B. LESCHEN10, ALEXEY SOLODOVNIKOV2,6 and JEREMY R. DETTMAN1

1Agriculture and Agri-Food Canada, Ottawa, ON, Canada, 2Natural History Museum of Denmark, Zoological Museum, Copenhagen, Denmark, 3Department of Biology, Aarhus University, Aarhus, Denmark, 4Natural History Museum Aarhus, Aarhus, Denmark, 5X-BIO Institute, University of Tyumen, Tyumen, Russia, 6Zoological Institute of Russian Academy of Sciences, Saint Petersburg, Russia, 7Bioinformatics Institute, Saint Petersburg, Russia, 8Australian National Insect Collection, National Collections Australia, CSIRO, Canberra, Australia, 9Department of Entomology, National Museum, Prague, Czech Republic and 10New Zealand Arthropod Collection, Maanaki Whenua – Landcare Research, Auckland, New Zealand

Abstract. Rove beetles of the tribe Quediini are abundant predators in humid microhabitats of forested, open, synanthropic or subterranean ecosystems, with just over 800 species distributed across the temperate and subtropical regions of the Northern Hemisphere. Previous molecular phylogenies included only a limited representation of this diversity but have already indicated that *Quedius*, containing the majority of Quediini species, is polyphyletic. Six genera, historically associated with Quediini but now *Staphylininae incertaesedis*, are known only from few pinned specimens and have never been sequenced. Recent synergy between target enrichment phylogenomics, low-input sequencing of dry, pinned insect specimens and advances in alpha taxonomic knowledge have made comprehensive sampling of Quediini tractable. Here we developed a novel probe set specialized for anchored hybrid enrichment of 1229 single-copy orthologous loci in Staphylinidae. In one of the largest target enrichment phylogenies of insects to-date, we sequenced 201 ingroup taxa to clearly delimit monophyletic Quediini within Staphylininae and resolve relationships within this tribe, with 46% of sampled taxa derived from pinned specimens (0–45 years old). Maximum likelihood and coalescent phylogenetic analyses produced well-resolved, congruent topologies that will serve as a framework for further exploration of this radiation and its necessary generic revision. The inclusion of nearly all remaining Staphylininae *incertaesedis* genera, all known only from pinned specimens, resulted in the creation of Quelaestrygonini Brunke, trib. n. and revised concepts for Cyrtoustedini and Indoquedini. Quediini was resolved as monophyletic with the transfer of *Q. elevatus* and *Q. nigropolitus* to other tribes but *Quedius* and its subgenera *Microsaurus*, *Distichalius* and *Raphirus* were shown to be para- or polyphyletic. Based on the results of our analyses, *Velleiopsis* Fairmaire, 1882 syn. n. and *Megaquedius* Casey, 1915 syn. n. are synonymized with *Microsaurus* Dejean,
1833 resulting in: Q. (Microsaurus) marginiventris (Fairmaire) comb. n., Q. (M.) varendorffi (Reitter) comb.n. Several species of Quedius were transferred from Microsaurus to Distichalius (Q. aethiops Smetana, Q. biann Smetana, Q. cingulatus Smetana and Q. taruni Smetana), Distichalius to Raphirus (Q. fagelianus Scheerpeltz) and Microsaurus to Raphirus (Q. mixtus Eppelsheim and Q. persicus Korge).

Introduction

The rove beetle tribe Quediini (alternatively subtribe Quediina) is a diverse group of just over 800 species (updated from Newton, 2019) distributed in the temperate and subtropical regions of the Northern Hemisphere, extending southward at successively higher elevations (Brunke et al., 2016; Smetana, 2017; Salnitska & Solodovnikov, 2019). Quedines are predators and often abundant in moist, forest-based microhabitats such as wet moss, leaf litter, rotting wood and fungi (Smetana, 2017). Many other species occur in debris or under stones in unforest environments, including arctic and alpine, or live in subterranean microhabitats (e.g. Smetana, 1971, 1988; Solodovnikov & Hansen, 2016; Salnitska & Solodovnikov, 2018a, 2018b). Some species have formed facultative or obligate associations with the nests of ants, wasps, birds and mammals (nidicolous) (Assing & Schülke, 2012; Brunke & BUFFAM, 2018). Some quedines thrive under the synanthropic conditions of agricultural and suburban landscapes, and have been transported around the world by human activity (Klimaszewski & Brunke, 2018).

Since the beginning of modern systematics research on the subfamily Staphylininae sensu lato (including Xantholininae and Platyprosopinae sensu Zyla & Solodovnikov, 2020), the composition of Quediini has been a central issue (Solodovnikov & Newton, 2005). Traditionally, Staphylininae has been roughly divided into a quedine group with a broad, shield-shaped pronotum and a staphylinine group with a more cylindrical pronotum (e.g. Smetana, 1977). Phylogenetic analyses showed that the ‘quedine’-type pronotal shape was in fact the plesiomorphic composition of Quediini has been a central issue (Solodovnikov 2019) have been published, complementing recent reviews of Quediini in China (Smetana, 2017), Middle Asia (Salnitska & Solodovnikov, 2018c) and Russia (Salnitska & Solodovnikov, 2019) have been published, complementing...
previous efforts for North America (Smetana, 1971) and the West Palaearctic (Coiffait, 1978) such that this diversity is easier to navigate for phylogenetic sampling using informal species groups and other morphological groupings elucidated by keys. However, only a fraction of the hundreds of taxa needed for adequate representation of Quedini are optimally preserved for the high quality of DNA required for the PCR-based workflows that have become standard in the aforementioned phylogenetic studies. Optimally preserved samples are also heavily biased towards North America and Central Europe, and for taxa readily collected by standard methods. Conversely, a geographically and taxonomically rich diversity of Quedini samples is preserved and available as pinned museum specimens. Low concentrations of highly fragmented DNA as preserved in pinned insect specimens have become readily amenable using a combination of extraction and library-preparation protocols that require increasingly smaller DNA inputs (e.g. Sproul & Maddison, 2017; Maddison & Sproul, 2020). Next-generation sequencing uses massively parallel short-read technologies to read these short DNA library fragments that are then assembled into longer target gene regions using bioinformatics pipelines. These advances can be combined with sequence capture methods, which target hundreds to thousands of single-copy loci using a set of short probe sequences, to attain comprehensively sampled phylogenomic datasets (St. Laurent et al., 2018; Hamilton et al., 2019; Buenaventura et al., 2020).

Anchored hybrid enrichment (AHE) is one such sequence capture method, which targets orthologous nuclear protein-encoding gene regions and has been successfully applied to beetles (e.g. Haddad et al., 2018; Martin et al., 2019). However, as sequence capture success declines with phylogenetic distance from the model taxa used to develop the probes, probe sets ‘tailored’ for specific beetle lineages have been developed to maximize the number of recovered loci (Martin et al., 2019; Gustafson et al., 2020). The AHE studies have focused on two clades: the Phytophaga (e.g. Haddad et al., 2018) and the family Lampyridae (Martin et al., 2019), both distant from Staphylinidae and the superfamily Staphylinioidea to which it belongs (Mickenna et al., 2019). As Staphylinidae was already diverse by the mid-Jurassic (Chatzimanolis, 2018; Fikáček et al., 2020) and is the largest family of organisms with more than 60,000 species (Newton, 2019), rove beetle systematics would undoubtedly benefit from the development of a specialized AHE probe set.

Here we developed such a resource for sequence capture in Staphylinidae and tested its efficacy to resolve the limits of, and relationships within, the diverse Quedini. Using low-input extraction and library preparation protocols, we targeted rare taxa available only as pinned museum specimens and attempted to amplify DNA from as many named supraspecific taxa and species groups of the heterogeneous Quedius as possible. We used the resultant genomic dataset to test the monophyly of Quedini, Quedius and its subgenera, and to produce a comprehensive phylogeny that may serve as a framework for a greatly needed generic revision of the tribe.

Methods

Higher classification of Staphylininae

Recently, Zyła & Solodovnikov (2020) recovered enigmatic genus Coomania Cameron as the sister group of the morphologically well-defined clade Staphylinini, and elevated each of these to subfamily rank. They, in turn, elevated most former subtribes of Staphylinini, including Quedini, to tribe status. Staphyliniinae in the former, broadest sense was found to be monophyletic and sister to Paederinae, and systematic changes were not required based on topology alone. Changes in rank were made in order to allow Staphyliniinae to be more easily diagnosed morphologically, compared to treating Coomania and Staphylinini together as Staphyliniinae, or treating these taxa, along with tribes Arrowini, Platyprosopini, Othiini, Maorothiini and Xantholinini as the traditional, broadly defined Staphyliniinae. Shortly thereafter, Tihielka et al. (2020) reanalysed the dataset of Zyła & Solodovnikov (2020) and recovered a slightly different topology but with Coomania again sister to Staphylinini and the traditional Staphyliniinae and Paederinae as sister groups. They argued against the proliferation of subfamily rank names and instead returned to the traditional broad Staphyliniinae, downgrading Coomaniiinae to Coomantini. We here prefer the system proposed by Zyła & Solodovnikov (2020) for its greater diagnostic value and treated Cyrtosquetidini, Quedini, etc. as tribes herein.

Taxon sampling

As Quedini has been repeatedly recovered within a well-supported NHC (Brunke et al., 2016, 2019; Chani-Posse et al., 2018; Jenkins Shaw et al., 2020), taxa were sampled from within this latter clade and Heterothops sp., a staphyline outside of the NHC, was used to root the trees. The species of Heterothops used is an undescribed species from the Neotropics but belongs to the ‘core’ of Heterothops as defined in Jenkins Shaw et al. (2020) and therefore to the Southern Hemisphere clade Amblyopini. All six major clades of the NHC recovered by Brunke et al. (2016) and treated as tribes or subtribes (Tihielka et al., 2020; Zyła & Solodovnikov, 2020) were represented in the taxon sample. Although Quedius still contains many species that belong in Amblyopini, these were ignored in the sampling scheme based on morphological diagnoses of tribes given by Brunke et al. (2019). Pinned museum specimens were available for the Staphyliniinae incertae sedis genera Alesiella Brunke & Solodovnikov, Beeeria Hatch, Quedio macrurus Sharp, Quelaestrygon Smetana and Strouhalium Scheerpeltz (see Supplementary File S1). We densely sampled Quedini by representing all described genera and subgenera except Velleiopis Fairmaire, which is similar to the sampled Quedius (Megaquetus) Casey (see Discussion), and nearly all species groups of the large genus Quedius. Quedius nigropolitus Cameron from Java, known only from the holotype collected in 1937, is the only species of the genus from southeast Asia (south of northern Thailand, Laos and Vietnam) that has not yet
been moved to another genus. We sampled a closely related but undescribed species from Vietnam and so this taxon is hereafter referred to as *Q. nr. nigropolitus*. Staphylininae *incertae sedis* genus *Descarpentriesiellus* Jarrige from Madagascar was successfully sequenced and included in initial, exploratory analyses. It formed a well-supported clade with *Heterothops* (i.e. not NHC) in unrooted trees and was excluded from final datasets to prevent problems with rooting the tree. Its phylogenetic position will be the topic of a future study with greater taxon sampling of the Southern Hemisphere lineages. The only Staphylininae *incertae sedis* genus unaccounted for in the present study is the quedine-like genus *Lonia* Strand, which was unavailable for sequencing and has not been collected since 1941 (Brunke & Solodovnikov, 2013). A total of 202 taxa were included in the analyses (see Supplementary File S1). Identifications of nontype material were made by AJB, A. Smetana, A. Solodovnikov, AKH and MS using type material or the literature cited in the Introduction.

