Systematic Entomology

Systematic Entomology (2021), **46**, 396–421 DOI: 10.1111/syen.12468

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

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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 *incertae sedis*, 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 *incertae sedis* genera, all known only from pinned specimens, resulted in the creation of Quelaestrygonini Brunke, **trib. n.** and revised concepts for Cyrtoquediini and Indoquediini. 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,

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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). Quediines 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 unforested 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 (nidicoly) (Assing & Schülke, 2012; Brunke & Buffam, 2018). Some quediines 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* Żyła & Solodovnikov, 2020), the composition of Quediini has been a central issue (Solodovnikov & Newton, 2005). Traditionally, Staphylininae has been roughly divided into a quediine 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 'quediine'-type pronotal shape was in fact the plesiomorphic state for Staphylininae and that 'quediines' distributed in the Southern Hemisphere were only superficially similar to those of the Northern Hemisphere, the latter including the type species of the type genus *Quedius* Stephens (Solodovnikov & Newton, 2005; Solodovnikov, 2006; Solodovnikov & Schomann, 2009). To complicate matters further, there have been multiple reversals back to the 'quediine-type' pronotum shape and multiple origins of the 'staphylinine-type' pronotum, leading to erroneous placements in Quediini or the subtribes of Staphylinini *sensu* Żyła & Solodovnikov (2020) (Smetana, 1977; Solodovnikov & Schomann, 2009; Schillhammer & Brunke, 2018). Recent molecular and total-evidence analyses of Staphylininae (then as tribe Staphylinini) recovered the Southern Hemisphere lineages as either a grade or a clade, leaving the remaining taxa (including Quediini) to consistently form a 'Northern Hemisphere clade' (hereafter NHC) supported by the synapomorphic 'sinuate basal elytral ridge' (Brunke *et al.,* 2016, 2019; Chani-Posse *et al.,* 2018; Jenkins Shaw *et al.,* 2020). Within the NHC, Quediini in the broad sense was shown to be nonmonophyletic and formed multiple higher clades that were treated formally as subtribes but elevated to tribe level by Żyła & Solodovnikov (2020). Based on the revised morphological diagnosis of Quediini by Brunke *et al.* (2016), the lineage is completely absent from South America, the Caribbean, the Afrotropics, the Sunda region of Asia and the Australasian region. Currently, a number of species from the Southern Hemisphere or the northern Neotropical region remain in *Quedius* but need to be moved to Amblyopinini, a tribe which does not belong to the NHC (Jenkins Shaw *et al.,* 2020).

Though the revised concept of Quediini given by Brunke *et al.* (2016) was demonstrated to be monophyletic, less than 3% of the total described diversity have been included in past analyses and a number of morphologically unusual but rarely collected genera, historically listed as Quediini (e.g. Herman, 2001), were unavailable for sequencing. These taxa were excluded from this new concept of Quediini and placed as *incertae sedis* within Staphylininae by Brunke *et al.* (2016). Without a more robust and representative test of quediine monophyly, the current, restricted morphological diagnosis of Quediini remains provisional. Additional phylogenetically isolated lineages, important to the higher systematics of Staphylininae and study of its evolution, may still be hidden within the morphologically heterogeneous genus *Quedius*, further emphasizing the need for comprehensive taxon sampling. Much morphological diversity is also obscured by the current subgeneric system of *Quedius* consisting of the subgenera *Distichalius* Casey, *Megaquedius* Casey, *Microsaurus* Dejean, *Paraquedius* Casey, *Quedius* Stephens, *Raphirus* Stephens and *Velleius* Leach. This system has been greatly improved (e.g. Smetana, 1971, 2017) from its historical usage (e.g. Mulsant & Rey, 1876; Casey, 1915; Gridelli, 1924) but still struggles to account for the morphological diversity of Quediini globally. Despite the low level of representation of Quediini in previous phylogenetic analyses, it has already been possible to identify major systematics problems within the tribe including the polyphyly of *Quedius* and the paraphyly of its subgenera *Microsaurus* Dejean and *Raphirus* Stephens (e.g. Brunke *et al.,* 2019).

Recently, achieving a comprehensively sampled phylogeny of Quediini has become more tractable through a combination of significant taxonomic and methodological advances. During the past 3 years, regional taxonomic 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 Quediini 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 Quediini 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 Staphylinoidea to which it belongs (Mckenna *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 Quediini. 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 Quediini, *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, Żyła & 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 Quediina, to tribe status. Staphylininae 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 Staphylininae to be more easily diagnosed morphologically, compared to treating *Coomania* and Staphylinini together as Staphylininae, or treating these taxa, along with tribes Arrowinini, Platyprosopini, Diochini, Othiini, Maorothiini and Xantholinini as the traditional, broadly defined Staphylininae. Shortly thereafter, Tihelka *et al.* (2020) reanalysed the dataset of Żyła & Solodovnikov (2020) and recovered a slightly different topology but with *Coomania* again sister to Staphylinini and the traditional Staphylininae and Paederinae as sister groups. They argued against the proliferation of subfamily rank names and instead returned to the traditional broad Staphylininae, downgrading Coomaniinae to Coomaniini. We here prefer the system proposed by Żyła & Solodovnikov (2020) for its greater diagnostic value and treated Cyrtoquediini, Quediini, etc. as tribes herein.

Taxon sampling

As Quediini 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 staphylinine 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 Amblyopinini. All six major clades of the NHC recovered by Brunke *et al.* (2016) and treated as tribes or subtribes (Tihelka *et al.,* 2020; Żyła & Solodovnikov, 2020) were represented in the taxon sample. Although *Quedius* still contains many species that belong in Amblyopinini, 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 Staphylininae *incertae sedis* genera *Alesiella* Brunke & Solodovnikov, *Beeria* Hatch, *Quediomacrus* Sharp, *Quelaestrygon* Smetana and *Strouhalium* Scheerpeltz (see Supplementary File S1). We densely sampled Quediini by representing all described genera and subgenera except *Velleiopsis* Fairmaire, which is similar to the sampled *Quedius* (*Megaquedius*) 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 quediine-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 v4.5 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 Staphylinoidea (Supplementary File S2): published genomes for the beetles *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)*; Orussus abietinus* (Scopoli) (Hymenoptera) and *Drosophila melanogaster* Meigen (Diptera); and newly sequenced low coverage genomes and transcriptomes of Staphylinoidea: 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 (Pryszcz & 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 Endopterygota 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 Staphylinoidea 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 Staphylinoidea 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-BICoE/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 Hedin *et al.* (2018).