**Specimen study and imaging**

Morphological terms follow those of Brunke et al. (2016), Brunke et al. (2019) and Brunke & Smetana (2019). Scutellum refers to the part of the mesoscutellum visible between the elytral bases. Specimens from the following collections were used specifically for morphological study: Canadian National Collection of Arthropods, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada; A. Smetana collection (National Museum of Nature and Science, Tokyo, Japan; Y. Hayashi collection, Kawanishi City, Japan; Naturkundemuseum, Erfurt, Germany; Naturhistorisches Museum Wien, Vienna, Austria; Shanghai Normal University Insect Collection, Shanghai, China; Zoological Institute, St. Petersburg, Russia). Images were taken using a motorized Nikon SMZ25 stereomicroscope and NIS Elements BR v.4.5 for photomontage. Photos were processed in Adobe® Photoshop™ CC-2019 and plates were prepared using either Adobe® Illustrator™ or InDesign™ CC-2019.

**StaphBaits probe design**

Probes were designed based on genome-scale datasets from 34 insect taxa, focussing on Staphylinoidae (Supplementary File S2); published genomes for the following collections include *Nicrophorus vespilloides* Herbst (Silphidae); *Anoplophora glabripennis* (Motschulsky) (Cerambycidae); *Agrilus planipennis* Fairmaire (Buprestidae); *Leptinotarsa decemlineata* (Say) (Chrysomelidae); *Onthophagus taurus* (Schreber) (Scarabaeidae); *Tribolium castaneum* (Herbst) (Tenebrionidae); *Dendroctonus ponderosae* Hopkins (Curculionidae) and the outgroup taxa *Bombyx mori* Linnaeus (Lepidoptera); *Oryctes abietinus* (Scopoli) (Hymenoptera) and *Drosophila melanogaster* Meigen (Diptera); and newly sequenced low coverage genomes and transcriptomes of Staphylinoidae: *Ptiliidae* (1 sp.), *Leiodidae* (2 spp.), *Silphidae* (1 sp.) and *Staphylinidae* (20 spp.) (transcriptomes available under NCBI project number PRJNA669070 and genomes under PRJNA673872). NCBI repositories and respective SRA numbers are provided in Supplementary File S2. Low coverage genomes and transcriptomes were preprocessed, assembled and mined for orthologs using custom pipelines described in Kypke (2018). Briefly, all data were generated from Illumina platforms as paired end short reads. Low coverage genomes were assembled with SparseAssembler (Ye et al., 2012) and processed with Redundans (Przybysz & Gabaldón, 2016). The transcriptomes were assembled with Trinity v. 2.3.2 (Grabherr et al., 2011). In both cases, gene content and metrics were assessed with BUSCO v. 3.0 (Simão et al., 2015) and Quast (Gurevich et al., 2013), respectively. Staphylinid taxonomic coverage included multiple taxa from each of the informal subfamily groupings as given by Thayer (2016).

We used OrthoDB v9.1 (Zdobnov et al., 2017) to create a phyloprofile of single copy protein coding orthologous genes customized for Staphylinidae using the beetle and outgroup insect genomes mentioned above, also detailed in Kypke (2018) and summarized here. The OrthoDB database at the time lacked any genomes of Staphylinidae or their closest relatives, so we used its website capabilities to add the only available genome of the next-closest relative, *N. vespilloides* (Silphidae), to the phyloprofile. The *N. vespilloides* coding sequences (cds) were preprocessed by selecting one isoform and their headers were adjusted as required by OrthoDB. The cds were then mapped to OrthoDB using Endopyertygota as hierarchical-level. Next, we used a custom perl script, created by Robert Waterhouse and available upon request (University of Lausanne, Switzerland), to retrieve a table with EOG (Eukaryotic Ortholog Group) identifiers and respective sequence headers of the genomic data from OrthoDB API. EOGs were filtered (custom shell scripts by HE) due to multiple occurrences, putative paralogy, in *N. vespilloides*, or low representation (<3 taxa), in the reference species. The final ortholog set (3822 EOGs) was used by the software pipeline Orthograph v 0.6.2 (Petersen et al., 2017) to identify, by best reciprocal hits and profile hidden Markov models, single copy orthologs among the Staphylinioidea genomes and transcriptomes available. Orthograph generated a FASTA file (nucleotide and amino acid) for every ortholog group (EOG) that was used for downstream analysis.

While we briefly describe probe design here, full probe design methodology, scripts and the probe set itself can be found at https://github.com/AAFC-BICoE/staphylinidae-ortholog-baitset. Orthologs were aligned using T_Coffee 11.0.8 (Magis et al., 2014) for amino acids followed by Tranalign (EMBOSS 6.6.0) (Rice et al., 2000) for nucleotides. A custom python script used a sliding window approach to identify conserved blocks in the amino acid alignments and excise the corresponding regions from the nucleotide alignments. To limit the size and cost of the probe set, 10 of the 20 staphylinid reference taxa were prioritized (maintaining subfamily grouping diversity) for downstream loci selection (see Supplementary File S2). Loci that were at least 300 bp in size and found in at least five priority reference taxa were selected, resulting in 1229 target regions. These target regions were submitted as a multi-FASTA file to Arbor Biosciences (Ann Arbor, MI, U.S.A.) for development.
of a myBaits Custom probe kit. After optimization by Arbor Biosciences, the probe set was first tested in silico with all 18 beetle genomes then available on NCBI (see github link above) using the corresponding part of the Phyluce pipeline (Faircloth, 2016), after first converting FASTA headers to the format required by Phyluce. In silico recovery using Phyluce ranged from 420 to 992 loci, with the two highest numbers belonging to Staphylinoida taxa. The final probe set contained 39 938 bait sequences of 100 nt length with staggered placement at 120 nt intervals.

Sample preparation and DNA extraction

All vouchers were deposited in institutions and given identifiers as indicated in Supplementary File F1. Most rove beetles were severed at the connection between prothorax and elytra and then either a forebody (> 1 cm length) or both pieces were used for DNA extraction. In the case of the largest taxa (>2 cm), a foreleg was used. Nonextracted parts of vouchers were kept frozen in 96% ethanol and extracted specimens were mostly card mounted dry after washing in ethanol. In all cases, signs of extraction were minor (slight lightening) or undetectable (nearly all specimens). Specimens varied in age from 45 years to less than 1 year old at time of extraction (1973–2019). Before nondestructive extraction, ethanol-preserved specimens were dried in a vacuum centrifuge to remove residual ethanol. Alcohol-preserved specimens were extracted using a DNeasy™ Blood and Tissue Kit (Qiagen, Montreal, Canada), whereas pinned specimens were extracted using a Qiagen QIAamp DNA Micro Kit (standard protocol with RNA carrier added). To remove RNA, 4 μL of RNase A (100 mg/mL) were added to each high quality, alcohol preserved sample, followed by a 2 min incubation at room temperature. In all cases, elution buffer was preheated to ~60°C and DNA was eluted in 30 μL buffer EB after a 10 minute incubation. This step was repeated twice for a final elution volume of 60 μL.

Library preparation, hybridization and sequencing

Sample DNA concentration was quantified using a Qubit 3.0 fluorometer (Invitrogen, Burlington, Canada), and the DNA fragment size range was measured using a 4200 Tape Station (Agilent Technologies, Mississauga, Canada) with either a gDNA or D5000 assay, depending on DNA concentration. DNA libraries were prepared using an NEBNext DNA Ultra II FS Kit for Illumina (New England BioLabs, Ipswich, MA). DNA was first sheared enzymatically to target an average length of 200–450 bp using incubation times of 1–15 min depending on starting fragment size. Adaptors were diluted to 0.6 μM for DNA input <50 ng and adaptor ligated inserts were eluted in 33 μL 0.1X TE. Libraries were dual-indexed using corresponding NEBNext Multiplex Oligos for Illumina (Dual Index Primers Set 1) (New England BioLabs) and PCR amplified for 5–13 cycles (default amplification protocol) depending on the amount of original input DNA of each sample (highest cycles for the lowest DNA concentrations). Post-PCR, indexed libraries were quantified with another Qubit assay and fragment size was measured for representative samples from each PCR group using 4200 TapeStation D5000 or HS D1000 assays. Post-PCR, indexed libraries were first grouped according to DNA concentration (as a subjective indicator of quality) and then pooled at equal concentrations with a target of ~500 ng input to the hybridization reaction, provided there was sufficient total DNA per sample. Pools composed of degraded samples contained much less total input (100–400 ng, 10–40 ng per sample). Pooled libraries were reduced to ~7 μL volumes for hybridization using a vacuum centrifuge. Reduced, pooled libraries were hybridized with the DNA probes using a myBaits Hyb Capture Kit (Arbor Biosciences) according to the myBaits v.4.01 protocol, following the KAPA HiFi on bead PCR method, with 20–25 h of hybridization (arborbiosci.com). Purified, hybridized libraries were quantified with a Qubit assay and then amplified with 14–22 cycles of PCR, depending on concentration. To determine molarity for equimolar pooling and overall sequencing viability, reamplified libraries were purified and then assessed by Qubit, 4200 TapeStation HS D1000 assay and by qPCR (KAPA Library Quantification Kit) on a Roche LightCycler 480. Equimolar pooled libraries were sequenced at the Molecular Technologies Laboratory (Agriculture and Agri-Food Canada, Ottawa, ON, Canada) in multiple runs (6–60 samples each) on an Illumina MiSeq using 600 (v3) or 500 (v2) cycle kits. Demultiplexed, raw read FASTq files were deposited in the NCBI SRA under BioProject PRJNA661133 (Supplementary File F1).

Read assembly and orthology assessment pipeline

A bioinformatics pipeline, heavily drawing upon elements of the Phyluce package (Faircloth, 2016), was developed using Snakemake (Köster & Rahmann, 2012) to input raw Illumina reads and output aligned target loci for a variety of target enrichment projects (full details at: https://github.com/AAFC-BIOe/snakemake-partial-genome-pipeline). Briefly, raw reads were first adapter-trimmed using BBduk (Bushnell et al., 2017, sourceforge.net/projects/bbmap/), then single reads were de novo assembled using three different assemblers: Abyss (Jackman et al., 2017) SPAdes (Nurk et al., 2013) and rnaSPAdes (Bushmanova et al., 2019). Reads were merged using BBMerge and then assembled via a second run of Abyss. The output of each of the four assembly methods, plus the probe sequences were separately input to Phyluce, where assemblies were matched to target loci with minimum 80% identity and 82% minimum coverage (defaults) to exclude contaminants and nonorthologous sequences. Assemblies matching multiple target loci were filtered out with Phyluce, as were target loci with probes matching to multiple assemblies considered to be different. The results of these four assembly methods were compared and the longest fragment of each target locus was retained. We have found that using multiple assemblers drastically increases the number of recovered targets, in agreement with the results of Hedlin et al. (2018).

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Alignment and internal trimming were performed using elements of the Phyluce pipeline under default settings (Faircloth, 2016) unless otherwise stated. Alignment of each locus was performed in MAFFT (Katoh et al., 2002) with edge trimming turned off. Internal trimming of ambiguously aligned regions was performed in Gblocks (Talavera & Castresana, 2007). Trimmed, single locus alignments were manually inspected in Geneious v10.2.6 to find the reading frame, trim alignments to start with codon position 1, remove taxa with empty alignment (an artefact of earlier Gblocks step), remove taxa with very short sequences (<9 bp) as a result of trimming and other alignment artefacts. Noncoding, flanking regions were trimmed and only gaps divisible by 3 were allowed. Dubious gaps in coding probe regions and downstream nucleotides affected by the frameshift were converted to ambiguous (N’s). Nonorthologous sequences and contamination not already filtered by Phyluce were both identified by the broad disagreement to the amino acid level consensus and were removed. When two widespread paralogs were identified in an alignment, the most common was retained to preserve as much data as possible.

### Phylogenetic analyses

Single locus alignments were grouped into two sets, with 50 and 75% of taxa present, using the Phyluce script ‘phyluce_align_get_only_loci_with_min_taxa’ (Faircloth, 2016). Alignments from each set were concatenated into 50 and 75% datasets using AMAS (Borowiec, 2016). Seven loci were further excluded from analyses as they were less than 30 bp.

All analyses were performed at the nucleotide level. Concatenated alignments were analysed as partitioned (CP50, CP75) and unpartitioned (CU50, CU75) data, using maximum likelihood (ML) in IQ-TREE v1.6 (Nguyen et al., 2015). The alignment was initially partitioned by codon position per locus and submitted to PartitionFinder 2 (Lanfear et al., 2017) to determine the optimal partitioning scheme using Bayesian Information Criterion (BIC). Branch lengths were set to ‘linked’ and the search was set to use the relaxed clustering algorithm (rcluster) (Lanfear et al., 2014) in RAxML (Stamatakis, 2014), with only the top 10% of schemes examined. To reduce computational burden following Espeland et al. (2018) and Gough et al. (2020), models were restricted to variants of GTR. Merged partitions were then submitted to IQ-TREE where model selection was performed with all models considered (–m TESTNEW). Extremely small final partitions containing only one position of one locus (<80 bp) were excluded as these caused the IQ-TREE analysis to fail at various points. Partitioned analyses in IQ-TREE were performed with the -spp option following Duchêne et al. (2019) and clade support was assessed using 1000 iterations of both the ultrafast bootstrap (UFB) (Hoang et al., 2018) and an SH-aLRT test (SHT) (Guidon et al., 2010); the -nni option was used to avoid overestimation of bootstrap support in the presence of violation of model assumptions (Nguyen et al., 2015). Of the several phylogenetic results generated by our analyses that suggest the need for significant systematic changes to the higher classification of Staphylininae, alternative, yet unsupported topologies were found for two of these. To test the statistical robustness of these two phylogenetic results, we applied four-cluster likelihood-mapping (FcLM) tests on the unpartitioned 50% completeness matrix. In FcLM, taxa are grouped into four taxon sets that represent a condensed topology around the node in question. These sets are assumed to be monophyletic. FcLM outputs the proportion of taxon quartets that support each of the three possible topologies. FcLM analyses were performed in IQ-TREE 1.6 using -lmclust -Imap ALL and -n 0 options. For further information on FcLM and its extended applications, see Misof et al. (2014) and Vasilikopoulos et al. (2019).

Additional coalescent analyses were performed in ASTRAL III v.3 (Zhang et al., 2018) (50A, 75A). Individual locus trees were generated using IQ-TREE: the substitution model was selected by BIC using ModelFinder (–m MFP) and near-zero branch lengths were collapsed using the ‘-polytomy’ option. The latter collapses clades with extremely low support values (<10 UFB), which can cause errors in the reconstruction of the species tree in ASTRAL (Zhang et al., 2018). Analyses in ASTRAL were run with default parameters and clade supports were calculated as local posterior probability (LPP). All analyses were run either on the NCR-HPC-Biocluster at Agriculture and Agri-Food Canada (Ottawa, Canada) or the CIPRES Science Gateway v3.3 (phylo.org). Both 50 and 75% concatenated matrices, partition files and single locus alignments were uploaded to FigShare and are available: https://doi.org/10.6084/m9.figshare.13064144.v1

We considered UFB values ≥0.95, SHT values ≥0.80 or LPP ≥0.85 to indicate support. Nodes with support from UFB and SHT ≥0.95 or LPP ≥0.95 were considered strongly supported. Nodes with support from only UFB or SHT, or LPP = 0.85–0.94 were considered weakly supported. Tree-diagrams were visualized in FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and then annotated in Adobe® Illustrator™ CC-2019.

### Results

**Dataset and target capture**

Of the 1229 targeted loci, 905 were successfully recovered, with 19–691 loci recovered from each sample, after phyluce quality control filtering (Supplementary File S1). While pinned museum specimens, comprising 46% of the samples, yielded distinctly fewer loci on average than ethanol preserved specimens (mean 417 ± 18 vs 601 ± 5 loci, respectively), considerable success was attained for oldest specimens (mostly pinned) collected in the 1970s (7 specimens, 368 ± 67 loci), 1980s (12 specimens, 287 ± 55 loci), 1990s (15 specimens, 437 ± 41 loci) and 2000s (22 specimens, 495 ± 30 loci). Over 500 loci each were sequenced from three specimens collected in the 1970s. Eight samples yielded less than 100 loci: Q. lesagei Smetana (19, 1984); Genus 1 sp. 2 (20, 2005); Q. liang Smetana (36, 1981); Q. regularis Bernhauer & Schubert (37, 2005); Q. montivagus Smetana (66, 1975); Q. inflatus Fauvel (68, 1999);
Fig. 1. Phylogeny of the Northern Hemisphere Clade of Staphylininae, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. An asterisk (*) indicates node support when *Acylophorus caseyi* Leng was removed from ASTRAL analyses. A plus (+) next to a taxon name indicates a corresponding illustration to the right. Photos of *Algon jaechi* Schillhammer and *Stevensia longipennis* Cameron by H. Schillhammer. Abbreviations: O, Oriental; N, Nearctic; NT, Neotropical; P, Palaearctic; e, east; w, west. [Colour figure can be viewed at wileyonlinelibrary.com].

**Alesiella lineipennis** (Cameron) (79, 2015); **Q. tanderi** Smetana (82, 1981). After manual processing of single-locus alignments, the 50 and 75% occupancy datasets contained 487 (95 028 bp) and 239 loci (58 770 bp), respectively. Concatenated datasets, according to the best scheme of PartitionFinder2, were divided into 107 (50CP) and 71 (75CP) final partitions.

**Phylogenetic analyses**

Topologies generated by the various analyses were well resolved and highly congruent; the few conflicts were limited to differences between concatenated and coalescent analyses. The majority of these concerned more derived clades or the position of a single taxon, leaving the composition of clades otherwise identical. Overall, concatenated topologies were more strongly supported than coalescent analyses. In general, the inclusion of more loci (e.g. 50% datasets) and dataset partitioning resulted in greater support for clades, though there were some exceptions. Therefore, the 50CP topology is shown in Figs. 1–6 and only strongly supported conflicts between concatenated and coalescent analyses are discussed below. In coalescent analyses, *Acylophorus caseyi* Leng was resolved as the sister group to the other members of the NHC but without support, in direct conflict with concatenated analyses and previous molecular and integrated phylogenies demonstrating the monophyly of Acylophorini (Brunke et al., 2016; Schillhammer & Brunke, 2018). We treat this result as an artefact (likely long
Fig. 2. Backbone phylogeny of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. A plus (+) next to a taxon name indicates a corresponding illustration to the right. Photos of *Queskallion* Smetana by L. Tang and *Quedius seriatus* Horn by Centre for Biodiversity Genomics. Abbreviations: N, Nearctic; NT, Neotropical; P, Palaearctic; e, east; w, west. [Colour figure can be viewed at wileyonlinelibrary.com].

Within the NHC, tribe Staphylinini (former ‘Staphylinini Propría’) was resolved as a clade sister to the remaining tribes (Fig. 1). Relationships between tribe-level clades were generally weakly to strongly supported depending on the partitioning scheme or amount of data used (Fig. 1). Within Staphylinini, Xanthopygina formed the sister group to the remaining sampled subtribes. Anisolinina and Staphylinina were resolved as sister groups, and the monophyly of Staphylinina was supported in all analyses. Subtribes Algonina and Philonthina formed a clade in all analyses but the monophyly of Algonina was rejected (clade *Rientis + Hesperus* weakly supported) by most concatenated analyses (Fig. 1). *Quelaestrygon puetzi* Smetana was resolved in an isolated position as the sister group to the remaining tribes of the NHC, except Staphylinini. Its position was not resolved with support by coalescent analyses but in analysis 50A it was recovered as the sister group of Staphylinini, whereas in 75A it was recovered in the same position as concatenated analyses. Tribes Indoquediini *sensu n.* (including *Strouhalium gracilicorne* Scheerpeltz and *Quediuselevatus* Hatch) and *Cyrtoquediini sensu n.* (including *Alesiellalineipennis*, *Quediomacrus pollens* Sharp and *Quedius nr. nigropolitus*) were each recovered as clades by all analyses. The tribe Quediini was rendered polyphyletic due to the
Fig. 3. Phylogeny of the Microsaurus lineage of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP = 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black — strong; grey — weak; white — unsupported; slash — in strongly supported topological conflict. An asterisk (*) indicates node support when *Quedius lesagei* Smetanawas removed from ASTRAL analyses. A plus (+) next to a taxon name indicates a corresponding illustration to the right. Photos of *Anthosaurus caelestus* Smetana, *Korgella sichuanensis* Smetana, *Q. jyr* Smetana and *Q. bito* Smetana by L. Tang, *Q. dilatatus* by M.E. Smirnov. Abbreviations: O, Oriental; N, Nearctic; NT, Neotropical; P, Palaearctic; e, east; w, west. [Colour figure can be viewed at wileyonlinelibrary.com].

positions of *Q. elevatus* and *Q. nr. nigropolitus* each in different tribes but, excluding these taxa, was monophyletic in all analyses and the sister group to a clade including *Indequediini*, *Cyrtquediini*, *Acylophorini* and *Erichsoniini*. *Acylophorini*, *Erichsoniini* and *Beeria nemaotocera* (Casey) were recovered together as a clade in all analyses. *Acylophorini* (minus *Acylophorus* in coalescent analyses, see above) was recovered as monophyletic in all analyses. *Beeria nemaotocera* was recovered as the sister group of *Erichsoniini* in concatenated analyses, whereas in coalescent analyses *Beeria* was sister to *Acylophorini*+*Erichsoniini* but without support. Within *Indequediini*, *Q. (R.) elevatus* was resolved as the sister group of *Indequedius* Blackwelder in concatenated analyses, but sister to *Strouhalium* in coalescent analyses. *Alesiella* and *Quediomacrus* were resolved as sister groups in concatenated analyses, whereas coalescent analyses resolved *Quediomacrus* and *Bolitogyrus* Chevrolat as sister groups.