Alignment, trimming and manual inspection

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 -lmap 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.X (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 ≥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);

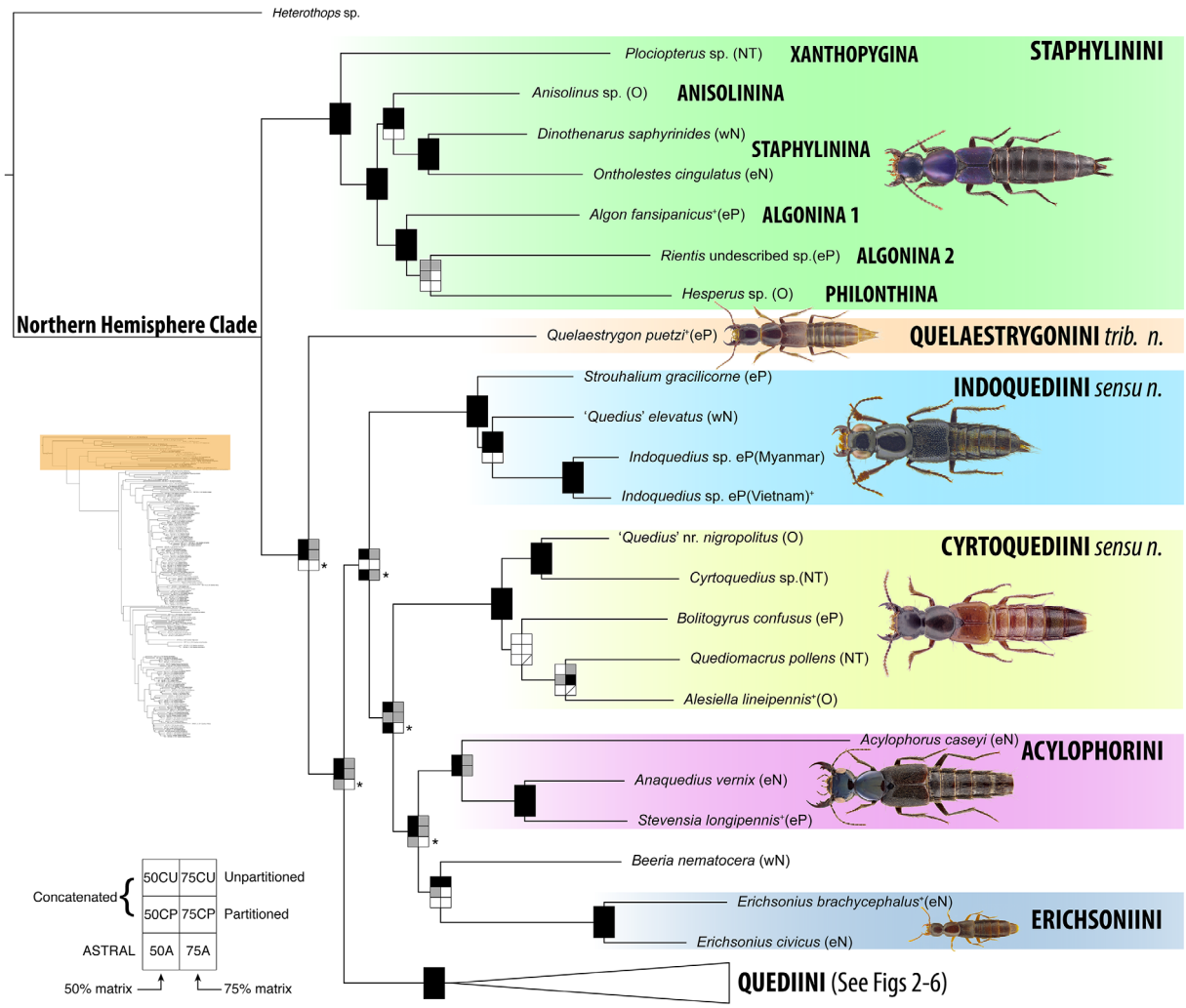

Fig. 1. Phylogeny of the Northern Hemisphere Clade of Staphylininae, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; 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