The backbone phylogeny of *Quediini* was generally well resolved, with only a few points of conflict among analyses (Fig. 2). All analyses recovered a *Quedionuchus* clade consisting of *Quedionuchus* and *Queskallion*. This clade was sister to all other *Quediini* in concatenated analyses but its position

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Fig. 4. Phylogeny of the Microsaurus lineage of Quedini continued, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. A plus (+) next to a taxon name indicates a corresponding illustration to the right. Photos of Quedius lualu Smetana, Q. adjacens Cameron, Q. raan Smetana by L. Tang, Q. griffinae Hatch and Q. rainieri Hatch by Centre for Biodiversity Genomics. Abbreviations: O, Oriental; N, Nearctic; NT, Neotropical; P, Palaearctic; e, east; w, west. [Colour figure can be viewed at wileyonlinelibrary.com].

was not resolved by coalescent analyses. Within this lineage, the monophyly of Quedionuchus was rejected by all analyses (Fig. 2). Queskallion Smetana was recovered as monophyletic by all analyses. Clade A was recovered by all concatenated analyses (except 75CU) and consisted of Q. (R.) amabilis Smetana, Q. (R.) prostans Horn and Q. (R.) seriatus Horn. In partitioned concatenated analyses, clade A was resolved as the sister group to the Microsaurus lineage, which was recovered by all analyses. Clade A was not recovered by coalescent analyses or by 75CU; instead, Q. prostans and Q. seriatus formed a clade sister to the Microsaurus lineage, while Q. amabilis formed a clade with Q. (Paraquedius) puncticeps that was sister to the remaining Quedini. In partitioned analyses, Q. puncticeps was resolved as the sister group to the remaining Quedini (Fig. 2). In all analyses, Q. (R.) nanulus was resolved as the isolated sister group of a clade containing the remaining Quedini lineages (Fig. 2). In all analyses, Quedius (R.) riparius Kellner, Q. (D.) vilis Smetana and Q. (R.) scintillans (Gravenhorst) formed clade B, sister to a clade consisting of the Quedius, Distichalius and Raphirus lineages. In all analyses, the Quedius lineage formed the sister group to clade containing the Distichalius and Raphirus lineages (Fig. 2).

In all analyses, Pseudorientis Watanabe was resolved as the sister group to all other members of the Microsaurus lineage (Fig. 3). All Quedius currently classified in the subgenus Microsaurus (except two species forming clade U3) were resolved in this lineage, together with genera Anthosaurus and Korgella Özdikman, and subgenera Megaquedius and Velleius (Fig. 3), rendering the subgenus as polyphyletic. Clade C, recovered by all analyses, consisted of the placidus and zeuxis groups and monotypic kurbatovi group of Smetana (2017), and two species of a putatively undescribed genus. Clade D, recovered by all analyses, consisted of species belonging to the apicicornis and beesoni groups.

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Fig. 5. Phylogeny of the *Quedius* (A) and *Distichalius* (B) lineages of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. A plus (+) next to a taxon name indicates a corresponding illustration to the right. Photos of *Quetarsius* sp.*er* Solodovnikov, *Quemetopon grandipenis* Zhu et al., *Quedius collinsi* Smetana, *Q. chinensis* Bernhauer, *Q. ou* Smetana and *Q. biann* Smetana by L. Tang, *Q. montivagus* Smetana, *Q. frater* Smetana and *Q. transparens* Motchulsky by Centre for Biodiversity Genomics. Abbreviations: O, Oriental; N, Nearctic; NT, Neotropical; P, Palaearctic; e, east; w, west. [Colour figure can be viewed at wileyonlinelibrary.com].
Fig. 6. Phylogeny of the Raphirus lineage of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. An asterisk (*) indicates node support when Quedius inflatus Faüvel was removed from ASTRAL analyses. A plus (+) next to a taxon name indicates a corresponding illustration to the right. Photo of Quedius hegesias Smetana by L. Tang. Abbreviations: O, Oriental; N, Nearctic; NT, Neotropical; P, Palaearctic; e, east; w, west. [Colour figure can be viewed at wileyonlinelibrary.com].

to the mesomelinus group. Clade K was recovered by all analyses, albeit with varied support, and consisted entirely of East Palaearctic species of the adjacens, euryalus (K3), szechuanus (K1) and mukuensis (K2 in part) groups of Smetana (2017) (Fig. 4).

Within the Quedius lineage, clade L was recovered by all analyses and was composed of the multipunctatus and intricatus groups of Quedius (Raphirus) (Smetana, 2017) (Fig. 5). Clade M was recovered by all concatenated analyses and represented the himalayicus and liangtangi groups of Quedius (Raphirus) sensu Smetana (2017). Within clade M, the position of Q. (R.) liangtangi could not be resolved with confidence. The position of Q. liangtangi Smetana could not be confidently resolved by coalescent analyses either but in these analyses, it was
never placed in a clade with the himalayicus group. In concatenated analyses, clade L was resolved as the sister group to the remaining members of the Quedius lineage with strong support, whereas coalescent analyses resolved clade M in this position with strong support. Clades N and O were resolved as sister groups in all analyses. Clade N contained members of the bleptikos and meei groups of Quedius (Raphirus) (Smetana, 1995, 2017) and the genus Quetarsius Smetana (Fig. 5). Clade O was entirely composed of the pluvialis group of Quedius (Raphirus) (Smetana, 2017). Clade P was resolved by all analyses and contained all sampled members of subgenus Quedius s.str. (Fig. 5).

Within the Distichalius lineage, two major clades were resolved as sister groups: one (clades Q, R and S) containing mostly Nearctic taxa and eastern Russian Q. (R.) jenisseensis (Sahlberg), and another (clades T, U and Quemetopon) containing mostly Palaearctic taxa and eastern Russian Q. (D.) transparens Motschulsky (Fig. 5). Clade Q was recovered by all concatenated analyses and contained representatives of the transparens and capucinus groups of Q. (Distichalius) (Smetana, 1971). Clade R, recovered by all analyses, represented the fenderi group of Q. (Distichalius) (Smetana, 1971). Sister to this clade was clade S, which was recovered by all analyses, and represented the brunnipennis group sensu Smetana (1976), with members placed in either Q. (Distichalius) or Q. (Raphirus) (Smetana, 1971, 2017). Quemetopon Smetana was resolved as the sister group to a clade containing clades T and U (Fig. 5). Clade T was recovered by all analyses and contained members of the annectens and regularis groups (Smetana, 1995, 2017) of Q. (Distichalius). Clade U was recovered by all analyses and consisted of a member of the transparens group, members of the ladas group and members of the cinctus group of Q. (Distichalius), plus two members currently placed in the euryalus group of Q. (Microsaurus) (Smetana, 1971, 2017) but forming clade U3 (Fig. 5).

The Raphirus lineage was resolved as a group consisting of large-eyed Quedius species forming sister clades V and W, and genus Euryporus to the smaller-eyed and mostly West Palaearctic Quedius of clade X (Fig. 6). Clade V was recovered by all analyses and consisted of the probus and vulpinus groups of Q. (Raphirus) (Smetana, 1971) and species treated as Microquedius (= Raphirus) by Coiffait (1978). Clade W was recovered by all analyses and consisted of species from the boops and musicola groups of Q. (Raphirus) (Smetana, 1971, 2017). Euryporus was recovered as the sister group of clade X by all analyses. Clade X consisted of the Nearctic Q. (R.) oculus (sublimbatus group) (Smetana, 1971) and numerous West Palaearctic species of Q. (Raphirus), including its type species Q. (R.) limbatis (Heer). The position of Q. inflatus within clade X was not resolved with confidence and was placed in either subclade X3 (concatenated) or as the sister group to all other members of clade X (coalescent) (Fig. 6). Quedius (D.) fagelianus Coiffait from Israel and Lebanon was resolved within clade X2 with members of the West Palaearctic lateralis group of Q. (Raphirus) (Coiffait, 1978).

FcLM analysis showed an overwhelming proportion (94.3%) of quartets in support of the position of Quelaestrygon as sister to all remaining taxa, except Staphylinini and the outgroup (Fig. 7A). A second FcLM analysis showed approximately equivocal support for the position of Beeria as either sister to Erichsoniini (Erichsonius) (36.0%) or sister to Erichsoniini + Acylophorini (49.3%) (Fig. 7B).

**Discussion**

Our novel, staphylinid-focused AHE probe set successfully enriched as many as 691 loci per specimen and resolved both tribe-level clades within the NHC and lineages within the megadiverse Quediini, the focal group of this study. In corroboration with previous studies (e.g. St. Laurent et al., 2018; Buenaventura et al., 2020), we showed that target capture datasets heavily derived from pinned insect specimens (up to 46%) can recover well-resolved phylogenies. The combination of low-input lab protocols, target enrichment and next-generation sequencing allowed for extensive sampling of Quediini and incertae sedis Staphylininae through the inclusion of pinned museum specimens, which formed nearly half of the taxon sample. Such a representative sample of this diverse lineage would have been otherwise prohibitively resource-intensive or even impossible to recollect anew into 96% ethanol, given that many of these species are only known from a few specimens. These methods provide broad access to the molecular data held by the extensive material kept in natural history museums worldwide (recently coined as Museomics) and further highlights the importance of these collections.