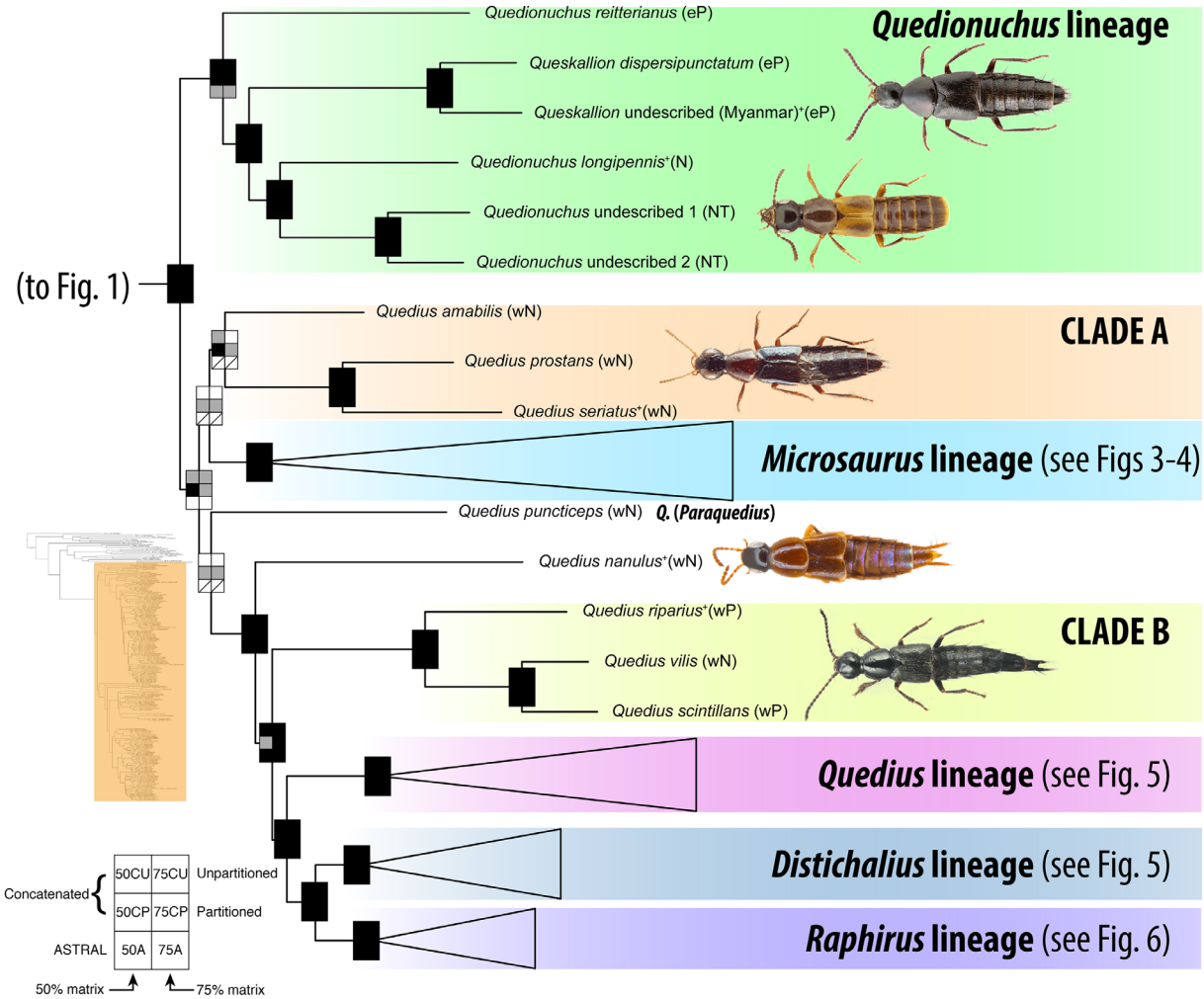

Fig. 2. Backbone phylogeny of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; 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].

branch attraction in single gene trees) and all discussions of node congruence between analyses ignore the position of this taxon (nodes marked with * in Fig. 1). Similarly, discussions of node congruence within clades C and X are given ignoring the positions of *Q. lesagei* and *Q. inflatus*, respectively, in ASTRAL analyses (* in Figs. 3, 6), which were unresolved likely due to very low numbers of target loci. ASTRAL analyses with these taxa removed were otherwise identical. Tree files for all six analyses are provided in Supplementary File S3.

Within the NHC, tribe Staphylinini (former 'Staphylinini Propria') 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 *Quedius elevatus* Hatch) and Cyrtoquediini *sensu n.* (including *Alesiella lineipennis*, *Quediomacrus pollens* Sharp and *Quedius* nr. *nigropolitus*) were each recovered as clades by all analyses. The tribe Quediini was rendered polyphyletic due to the

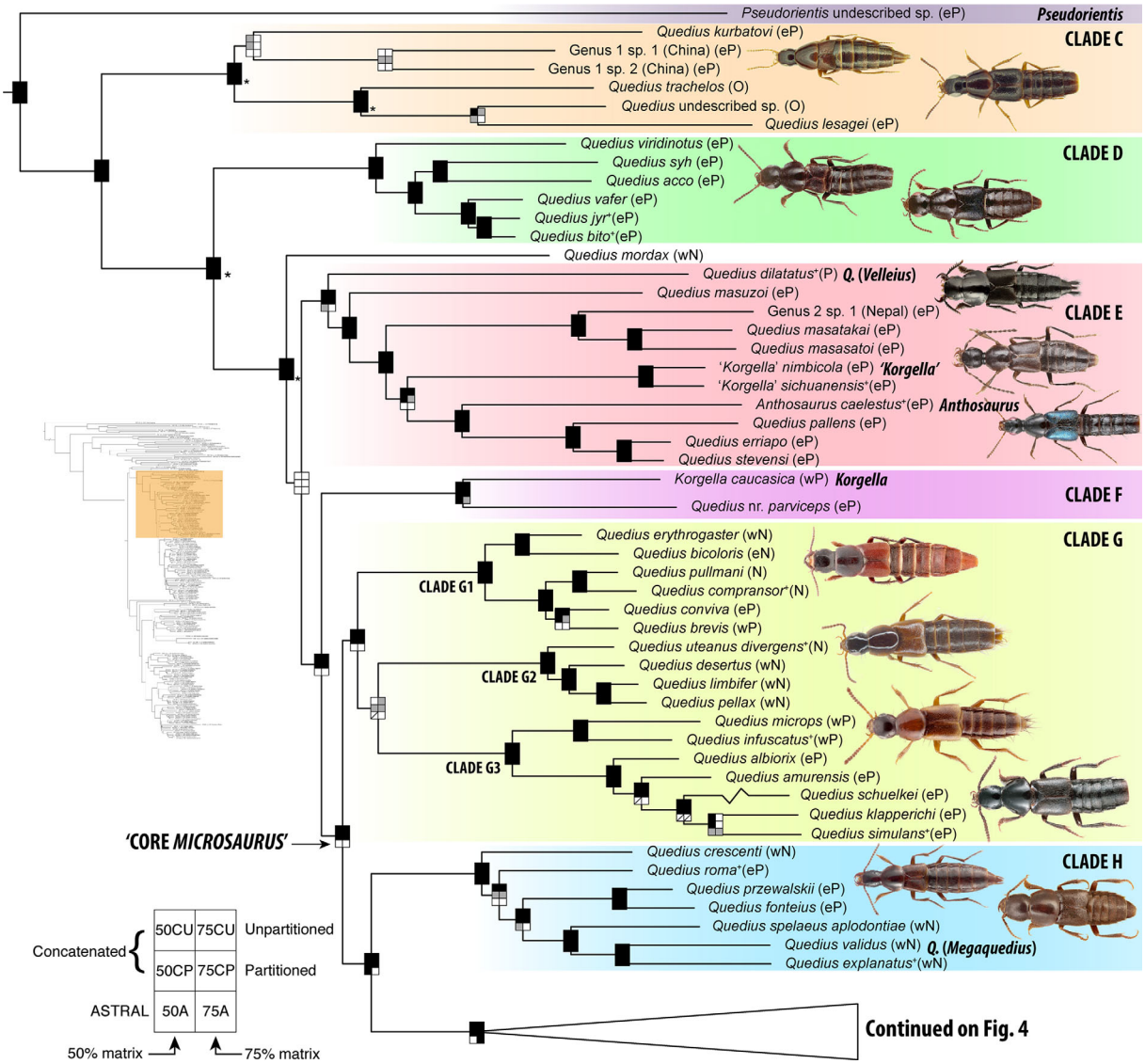

Fig. 3. Phylogeny of the *Microsaurus* lineage of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. An asterisk (*) indicates node support when *Quedius lesagei* Smetana was 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 Indoquediini, Cyrtoquediini, Acylophorini and Erichsoniini. Acylophorini, Erichsoniini and *Beeria nematocera* (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 nematocera* was recovered as the sister group of *Erichsonius* in concatenated analyses, whereas in coalescent analyses *Beeria* was sister to Acylophorini+*Erichsonius* but without support. Within Indoquediini, *Q.* (*R.*) *elevatus* was resolved as the sister group of *Indoquedius* 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

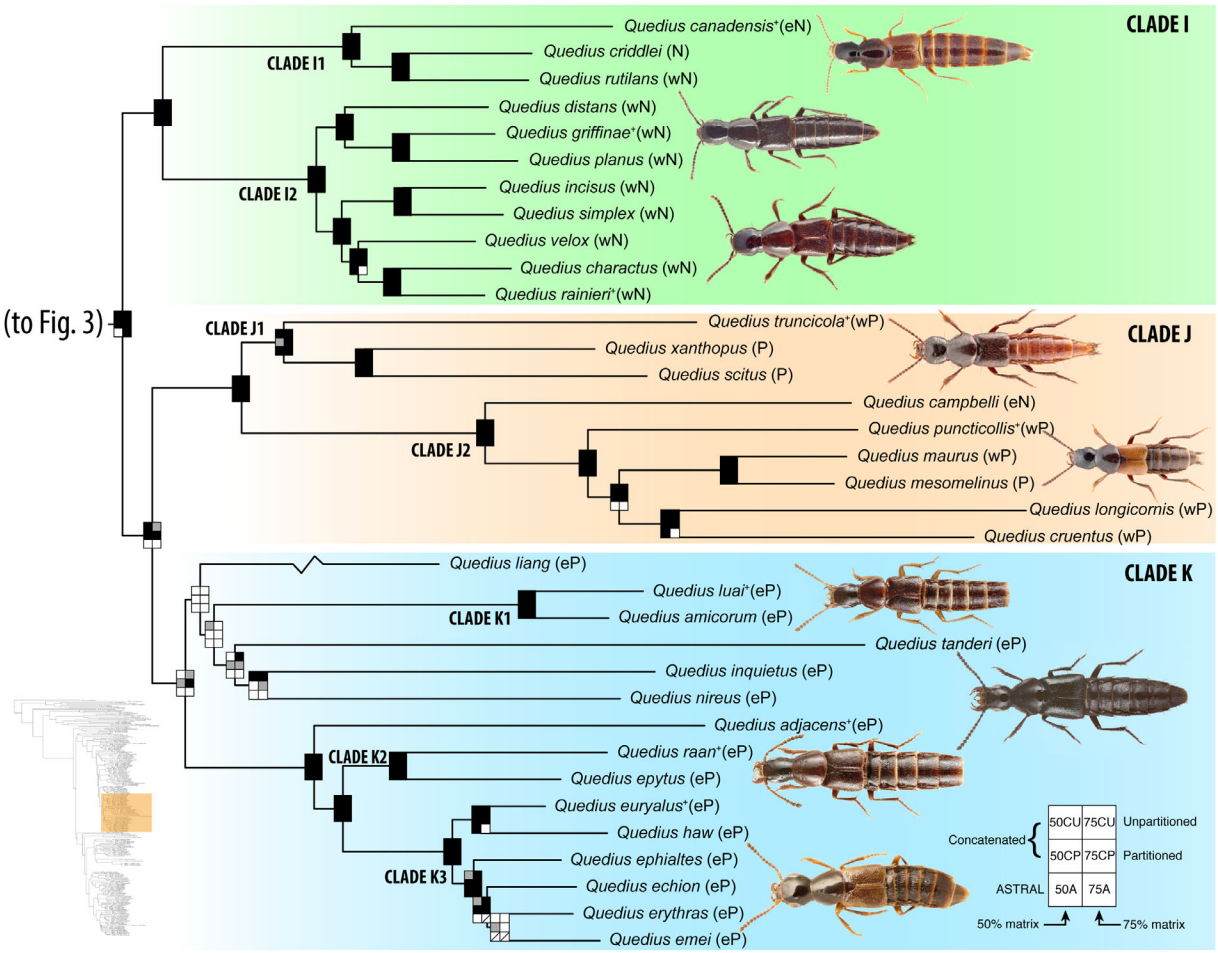

Fig. 4. Phylogeny of the *Microsaurus* lineage of Quediini *continued*, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; 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 luai* 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 Quediini. In partitioned analyses, *Q. puncticeps* was resolved as the sister group to the remaining Quediini (Fig. 2). In all analyses, *Q.* (*R.*) *nanulus* was resolved as the isolated sister group of a clade containing the remaining Quediini 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 (Smetana, 2017). The sister