**Target enrichment of DNA from pinned specimens**

As reported by previous authors (e.g. Blaimer et al., 2016; Van Dam et al., 2017; St. Laurent et al., 2018; Buenaventura et al., 2020), we observed a gradual decline in the number of loci recovered with increasing age in pinned specimens. Specimens from the 1970s and 1980s were the oldest pinned samples in the present study, about 32–45 years old at the time of extraction, respectively, and regularly yielded hundreds of loci (postfiltering) for phylogenetic inference (Supplementary File S1). Although previous authors have recommended a cut-off of approximately 20 years (e.g. Blaimer et al., 2016), we demonstrated that successful enrichment should be routinely possible for much older pinned specimens using the extraction, library preparation and enrichment protocols given in the Methods section. Even older (>45 years) specimens are worth trying, especially those of critical taxa, as we found other unknown factors, most likely related to collection and storage, to be important for results (e.g. Genus I sp. 2 (20 loci, 2005) vs Q. brunnipennis Mannerheim (544 loci, 1973)). Many staphylinids are much smaller than the staphylinines sequenced in the present study (1–3 mm vs >5 mm body length) but we do not expect limited tissue input per se to pose a problem for locus recovery using these protocols. In this and other studies (e.g. Toussaint et al., 2018; Buenaventura et al., 2020), low
Fig. 7. Results of an four-cluster likelihood-mapping (FcLM) analysis on the unpartitioned, 50% completeness matrix for: A) position of Quelaestrygon; B) position of Beeria. Photos of Algonjaechi Schillhammer and Stevensia longipennis Cameron by H. Schillhammer. [Colour figure can be viewed at wileyonlinelibrary.com].

concentrations of DNA (<1 ng/μL) regularly resulted in successful target capture and all specimens of the present study yielded at least some loci suitable for downstream phylogenetic analyses.

Although the eight taxa with the poorest enrichment success (<100 loci, see Results section) were generally resolved with confidence within major clades, their exact sister groups were often resolved with weak support or were unable to be resolved entirely (Q. liang, Q. inflatus). Small alterations to the data filtering parameters of the preanalysis pipeline used in this study may have allowed for the retention of slightly more sequence data for these taxa, while maintaining high levels of quality control. The default identity and coverage thresholds in Phyluce (80/82%, respectively) (Faircloth, 2016) may have been too strict for the present dataset, where a large proportion of pinned samples yielded, in some cases, lower quality or shorter assemblies. Derkarabetian et al. (2019) demonstrated that UCE datasets generated from degraded specimens and constructed under default and more relaxed parameters (65/65%) of Phyluce resulted in phylogenies that were highly similar, despite the latter containing an average of about one third more target loci. Alignment trimming using Gblocks is another aspect of our preanalysis pipeline that may have overfiltered data, especially for degraded samples. Tan et al. (2015) found that alignments trimmed by many standard methods, including the ‘relaxed’ settings of Gblocks, default in Phyluce (Faircloth, 2016), contained less ‘true’ phylogenetic signal than untrimmed datasets, despite the retention of dubiously aligned regions. Phyluce and Gblocks thresholds were both relaxed beyond the defaults by Buenaventura et al. (2020), who resolved the higher phylogeny of oestroid flies using UCEs and a high percentage of pinned museum specimens. The evolution of bioinformatics pipelines towards customization for special challenges, such as high proportions of degraded samples, may be an important future direction in phylogenomics and specifically museomics.

Higher phylogeny of the NHC

Sister group relationships between tribes or clades of tribes within the NHC were generally well-resolved in our analyses but node support was noticeably higher when more loci were included. While all tribe-level clades corroborate the results.
of previous molecular and integrated analyses, the recovered backbone topology differs strikingly, likely due to our limited taxon sample outside of the NHC compared to other studies (Brunke et al., 2016; Chani-Posse et al., 2018; Brunke et al., 2019; Cai et al., 2019; Jenkins Shaw et al., 2020; Zyla & Solodovnikov, 2020). These relationships were outside of the focus of the present investigation but our taxon sample should later be expanded to include the diversity of Southern Hemisphere Staphylininae and more distantly related subfamilies Arrowininae, Coomaninae and Xantholininae (Zyla & Solodovnikov, 2020). In contrast to the backbone phylogeny of Staphylininae, tribe-level clades in the present study were congruent with those of all previous studies since Brunke et al. (2016), indicating that the higher systematics of at least the NHC clade of Staphylininae are stabilizing and that the tribes very likely represent natural groupings. This is further supported by the inclusion in our taxon sample of nearly all remaining Staphylininae incertae sedis genera (see Methods), which resulted in only one additional tribe and revealed the diversity of Cyrtoquediini and previously monotypic Indokoedini to be greater than expected (Brunke et al., 2016).

The addition of molecular data here for Quelaestrygon resulted in the exciting discovery that this monotypic and rarely collected genus represents a relictual, phylogenetically isolated tribe (Figs. 1, 7; see Systematics) known only from the higher mountain forests of southwestern China (Smetana, 1999, 2017; Cai et al., 2020). Our analyses unequivocally demonstrated that this genus is an isolated lineage, outside of all described tribes and either sister to all NHC tribes except Staphylinini (also supported by FcLM) or the sister group of Staphylinini (50A, unsupported). The previously hypothesized close relationship of this genus with large-bodied Staphylininae incertae sedis genera Lonia, Alesiella and Quediomacrus, based on morphology (Brunke & Solodovnikov, 2013), is here revealed to have been an artefact of convergence in glabrous elytra and setal arrangements on the ventral surface of the tarsi. Quelaestrygon lacks the characteristic synapomorphies of Staphylinini (see Systematics) and we argue that, even if it is later shown to be its sister group, it should not be incorporated into that tribe. The posteriorly developed postmandibular ridge on the head, the hypostomal cavity and traces of the posterior transverse basal ridges on the abdominal tergites of Quelaestrygon are found in both non-NHC Staphylininae and within Staphylinini but never within the recovered clade containing all other ‘quediine-like’ lineages (Fig. 1). Our analyses suggest that these states are plesiomorphies retained in Quelaestrygonini and Staphylinini and may explain why posterior transverse basal lines or their possible derivatives occur in non-NHC Staphylininae and related subfamilies, but also within the Staphylinini.

The widely disjunct, rarely collected and morphologically similar genera Alesiella (southeast Asia) and Quediomacrus (Central America) (Brunke & Solodovnikov, 2013) were resolved with strong support as sister groups within Cyrtoquediini. Alesiella was not available for study during the original description of Cyrtoquediini but it does bear the row of impressed, epipleural punctures characteristic of this tribe (Brunke et al., 2016), while in Quediomacrus they have apparently been lost. We here updated the morphological diagnosis of Cyrtoquediini from Brunke et al. (2016) to account for those few taxa that have lost the epipleural setae or for which they are obscured (see Systematics). The inclusion of Javan ‘Quedius’ nigropolitus in Cyrtoquediini is supported morphologically as it is rather similar to its Neotropical sister group Cyrtoquedius. With the results of the present analyses, there are now as many as three independent Oriental-Neotropical disjunctions within Cyrtoquediini. The disjunction within the charismatric cyrtquediine genus Bolitogyrus was recently demonstrated to be a result of climate cooling following the Early Eocene Thermal Maximum (Brunke et al., 2017) and a well-sampled, dated phylogeny of the tribe will be necessary to determine whether these distributions, uncommon in insects but widespread within Cyrtoquediini, share a common history.

In corroboration with molecular (Brunke et al., 2016) and total evidence (Schillhammer & Brunke, 2018; Brunke et al., 2019) phylogenies, Acylophorini and Erichsoniini formed a clade in all analyses. Staphylininae incertae sedis genus Beeria, here included in a molecular phylogeny for the first time, was also resolved as a member of this clade in all analyses. The exact sister group of Beeria could not be resolved with confidence and an FcLM analysis showed equivocal support for either Erichsoniini (Erichsonius) (concatenated) or Erichsoniini+Acylophorini (coal'escent) (Fig. 7B). The sole species of Beeria, B. nematocera, is distributed in the Pacific Northwest of North America and is rarely collected, likely due to a cryptic lifestyle within crevices in wet talus-like habitats (Smetana, 1977). Like Erichsonius, it was originally placed in Philonthina (Staphylinini), as a species of Philonthus (Casey, 1915), and was later considered to have an intermediate morphological configuration of the pronotum between Quedini (sensu lato) and Staphylinini (Smetana, 1977; Brunke & Solodovnikov, 2013). In addition to a similar habitus, Beeria and Erichsonius share a lack of empodial setae and presence of meshed microsculpture on the head and pronotum, both states missing in all members of Acylophorini. However, Beeria lacks an inflated apical antennomere bearing a broad microsetae field, a recently discovered structure found in all members of Acylophorini and Erichsoniini (Schillhammer & Brunke, 2018), and considered to be a synapomorphy of that clade. Future analyses with a greater taxon sample for Acylophorini and Erichsoniini should be conducted to resolve whether Beeria should be incorporated into Erichsoniini or a separate, new tribe. It is biogeographically noteworthy that northwestern North America, where Beeria is endemic, is one of the only major regions of the Northern Hemisphere lacking endemic species of Erichsoniini and Acylophorini (Smetana, 1971; Frank, 1975).

The tribe to undergo the greatest change in composition in the present study was the formerly monotypic Indokoedini. Originally erected for the moderately diverse Oriental and East Palaearctic genus Inodoquedius (Brunke et al., 2016), Indokoedini is here expanded to include ‘Quedius’ elevatus, a morphologically isolated species from western North America.
Fig. 8. A) Pronotal microsculpture, Quelaestrygon puetzi Smetana; B) apex of profemur, apical row of lateroventral spines (arrows), Cyrtquedius sp.; C) apex of protibia, subapical notch, Indoquedius sp. Scale bars: A = 1 mm; B, C = 0.25 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

den and the monotypic genus Strouhalium from high elevations in the Himalaya and China. Very little is known about Q. elevatus, placed in the ‘elevatus group’ of Q. (Raphirus) by Smetana (1971), except that it has been collected in wet debris along flowing water and occasionally in beaver houses. This species shares the characteristic, albeit smaller, brush of long setae on the penultimate labial palpomere with its sister group Indoquedius. The sole species of Strouhalium, S. gracilicorne, lacks this structure and is rather different in overall habitus from the other two members of Indoquediini, possibly as an adaptation to wet crevices on talus slopes and in caves (Smetana, 1993, 2007). However, posthoc examination of these taxa revealed that they share a unique feature in Staphylininae (as far as known): a subapical notch on the foretibia (Fig. 8C) that is likely to function as an antennal cleaner for the unusually long antennae found in all Indoquediini, analogous to that of Carabidae (Hlavac, 1971).

Even after accounting for the numerous species of Quedius in the Southern Hemisphere, long recognized as belonging to Amblyopinini (Jenkins Shaw et al., 2020), the monophyly of Quediini was still rejected in our analyses due to the positions of ‘Quedius’ elevatus and ‘Q.’ nr. nigropolitus, which should be transferred to other tribes of the NHC and treated as new genera (see above). These species do not fit the morphological diagnosis of Quediini sensu Brunke et al. (2016) and therefore it is not surprising that they were resolved as members of other tribes. The conflicting placement of Q. nigropolitus was known for several years by the lead author but Q. elevatus was newly examined for this study, emphasizing the importance of comprehensively sampling species groups, subgenera and genera in this large lineage. With these taxa excluded, the concept of Quediini remains essentially the same as given by Brunke et al. (2016) and can be most easily recognized using a combination of characters, including those added by Brunke et al. (2019) and Brunke & Smetana (2019) (see Systematics).