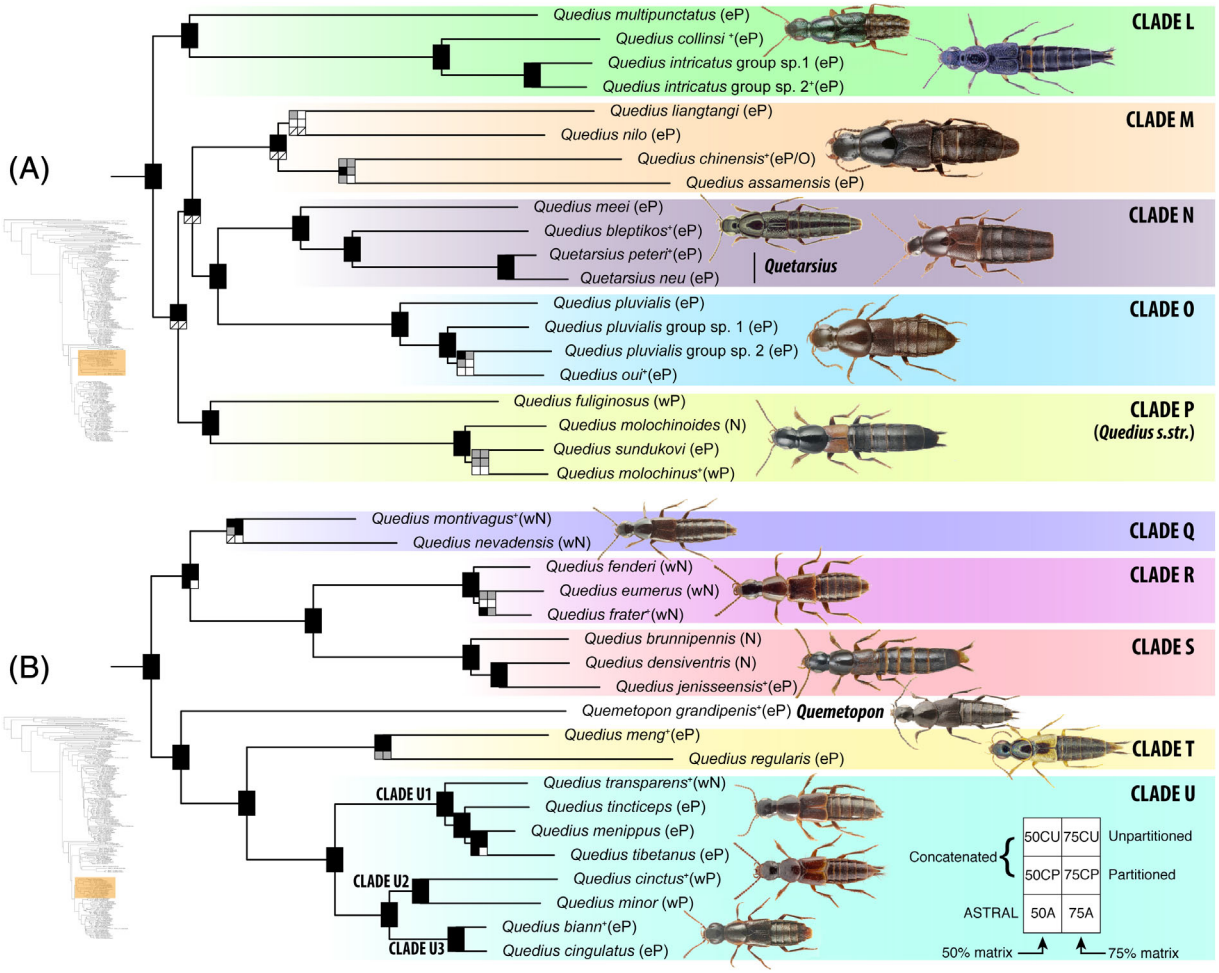

Fig. 5. Phylogeny of the *Quedius* (A) and *Distichalius* (B) lineages of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: 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 peteri* Solodovnikov, *Quemetopon grandipenis* Zhu et al., *Quedius collinsi* Smetana, *Q. chinensis* Bernhauer, *Q. oui* 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].

group of Nearctic *Q.* (*M.*) *mordax* Smetana could not be resolved (Fig. 3). Recovered in all analyses, clade E consisted of *Quedius* (*Velleius*) *dilatatus* (Fabricius), *Quedius masuzoi* Smetana of the abnormalis group (Hu *et al.,* 2020), *Q.* (*M.*) *masasatoi* Smetana of the apicicornis group (Smetana, 2017), a species of a second putatively undescribed genus, members of the ripicola and pallens groups (Smetana, 2017), the East Palaearctic representatives of the genus *Korgella*, and *Anthosaurus* Smetana. The monophyly of *Korgella* was rejected by our analyses as the West Palaearctic *Korgella* and a species related to *Q.* (*M.*) *parviceps* Sharp were resolved as members of clade F in all analyses. Clade F was resolved as sister to a clade containing all other members of the *Microsaurus* lineage and named here the 'core *Microsaurus*' clade (Fig. 3). Clade G was recovered by all analyses and was composed of the erythrogaster group (clade G1) (*sensu* Brunke *et al.,* 2020a), the Nearctic caseyi, desertus and limbifer groups of Smetana (1971) (clade G2), and clade G3 containing the West Palaearctic microps group (Coiffait, 1978) and the East Palaearctic kiangiensis group (Smetana, 2017). Clade H was recovered by all analyses and contained representatives of the criddlei, mnemon, przewalskii and spelaeus groups (Smetana, 1971, 2017; Solodovnikov & Hansen, 2016; Salnitska & Solodovnikov, 2018b) and *Quedius* (*Megaquedius*). Clade I was recovered by all analyses and consisted entirely of North American species of *Quedius* (*Microsaurus*) from the criddlei and canadensis groups (clade I1), and mesomelinus and planus groups (clade I2), both *sensu* Smetana (1971) (Fig. 4). Clade J was recovered by all analyses and contained species from the West Palaearctic, including *Q. mesomelinus* (Marsham) and Nearctic *Q.* (*M.*) *campbelli* Smetana (Fig. 4), both belonging

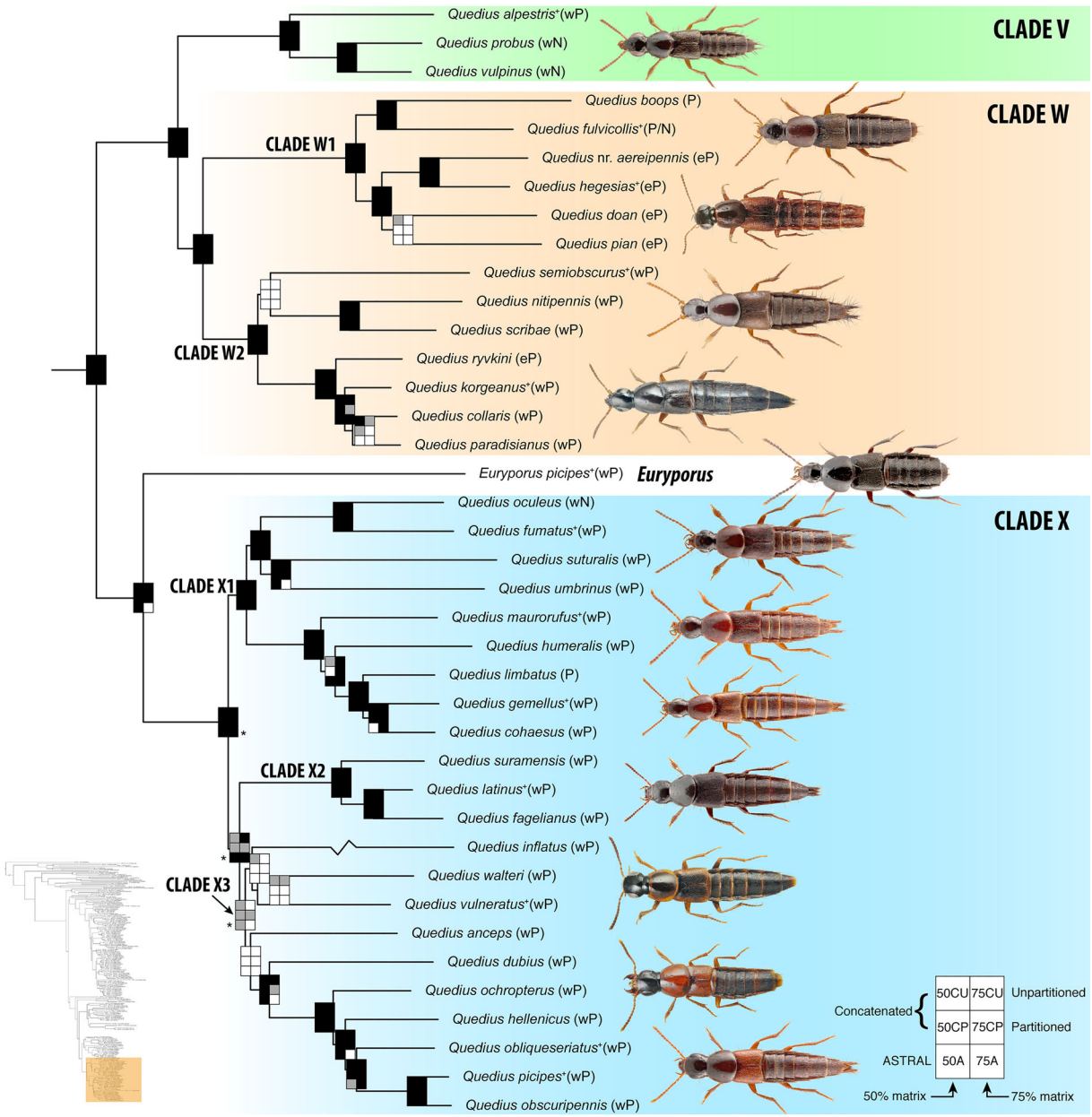

Fig. 6. Phylogeny of the *Raphirus* lineage of Quediini, inferred from a partitioned maximum likelihood analysis of the 50% completeness matrix (50CP – 487 loci). Node boxes correspond to individual analyses as indicated in lower left key and are shaded according to support: black – strong; grey – weak; white – unsupported; slash – in strongly supported topological conflict. An asterisk (*) indicates node support when *Quedius inflatus* Fauvel 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 the western Nearctic *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* sister 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 muscicola 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*.) *oculeus* (sublimbatus group) (Smetana, 1971) and numerous West Palaearctic species of *Q*. (*Raphirus*), including its type species *Q*. (*R*.) *limbatus* (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 1 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

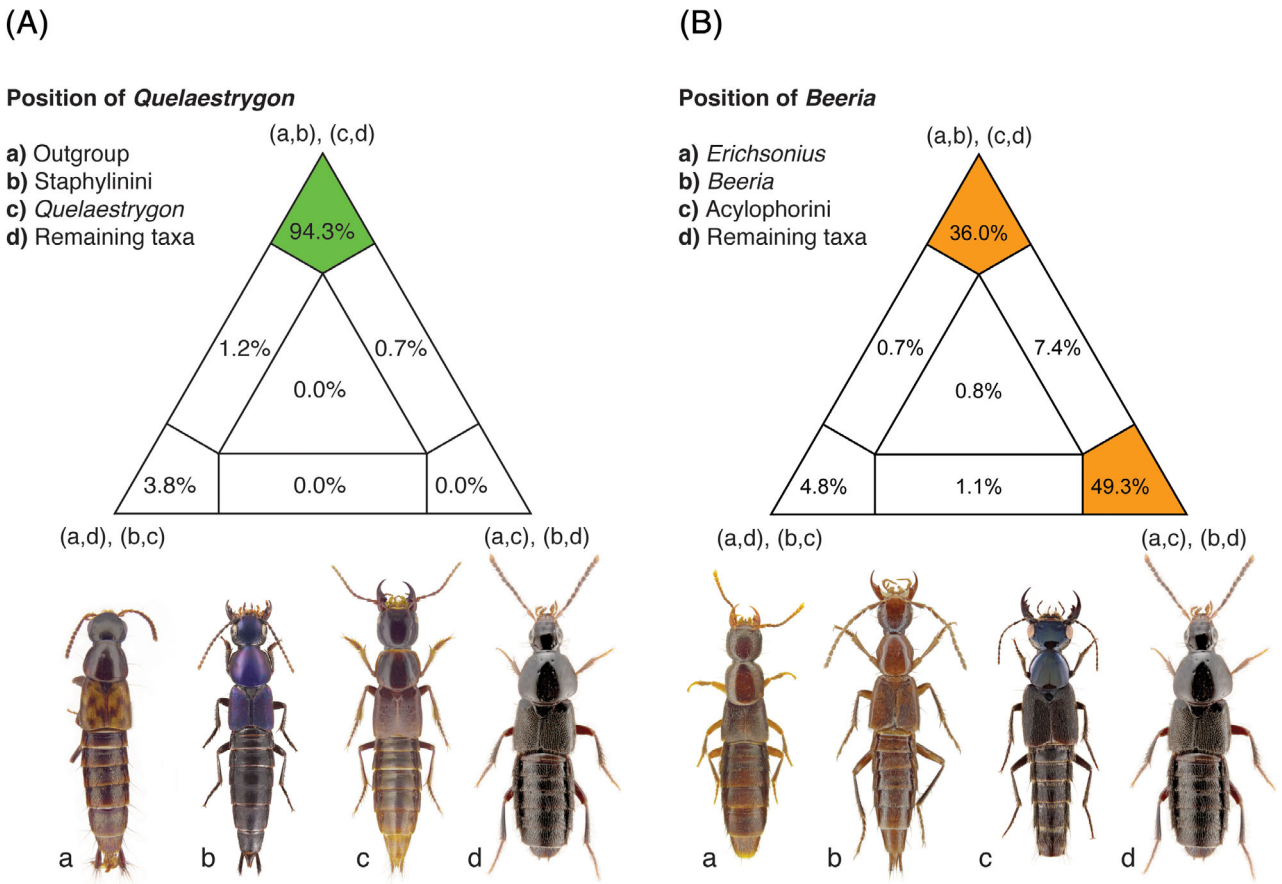

Fig. 7. Results of an four-cluster likelihood-mapping (FcLM) analysis on the unpartitioned, 50% completeness matrix for: A) position of *Quelaestrygon*; B) position of *Beeria*. Photos of *Algon jaechi* Schillhammer and *Stevensia longipennis* Cameron by H. Schillhammer. [Colour figure can be viewed 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; Żyła & 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, Coomaniinae and Xantholininae (Żyła & 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 Indoquediini 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 charismatic cyrtoquediine 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 (coalescent) (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 Quediini (*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 Indoquediini. Originally erected for the moderately diverse Oriental and East Palaearctic genus *Indoquedius* (Brunke *et al.,* 2016), Indoquediini is here expanded to include '*Quedius*' *elevatus*, a morphologically isolated species from western North America