The only Staphylininae genus presently incertae sedis and unaccounted for in our study is the monotypic, east Australian genus Lonia (see Methods). This genus was previously considered to belong to the ‘Quedionomacrus lineage’ clade (Brunke & Solodovnikov, 2013), which was here shown here to be a phylogenetic artefact of convergent morphological evolution. A re-examination of Lonia in the context of a recent integrated phylogeny (Brunke et al., 2019) showed that it is does not fit the diagnosis of Quediini and suggests that it may not even belong to the NHC based on a horizontal ridge near the base of the scutellum that may be interpreted as the sub-basal ridge, the broadly separated lobes of the labrum and a Valdivioide-s-like prosternum with blade-like ridge. The distribution of Lonia in eastern Australia, originally considered to be a result of long-distance dispersal from Asia (Brunke & Solodovnikov, 2013) is more easily explained as vicariance with potential relatives among the other Southern Hemisphere groups (Brunke et al., 2019).

Relationships within Staphylinini were not the focus of this study and we feel that taxon sampling within this clade was too low to discuss our results meaningfully. Overall, these relationships were mostly congruent with previously recovered
topologies, except for the weakly supported paraphyly of sub-family Algonina that is likely to be an artefact as all three genera of this group were resolved as a highly supported clade by Žyla & Solodovnikov (2020).

Framework for generic revision of Quediini

Using a comprehensive sample of nearly all species groups of Quediini, we thoroughly tested the monophyly of all its valid genera and subgenera except the West Palaearctic Velleiopsis Fairmaire, which is here synonymized with Microsaurus (see Systematics). Consistent with previous studies with far fewer Quediini (Chatzimanolis et al., 2010; Brunke et al., 2016, 2019), the genus Quedius was shown to be polyphyletic with respect to all genera of Quediini except Quedionuchus and Queskallion. It is clear that a generic revision of Quedius is needed in order to avoid treating nearly all species of Quediini as a single, morphologically heterogeneous genus. Quedius should be restricted to the current, well-defined concept of Quedius s.str. (e.g. Smetana, 1971; Assing & Schülke, 2012), while the subgenera Distichalius, Microsaurus, Paraquadius, Raphirus and Velleius should be (re-)elevated to genus rank after ensuring monophyly and diagnosis (see below). However, we refrain from these taxonomic actions here and prefer to make these changes in an incremental fashion to avoid large numbers of ‘orphaned’ species within Quediini as genera are (re-)defined. The monophyly of the subgenera Distichalius, Microsaurus and Raphirus was strongly rejected by our analyses, while the monotypic subgenus Paraquadius Casey was shown to represent a phylogenetically isolated, yet major lineage of Quediini (Fig. 2). Quedionuchus was unexpectedly recovered as paraphyletic with respect to Queskallion, despite a unique morphological diagnosis for the former genus based on the examination of all species, including many undescribed ones by Brunke et al. (2020b). Although the reitterianus and glaber groups of Quedionuchus (represented by Q. reitterianus (Bernhauer) and Q. longipennis (Mannerheim)) share a distinctly lobed female tergite X (Brunke et al., 2020b), this shape, along with the glabrous elytra characteristic of the genus, may actually be plesiomorphic states for the Quedionuchus lineage. A future analysis with a larger sample of diverse Quedionuchus is needed to further test the monophyly of this genus.

Distichalius lineage. Nearly all species currently placed in Q. (Distichalius) were resolved together in the Distichalius lineage but the subgenus was rendered paraphyletic by Quemetopon. Quedius (D.) fageliana Coiffait is clearly misplaced in this subgenus and is externally similar to other members of the lateralis group of Q. (Raphirus) in clade X2 (see Systematics). The current morphological diagnosis of Q. (Distichalius) (e.g. Smetana, 2017) is not unique among the global diversity of Quediini and excludes the most well-known member of the subgenus, the Palaearctic Q. (D.) cinctus Paykull. Therefore it will be necessary to redefine Distichalius in the future and we argue here that it should be treated at the genus level and restricted to clade U (Fig. 5). The members of clade U (~24 spp.), and the type species of Distichalius Q. (D.) capucinus (Gravenhorst), not sampled here), are easily recognized within Quediini by an extra puncture between pronotal lateral and sublateral rows, an additional puncture behind the eye (fig. 1 in Cai & Zhou, 2015) and the lack of a genal puncture on the head. Although not sampled here, the biplicitus group (1 sp.) from China (Smetana, 2017) would also belong in clade U. New genera would therefore need to be described for clades Q, R, S and T, for which species groups, or their clusters were already created (Smetana, 1971, 2017).

Microsaurus lineage. Except for Pseudorientis, all genera and subgenera of the Microsaurus lineage were recovered nested inside the large subgenus Microsaurus with strong support in all analyses. The nonmonophyly of (Q.) Microsaurus and the overall topology of the Microsaurus lineage are consistent with those of previous molecular and integrated phylogenetic analyses (Brunke et al., 2016, 2019) that sampled fewer taxa and different but fewer loci. With the exception of two species included in clade U and here moved to Distichalius (see Systematics), all Quedius species currently treated as Q. (Microsaurus) were resolved within the Microsaurus lineage. Numerous taxonomic solutions exist to circumcribe monophyletic genera in this large and morphologically diverse clade (~350 described species) but these vary widely in their balance of nomenclatural stability against the diagnostic value of named clades. Another complicating factor is the nomenclatural priority of the older name Velleius over both Microsaurus and Quedius (Smetana, 2013). With nine species across the Palaearctic region, Velleius is currently treated as a valid subgenus of Quedius (Smetana, 2017), though it was briefly synonymized with Microsaurus by Solodovnikov (2012). Our analyses resolved Q. (Velleius) as a member of the morphologically heterogeneous clade E of the Microsaurus lineage. Treating all species of the Microsaurus lineage as Microsaurus would not only create a nomenclatural problem in need of a successful application of suppression to the International Commission on Zoological Nomenclature (ICZN), it would also synonymize two additional genera and create a heterogeneous taxon with an unwieldy diagnosis. Treating all major clades (and subclades to preserve names) of the Microsaurus lineage as genera would similarly result in creation of numerous taxa with diagnoses based on difficult to observe or variable characters. We observed a substantial difference in the degree of morphological disparity within and between clades C–F versus that of more uniform clades G–K. Clades G–K also represent the majority of global Q. (Microsaurus) species (about 70%) and all of its West Palaearctic species, which form the subject of most nontaxonomic literature involving the subgenus. Therefore, we argue that the ‘core Microsaurus’ clade indicated in Fig. 3 is a useful delimitation for Microsaurus, which should be treated at the genus level in the future. This delineation results in the synonymy of only one genus-group name (Megaquedius) versus four, as Velleiopsis is synonymized herein regardless (see Systematics). The resolution of East and West Palaearctic Korgella in separate clades is supported morphologically by the different pronotum shape, chaetotaxy of the palpi and differently
shaped male and female genitalia (Gusarov & Koval, 2002; Smetana, 2017). As the type species was described from Turkey, a new genus will need to be described for the five East Palaearctic species.

**Polyphyly of Raphirus.** In its current taxonomic concept (e.g. Smetana, 2017), *Raphirus* is the most polyphyletic taxon of *Quedius*, being resolved in no less than seven major clades in our analyses. Its broad definition, generally lacking the features of other genera/subgenera, has made it a convenient dumping ground for morphologically divergent taxa. The species of clade A, *Q. (R.) nanulus* Casey (and related *Q. debilis* Horn), the species related to *Q. (R.) riparius* Kellner and the species related to *Q. (R.) scintillans* each represent major lineages of *Quedius* (Fig. 2) and should be treated as separate genera. The remaining *Q. (Raphirus)* species in our analyses were resolved in the *Quedius* and *Raphirus* lineages. Within the *Quedius* lineage, clades L and O consist of distinctive *Q. (Raphirus)* species groups that can be easily treated as genera. Clade M contains the well-defined himalayicus group of *Q. (Raphirus)* and the morphologically isolated *Q. (R.) lianguansi* from China, whose position within clade M was not confidently resolved by concatenated analyses. Coalescent analyses suggested a more isolated position as the sister group of clades N + O but with weak support. *Quedius lianguansi* does not possess the chaetotaxy of the himalayicus group (Smetana, 2017) but is similar in habitus and is most likely its sister group. Clade N is the morphologically most heterogeneous clade within the *Quedius* lineage, consisting of the morphologically well-defined meei and bleptikos groups of *Q. (Raphirus)* and genus *Quetarius*, which should each be treated as valid genera. Although nearly all species resolved within the *Raphirus* lineage are currently classified as *Q. (Raphirus)*, a single genus solution would be poorly defined and would result in the synonymy of the morphologically distinct West Palaearctic genus *Euyporus*. Instead, clades V, W, X and *Euyporus* can easily be recognized as genera using characters such as the size of the eyes, punctuation of the scutellum and shape of the labial palpus. In fact, the convenient, though nomenclaturally erroneous (see Assing, 2017) four-genus concept used by Coiffait (1978) for this lineage is perfectly corroborated by our molecular analyses (Fig. 6). *Raphirus* (*Sauridus* of Coiffait, 1978) should be restricted to clade X, which contains the type species *Q. limbatus* but also that of its current synonym *Sauridus* (*Q. picipes* (Mannerheim)). Species treated as *Raphirus* by Coiffait (1978) based on a misidentification of the type species (Assing, 2017), correspond to clade W and would take the available name *Arphirus* (Smetana 1977; but our results demonstrated that each of these belong to a different tribe and that the East and West Palaearctic species of *Korgella* have separate origins within the *Microsaurus* lineage of *Quedius*. Other instances of this ecomorph within *Quedius* include the more robust members of the distantly related abnormalis and przewalskii groups of *Q. (Microsaurus)*. An analogous phenomenon was reported in Western Nearctic harvestmen, where cave species were shown to repeatedly develop a predictable set of troglomorphic features that also evolved in surface crevice-dwellers living at higher elevations (Derkarabetian et al., 2010). Another recent example of taxonomic error due to an ecomorph is the ‘*Quedionuchus* group’ of Brunke & Solodovnikov (2013), with members demonstrated here to belong to at least three different tribes. This clade of flattened beetles was recovered based on the mostly glabrous elytra and dorsally glabrous tarsi, traits likely related to a shared microhabitat under bark. However, these characters were also indicative of common descent at shallower levels of divergence in the case of Oriental *Alesiella* and Neotropical *Quedionuchus*, confirmed here as disjunct sister genera and included as members of *Cyrt qedin*.
Biogeography

Although outside of the scope of this study, our well-resolved topology suggests a dynamic biogeographic history for Quediini, that is worth exploring to better understand the diversification of insects in the Northern Hemisphere. Recent divergence dating for Staphylininae suggests that Quediini are relatively young among other tribes (median age 46.6 Mya), postdating the Early Eocene Climatic Optimum (EECO) but appearing just before the emergence of temperate ecosystems at the Eocene-Oligocene boundary (Brunke et al., 2017). This is consistent with their primarily temperate diversity but also with the existence of some subtropical groups, such as the Neotropical members of Quedionuchus or early-diverging groups of the Microsaurus lineage (Figs. 2, 3). The New-Old World disjunctions repeated across the major lineages of Quediini (Figs. 2–6), in the context of a post-EECO evolution, suggest many dispersal events across Beringia, the only land bridge available at the time and supporting a subtropical to temperate climate (Brunke et al., 2017). Other major clades, such as clades I, J and K, are almost to entirely restricted to a biogeographic region, representing significant radiations in the Nearctic, West Palearctic and East Palearctic regions, respectively.