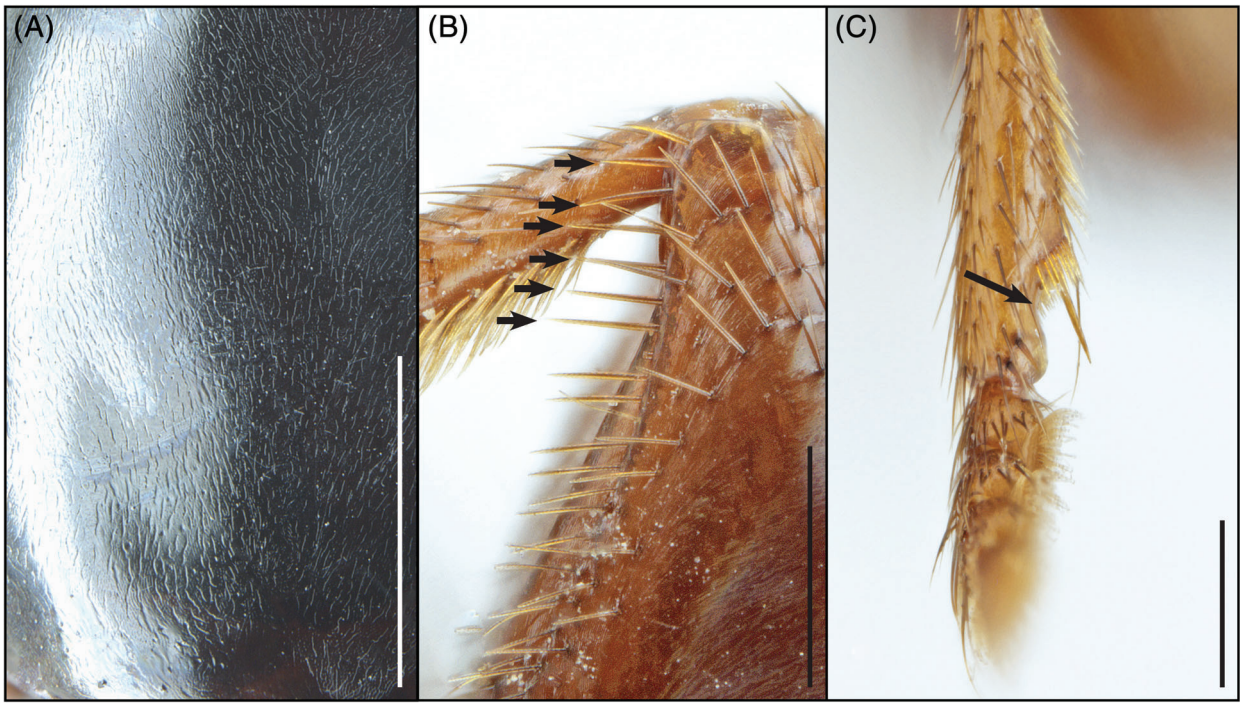

Fig. 8. A) Pronotal microsculpture, *Quelaestrygon puetzi* Smetana; B) apex of profemur, apical row of lateroventral spines (arrows), *Cyrtoquedius* sp.; C) apex of protibia, subapical notch, *Indoquedius* sp. Scale bars: A = 1 mm; B,C = 0.25 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

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 '*Quediomacrus* 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 *Valdiviodes*-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 subtribe Algonina that is likely to be an artefact as all three genera of this group were resolved as a highly supported clade by Żyła & 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*, *Paraquedius*, *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 *Paraquedius* 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*.) *fagelianus* 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 bipictus 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 circumscribe 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 Quediini, 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 Quediini (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*.) *liangtangi* 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 liangtangi* 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 *Quetarsius*, 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 *Euryporus*. Instead, clades V, W, X and *Euryporus* can easily be recognized as genera using characters such as the size of the eyes, punctation 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* Tottenham (type species: *Q. semiobscurus* Marsham). Those treated as *Microquedius* (current synonym of *Raphirus*) correspond to the Palaearctic members of clade V, represented by *Q. alpestris* (Heer). The concept of *Microquedius* should be expanded to include the Nearctic probus and vulpinus groups of Smetana (1971), something already hinted by Smetana (1971) for the probus group. One remaining issue concerns *Q. inflatus*, the only member of clade X to have a punctate scutellum and a species that could not be placed with confidence within clade X due to one of the highest amounts of missing data in our study. Although without support, coalescent analysis 50A placed *Q. inflatus* as the sister group to a maximally supported clade containing all other members of clade X. Whether this species should represent a separate genus or be placed in a more broadly defined *Raphirus* cannot be determined in the present study. In addition to morphological diagnosability, these generic concepts also correspond to ecological preferences for open landscapes (clade W), ever-wet moss and debris along fast-running water (clade V), wetlands (*Euryporus*) and forest litter or subterranean microhabitats (clade X) (Smetana, 1971; Assing & Schülke, 2012; Assing, 2017). Although clade X could be split further into *Raphirus* (clade X1) and *Sauridus* (clade X2 + X3), based on the positions of their type species (see above) (Fig. 6), we argue that stability and diagnosability are better served by treating these clades as a single genus.