Dataset exploration

Overall, varied analytical conditions such as differing amounts of missing data, partitioning and alternate methods of tree reconstruction resulted in highly similar topologies indicating strong phylogenetic signal for most clades. Although it has become a standard for phylogenomic analyses, filtering loci beyond 50% occupancy (i.e. 75%) generally did not improve phylogenetic resolution and often lowered node support. Molloy & Warnow (2018) demonstrated that as loci were filtered beyond 50% occupancy, phylogenetic accuracy and clade supports decreased for both coalescent, including ASTRAL, and concatenated methods (RAxML). Likely any artefacts created by missing data between the 50 and 75% occupancy datasets were far outweighed in our study by the decrease in phylogenetic signal accompanying the reduction in dataset size by nearly 40% (487 vs 239 loci). Three exceptions where the effect of filtering appeared to have a positive effect on node support involved taxa with some of the highest amounts of missing data: A. lineipennis (Fig. 1), Q. liang (Fig. 4) and Q. tanderi (Fig. 4). Conversely, partitioning loci by codon position had a positive impact on resolution of several backbone nodes in Quediini, the monophyly of clade A (also morphologically supported by the anteriorly convergent eyes), the position of monotypic Q. (Paraquadius) and the monophyly of ‘Genus 1’ and clade K of the Microsaurus lineage. As with filtering loci by missing data, partitioning increased support for clades involving taxa with high levels of missing data. Although partitioning by codon position appears to be uncommon among phylogenomic studies of insect phylogeny, likely due to increased computational burden, at least one study has demonstrated a positive impact on resolution (St. Laurent et al., 2018). However, we also observed a decrease in node support for some shallow clades and a few higher level clades outside Quediini, highlighting the importance of exploring the data with multiple analyses, especially where the inclusion of older pinned specimens dramatically increases the amount of missing data.

Coalescent analyses are commonly used in a complement to concatenation methods in phylogenomic studies to account for gene tree discordance due to incomplete lineage sorting (ILS) (Zhang et al., 2018; Young & Gillung, 2020). However, in the present study, the resulting ASTRAL topologies were in general more poorly resolved and less supported compared to the concatenated trees, with few strongly supported differences between concatenation and coalescent analyses, aside from very shallow clades. Most of these were found to be in conflict with morphological evidence (see above). This overall lower resolution indicates sources of gene tree discordance other than ILS, such as contamination, lack of phylogenetic signal or oversaturated loci (Van Dam et al., 2017). To further control for potential contaminants or other dubious data, we used TreeShrink (Mai & Mirarab, 2018) to prune sequences with excessively long branches but this either had no impact or generally lowered node supports (results not shown). More complicated filtering of loci, such as that used by Van Dam et al. (2017) to control for saturation may result in more strongly supported species trees using coalescent methods.

Conclusion

In one of the most comprehensively sampled target enrichment phylogenies of insects to-date, with just over 200 taxa, we used a newly developed AHE probe set to robustly test the monophyly of the diverse Quediini and provide a solid phylogenetic framework to understand its evolutionary history and biogeography, and identify areas for future taxonomic research. The use of AHE in combination with sensitive lab protocols and next generation sequencing (NGS) allowed for an extensive sampling of pinned museum specimens to include nearly all remaining Staphylininae incertae sedis taxa and all genera, subgenera and nearly all species groups of Quediini. Of the incertae sedis taxa, Quelaestrygon could not be accounted for in the existing systematic classification of Staphylininae and was demonstrated to represent a new tribe, while future analyses will hopefully determine whether Beeria should be placed in Erichsoniini or its own tribe. The remaining incertae sedis taxa were placed in tribes Cyrtquediini and Indoquediini, which were morphologically redefined. Given our comprehensive taxon sampling, we expect further tribe-level misplacement in the NHC of Staphylininae to be rare. Although it was outside of the scope of this study, a more representative sampling of all tribes, and related taxa Arrowinus Bernhauer and Coo mansia Cameron ( Zyła & Solodovnikov, 2020) will be needed to resolve the backbone phylogeny of Staphylininae. A generic revision of Quediini is greatly needed as the genus Quedius was shown to be polyphyletic with respect to almost all other genera of Quediini and all large subgenera of Quedius were shown
to be nonmonophyletic. The resolution and lineage representation necessary for such a revision were achieved by our analyses and major clades were found to be morphologically plausible, of which many are already recognized as species groups (e.g. Smetana, 1971, 2017).

**Systematics**

Quelaestrygonini Brunke, *trib. n.*

urn:lsid:zoobank.org:act:EFF6630F-5657-4B94-B142-F0FD3D24D59E7

Type genus: *Quelaestrygon* Smetana, 1999.

**Diagnosis.** The sole member of Quelaestrygonini can be recognized within Staphylininae by the unique microsculpture alone: disc of pronotum with thin, poorly impressed, scratch-like irregular elements (Fig. 8A). This tribe can also be recognized by the following combination of character states: obvious posterior frontal and basal punctures (fig. 1 in Brunke et al., 2019); head laterally with postmandibular ridge extending far posteriorly of eye; labrum broadly emarginate but not divided to base; antennomeres 1–4 without tomentose pubescence; protibiae without apical row of lateroventral spines; inframarginal tooth.

**Description.** Most relevant details were already published in a recent redescription of *Quelaestrygon* given by Brunke & Solodovnikov (2013) and very recently supplemented by Cai et al., (2020), who described the first male specimen. However, we here provide a full description of Quelaestrygonini that is comparable to those of Brunke et al. (2016) and Brunke et al. (2019).

Large Staphylininae, approximately 2 cm in length, brownish, with long appendages. **Head:** with frontoclypeal punctures absent, single basal puncture present, interocular, parocular and genal punctures absent; microsculpture of head composed of transverse lines combined with thicker fragments and that of pronotum composed of thin, poorly impressed, scratch-like elements (both unique in Staphylininae) (Fig. 8A); mentum with single seta (probably alpha); labrum broadly emarginate medially but not divided to base; infraorbital ridge thin and nearly obliterated at about basal third, from this point, continuing nearly to base of mandibles as faint ridge bordering impression, ventral of postmandibular ridge; postmandibular ridge well developed, extended far posteriorly of eye margin; nuchal ridge present dorsally and laterally; postgenal ridge present, dorsal basal ridge absent; gula with transverse basal impression just posterior of mandibles (hypostomal cavity of Chani-Posse et al., 2018); antennae nongenulate, antennomere 3 without dense pubescence, antennomeres 1–4 without tomentose pubescence, apical antennomere compressed in narrow profile, without broad microsetal sensory field; labial palpi without dense brushes of setae; right mandible with single, distinct proximal tooth. **Thorax:** pronotum with hypomeron slightly visible in lateral view; basisternum with pair of macrosetae; dorsal rows with only a single puncture; postcoxal process of hypomeron present, at base fused across inferior line; basisternum triangular, without longitudinal ridge, with lateral arms narrowed, pair of macrosetae present medially; pronotum not fused with prosternum in procoxal cavity. Elytra with sub-basal ridge complete, directed anteriad and forming scutellar collar, laterally with row of humeral spines; without epipleural row of impressed setose punctures (only fine punctures present); mesoscutellum glabrous, with posterior ridge present; wings well developed, with veins CuA and MP4 separate, vein MP3 present; protergal glands present as well-developed acetabulum. **Legs:** procoxae with internal ridge present and extending along external ridge; profemora with apical row of lateroventral spines; protibiae with lateral spines and apical spurs; protarsomeres with adhesive setae on ventral surface; mesoscoxae contiguous; metacoxae without transverse carina; metatibiae with only two very thin spines on outer face, otherwise spineless; meso- and metatarsomeres trapezoidal, flattened and setose on disc; all tarsi with pretarsus bearing pair of empodial setae, each pair about subequal in length. **Abdomen:** with tergites lacking accessory basal lines or curved lines, median fragment of posterior transverse basal line present on tergites III–V; sternite III with basal transverse carina forming an obtuse angle at middle; male sternite VIII with emargination; paramere fused in single structure bearing stiff, spike like setae on its underside but without peg setae, clearly not fused to median lobe; internal sac of aedeagus without out large sclerites. **Cytoquedini Brunke & Solodovnikov, 2016 sensu n.**

Type genus. *Cytoquedius* Bernhauer, 1917.

**Genera included.** Alesiella Brunke and Solodovnikov, Astrapaecus Gridelli, Bolitogyrus Chevrotail, Cytoquedius Bernhauer, Parisanopus Brèthes, Quediomacrus Sharp, Sedolinus Solodovnikov, Quwatanabius Smetana and an undescribed genus for ‘Quedius’ nigropolitus Cameron.

**Diagnosis.** Most Cytoquedini can be easily recognized by the unique row of coarse, impressed setose punctures on the elytral epipleuron (fig. 4 in Brunke et al., 2016). However, in some taxa this state is obscured by surrounding setae (Sedolinus) or has been independently reversed (Quediomacrus, termishophilous *Cytoquedius*) where the setae are still thicker than those surrounding but the punctures are finer and not impressed. All Cytoquedini can be recognized within Staphylininae based on the following combination of characters: microsculpture on disc of head and pronotum absent; obvious presence of both posterior frontal and basal punctures (fig. 1 in Brunke et al., 2019); profemora with apical row of lateroventral spines (near joint with protibia) (Fig. 8B); protibia without subapical notch; metatarsomeres 1–4 flattened and trapezoidal, not elongate and cylindrical.

**Redescription.** The original description of Cytoquedini given by Brunke et al. (2016) is here supplemented to accommodate *Alesiella* and *Quediomacrus*, and to provide character states for characters introduced since then (e.g. Brunke et al., 2019; Brunke & Smetana, 2019). **Head:** with antennomeres 1–3, 1–4...
(Alesiella, Quediacractus) or 1–5 (Bolitogyrus) without tomentose pubescence; apical antennomere compressed in narrow profile, without broad microsetal sensory field; head with extension of either nuchal or infraorbital ridge (homology unknown) extending along head capsule to near mandibles (or as a short basal fragment in Alesiella, Quediacractus); basal puncture single or doubled (Alesiella, Quediacractus); interocular and genal punctures absent; posterior frontal puncture present; labrum emarginate at middle but not broadly divided to base; mentum with alpha and beta setae (beta seta absent in Alesiella, Astrapeaus, Quediacractus); gula without distinct transverse basal impression; right mandible with either a single distinct tooth or with distinct proximal and distal teeth, each on a different plane (Alesiella, Bolitogyrus, Quediacractus). Thorax: pronotum lacking the ‘second puncture’ of the dorsal row sensu Brunke et al. (2019) (except in the falini group of Neotropical Bolitogyrus); postcoxal process with base fused across inferior line; basisternum triangular, with lateral arms narrowed. Elytra with epipleuron with row of regularly spaced, coarse setose and impressed punctures, sometimes doubled (Astrapeaus) (missing in one species of Cyrtogaeus; rows of macrosetae but not coarse impressed punctures present in Quediacractus); scutellum glabrous, at most with asetose coarse punctures (Bolitogyrus), or with micropunctures bearing short stiff setae basally (Alesiella, Quediacractus), or entirely covered with very fine setose punctures exactly the same as those covering entire forebody (Sedolinus). Legs: profemur with apical row of lateroventral spines (Fig. 8B); protibiae with lateral spines and apical spurs; mesoxoconch contiguous or moderately separated (Alesiella, Quediacractus); metatibiae either spinose or with at most two thin spines (Bolitogyrus, Alesiella, Quediacractus); pro- and metatarsomeres with setae on disc, setae not restricted to margins, (except Alesiella and Quediacractus); metatarsomere 4 with ventral spine-like setae (if present) distinctly interrupted medially and removed from apical margin (not interrupted in Alesiella, Quediacractus). Abdomen: with sternite III with basal transverse carina sharply produced posteriad, forming an acute angle (obtuse in Alesiella, Quediacractus). Aedeagus with (Alesiella, Bolitogyrus, Quediacractus) or without (all others) peg setae. Internal sac of aedeagus with a pair of well-sclerotized ventral copulatory sclerites (reduced to two thin sclerites in Bolitogyrus, slightly less so in Alesiella, Quediacractus) and a dorsal copulatory piece composed of two sclerites attached at their base (absent in Alesiella, Bolitogyrus, Quediacractus).

Indoquedini Brunke & Solodovnikov, 2016 sensu n. Type genus. Indoquedius Blackwelder, 1952.

Genera included. Indoquedius Blackwelder, Strouhalium Scheerpelz; also including ‘Quedius’ elevatus Hatch as incertae sedis.

Diagnosis. Indoquedini can be recognized by a combination of the following character states: head with obvious presence of both posterior frontal and basal punctures (fig. 1 in Brunke et al., 2019); protibiae subapically with distinct and unique notch (Fig. 8C); all antennomeres longer than wide.

Redescription. The original description of Indoquedini given by Brunke et al. (2016) is here supplemented to accommodate Strouhalium and ‘Quedius’ elevatus, and to provide character states for characters introduced since then (e.g. Brunke et al., 2019; Brunke & Smetana, 2019).

Head: with dorsal surface lacking microsculpture (Indoquedius) or with meshed microsculpture (Strouhalium, Q. elevatus); head with single basal puncture, interocular punctures (sensu Brunke et al., 2019) absent or present (Strouhalium), with 1–3 parocular punctures, genal punctures absent; antennae and legs relatively long compared to most Staphylininae, all antennomeres longer than wide; antennomere 3 with dense but not tomentose punctuation (except sparse in Indoquedius); apical antennomere compressed in narrow profile and lacking broad microsetal sensory field; penultimate labial palpmore with either brush of dense setae or not (Strouhalium); apical maxillary palpmores sparsely setose or not (Q. elevatus); right mandibles with single bicuspid tooth, protruding from inner margin. Thorax: pronotum with dorsal surface lacking microsculpture (Indoquedius) or with meshed microsculpture (Strouhalium, Q. elevatus); with 2 or 4 (Strouhalium) punctures in dorsal row; postcoxal process either interrupted by inferior marginal line or fused across this line (Q. elevatus). Elytra with sub-basal ridge sinuate and directed anteriad to form scutellar collar, or reduced to horizontal fragment, with evidence of scutellar collar still visible (Strouhalium, Q. elevatus); row of subequal humeral spines present (except Q. elevatus); protergal glands present, with well-developed acetabulum. Legs: protocoxae with internal procxal ridge not running parallel to external procxal ridge, ending distinctly before (fig. 9E in Brunke & Solodovnikov, 2013) (slightly overlapping in Strouhalium); protibiae with distinct notch subapically (Fig. 8C), without or with (Indoquedius) lateral spines; metatibiae spinose (except Q. elevatus, with only two thin spines); pretarsi with or without (Strouhalium) empodial setae; all pretarsi with one pair of empodial setae (absent in Strouhalium). Abdomen: with sternite III with basal transverse carina produced posteriad at a sharp angle (except Strouhalium); internal sac of aedeagus without large sclerites.

Comments. Previously (Brunke & Solodovnikov, 2013) reported empodial setae for Strouhalium but with multiple specimens available for re-examination, it is clear that they are absent as stated by Smetana (2007).

Quedini Kraatz, 1857. Type genus. Quedius Stephens, 1829.

Genera included. Anthosaurus Smetana, Euryporus Erickson, Korgella Özdikmen, Pseudorientis Watanabe, Quedionuchus Sharp, Quedius Stephens, Quemetopon Smetana, Queskallion Smetana and Quetarsius Smetana.

Diagnosis. Members of Quedini can be distinguished from all other Staphylininae using the following combination of characters: disc of head and pronotum with microsculpture, at least on lateral part of either head or pronotum; head with frontoclypeal punctures, and with posterior frontal and basal macropunctures (fig. 1 in Brunke et al., 2019) that are distinguishable from ground punctuation by their larger diameter and longer, thicker setae; pronotum shield-shaped, slightly elongate to strongly transverse; profemora without apical row of lateroventral spines; protibiae without subapical notch; all pretarsi with pair of empodial setae; all abdominal segments with only
anterior transverse line (no traces of posterior transverse line),
this line not encompassing spiracles. All Quedini also lack a
dorsal basal ridge, lack transverse lines on the metacoxae, have
a completely separated pronotum and prosternum, have sepa-
rate CuA and MP4 wing veins, and have the posterior carina on
the scutellum but these characters are more difficult to routinely
observe on specimens than those used in the diagnosis given
above.

Comments. The concept used here for Quedini remains
essentially that of Brunke et al. (2016). We here refrain from
providing a full description as the group is highly variable
for characters typically used in morphological phylogeny (e.g.
Brunke et al., 2019; Brunke & Smetana, 2019), aside from those
already provided above for the diagnosis.

Quedius (Microsaurus) sensu n.

Velleiopsis Fairmaire, 1882. Type species: V. marginiventris
Fairmaire, 1882 syn.n.

Megaquedius Casey, 1915. Type species: Quedius explanatus
LeConte, 1858 syn.n.

Although sufficient evidence exists for a revision of generic
limits within the Microsaurus lineage, the needed systemat-
ics effort (large number of new combinations, diagnostic mor-
phological characters, etc.) is outside of the scope of this
study. However, based on the recovered topology (Fig. 4), the
Nearctic subgenus Megaquedius (represented by Q. explanatus
LeConte and Q. validus Smetana) is deeply nested within the
Microsaurus lineage, well inside of the ‘core Microsaurus’ clade
(clade H). Therefore, we here synonymize Megaquedius with
Microsaurus. Velleiopsis, a poorly known genus from the south-
western Palaearctic, is the only genus or subgenus-level taxon
of Quedini that has not been sequenced for the present study.
However, we were able to examine nontype specimens of the type
species, V. marginiventris Fairmaire, and determined that it is
strikingly similar in morphology to Megaquedius (Fig. S1A,B).
Differences exist in the colouration (all black in Megaquedius,
reddish and black in Velleiopsis), antennomere length (middle
segments distinctly longer in Velleiopsis) and pronotal puncta-
tion (disc covered with fine, setose micropunctures in Velleiop-
sis). As with Megaquedius, we treat Velleiopsis as a synonym
of Microsaurus and assume that it belongs to clade H. The
other species of Velleiopsis, V. varendorffi Reitter, is quite dif-
ferent from the type species and is more general in appearance
(Fig. S1C), despite its thickened antennae that narrow apically,
a feature considered to be one of the defining characters of the
genus. However, similar antennae have evolved convergently
in mammal burrow-inhabiting species of clade H (Megaqua-
dius) and clade G (Q. (M.) compransor Fall and related, see
Brunke et al., 2020a), and this morphology may be functionally
related to a nidicolous lifestyle. Based on external morphology
(Fig. S1C) and the characteristic median lobe with longitudi-
nal ridges and lateral teeth (Coiffait, 1978), this taxon likely
belongs to the mostly Palaearctic clade J of core Microsaurus,
near Q. fulgidus and its relatives. The above synonyms result in
the following transfers: Q. (Microsaurus) marginiventris (Fair-
maire) comb.n., Q. (M.) varendorffi (Reitter) comb.n., Q. (M.)
explanatus LeConte, Q. (M.) martini Smetana, Q. (M.) syphax
Smetana and Q. (M.) validus Smetana.

Quedius (Distichalisus) Casey, 1915.

The small-bodied Chinese species Q. biann Smetana and
Q. cingulatus Smetana, currently placed as members of the
euryalus group of Q. (Microsaurus), were recovered as members
of clade U with strong support in all analyses. Morphological
examination of these and several others revealed that they lacked
a genal puncture, while possessing both an extra puncture
behind the eye and between the dorsal and sublateral rows
of the pronotum, supporting their placement in Distichalisus
s.str. (clade U). The following species are here transferred from
subgenus Microsaurus to Distichalisus: Q. aethiops Smetana, Q.
bicorn Smetana, Q. cingulatus and Q. taruni Smetana.

Quedius (Raphirus) Stephens, 1829.

The atypically large bodied and small-eyed species of Q.
(Raphirus) related to West Palaearctic Q. (R.) lateralis (Graven-
horst) have been previously placed in Q. (Microsaurus) but
were later moved to subgenus Raphirus when Microsaurus was
redefined. The present analyses recovered two representatives
of this species group, Q. latius Gridelli and Q. suramensis
Eppelsheim, as members of clade X2 within clade X, which
delineates Raphirus s.str. An additional species, Q. fagelianus,
was resolved within clade X2 and is here moved from Dis-
tichalius to Raphirus. Based on information given by Coif-
fait (1978), at least Q. mixtus Eppelsheim and Q. persicus Korge
also belong in this species group and we therefore transfer them
from Microsaurus to Raphirus.

Supporting Information

Additional supporting information may be found online in
the Supporting Information section at the end of the article.

Figure S1. Habitus of: A) Quedius (Microsaurus)
marginiventris (Fairmaire); B) Q. (M.) martini Smetana;
C) Q. (M.) varendorffi (Reitter) (holotype). Scale bars = 10 mm.

File S1. Specimen-level data for sequenced samples, includ-
ing identifiers, accession numbers, preservation type and tar-
get enrichment success.

File S2. Genomic resources used for development of Staph-
Baits target enrichment probe set.

File S3. Phylogenetic trees from each conducted maximum
likelihood analysis.

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