Convergent evolution of staphylinine ecomorphs

Our phylogeny demonstrates that the same morphological ecomorphs, presumably linked to similar ecology, have evolved multiple times across the tribes of Staphylininae (for Amblyopinini vs Quediini see Jenkins Shaw *et al.,* 2020) and also within Quediini itself. This phenomenon, in combination with the convergent evolution of the pronotum shape, is arguably the greatest contributor to taxonomic error in Staphylininae. An ecomorph that has created much systematic error in Staphylininae is the crevice/cave-dwelling or 'troglomorph' body type of Christiansen (1962). Generally, troglomorphic staphylinines have greatly elongated appendages, smaller or absent eyes, increased forebody setation and paler body coloration, presumably adaptations to crevices between boulders and talus in mountainous areas or for life in caves. Previously, the genera *Beeria*, *Korgella* and *Strouhalium* were considered to be closely related (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 Quediini. Other instances of this ecomorph within Quediini 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 *Quediomacrus*, confirmed here as disjunct sister genera and included as members of Cyrtoquediini.

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 Palaearctic and East Palaearctic 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.* (*Paraquedius*) 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 Cyrtoquediini 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 *Coomania* Cameron (Żyła & 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.**

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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 posteriad of eye; labrum broadly emarginate but not divided to base; antennomeres 1–4 without tomentose pubescence; protibiae without apical row of lateroventral spines; abdominal tergites III–V with posterior transverse basal line incomplete, as only median fragment (see fig. 2 in Cai *et al.,* 2020). Although *Quelaestrygon* possesses several character states found in some Staphylinini, it lacks all diagnostic characters of this tribe: dorsal basal ridge of neck; absence of posterior frontal puncture; transverse ridge on metacoxae; fusion of prosternum and pronotum inside procoxal cavity (Brunke *et al.,* 2016).

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, ventrad of postmandibular ridge; postmandibular ridge well developed, extended far posteriad of eye margin; nuchal ridge present dorsally and laterally; postgenal ridge present, dorsal basal ridge absent; gula with transverse basal impression just posteriad of mandibles (hypostomal cavity of Chani-Posse *et al.,* 2018); antennae nongeniculate, 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; mesocoxae contiguous; metacoxae without transverse carina; metatibiae with only two very thin spines on outer face, otherwise spineless; meso- and metatarsomeres trapezoid, 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 large sclerites.

Cyrtoquediini Brunke & Solodovnikov, 2016 **sensu n.**

Type genus. *Cyrtoquedius* Bernhauer, 1917.

Genera included. *Alesiella* Brunke and Solodovnikov, *Astrapaeus* Gridelli, *Bolitogyrus* Chevrolat, *Cyrtoquedius* Bernhauer, *Parisanopus* Brèthes, *Quediomacrus* Sharp, *Sedolinus* Solodovnikov, *Quwatanabius* Smetana and an undescribed genus for '*Quedius*' *nigropolitus* Cameron.

Diagnosis. Most Cyrtoquediini 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*, termitophilous *Cyrtoquedius*) where the setae are still thicker than those surrounding but the punctures are finer and not impressed. All Cyrtoquediini 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 Cyrtoquediini 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*, *Quediomacrus*) 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*, *Quediomacrus*); basal puncture single or doubled (*Alesiella*, *Quediomacrus*); 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*, *Astrapaeus*, *Quediomacrus*); 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*, *Quediomacrus*). **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 (*Astrapaeus*) (missing in one species of *Cyrtoquedius*; rows of macrosetae but not coarse impressed punctures present in *Quediomacrus*); scutellum glabrous, at most with asetose coarse punctures (*Bolitogyrus*), or with micropunctures bearing short stiff setae basally (*Alesiella*, *Quediomacrus*), or entirely covered with very fine setose punctures exactly the same as those covering entire forebody (*Sedolinus*). **Legs**: profemora with apical row of lateroventral spines (Fig. 8B); protibiae with lateral spines and apical spurs; mesocoxae contiguous or moderately separated (*Alesiella*, *Quediomacrus*); metatibiae either spinose or with at most two thin spines (*Bolitogyrus*, *Alesiella*, *Quediomacrus*); pro- and metatarsomeres with setae on disc, setae not restricted to margins, (except *Alesiella* and *Quediomacrus*); metatarsomere 4 with ventral spine-like setae (if present) distinctly interrupted medially and removed from apical margin (not interrupted in *Alesiella*, *Quediomacrus*). **Abdomen**: with sternite III with basal transverse carina sharply produced posteriad, forming an acute angle (obtuse in *Alesiella*, *Quediomacrus*). Aedeagus with (*Alesiella*, *Bolitogyrus*, *Quediomacrus*) 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*, *Quediomacrus*) and a dorsal copulatory piece composed of two sclerites attached at their base (absent in *Alesiella*, *Bolitogyrus*, *Quediomacrus*).

Indoquediini Brunke & Solodovnikov, 2016 **sensu n.**

Type genus. *Indoquedius* Blackwelder, 1952.

Genera included. *Indoquedius* Blackwelder, *Strouhalium* Scheerpeltz; also including '*Quedius*' *elevatus* Hatch as *incertae sedis*.

Diagnosis. Indoquediini 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 Indoquediini 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 punctation (except sparse in *Indoquedius*); apical antennomere compressed in narrow profile and lacking broad microsetal sensory field; penultimate labial palpomere with either brush of dense setae or not (*Strouhalium*); apical maxillary palpomeres 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**: procoxae with internal procoxal ridge not running parallel to external procoxal 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).

Quediini Kraatz, 1857.

Type genus. *Quedius* Stephens, 1829.

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

Diagnosis. Members of Quediini 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 punctation 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 Quediini also lack a dorsal basal ridge, lack transverse lines on the metacoxae, have a completely separated pronotum and prosternum, have separate 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 Quediini 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* Dejean, 1833) **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 systematics effort (large number of new combinations, diagnostic morphological 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 southwestern Palaearctic, is the only genus or subgenus-level taxon of Quediini 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 punctation (disc covered with fine, setose micropunctures in *Velleiopsis*). 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 different 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 (*Megaquedius*) 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 longitudinal 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 synonymies result in the following transfers: *Q.* (*Microsaurus*) *marginiventris* (Fairmaire) **comb.n.**, *Q.* (*Mi.*) *varendorffi* (Reitter) **comb.n.**, *Q.* (*Mi.*) *explanatus* LeConte, *Q.* (*Mi.*) *manitobensis* (Casey), *Q.* (*Mi.*) *martini* Smetana, *Q.* (*Mi.*) *syphax* Smetana and *Q.* (*Mi.*) *validus* Smetana.

Quedius (*Distichalius* 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 *Distichalius s.str*. (clade U). The following species are here transferred from subgenus *Microsaurus* to *Distichalius*: *Q. aethiops* Smetana, *Q. biann* 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* (Gravenhorst) 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. latinus* 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 *Distichalius* to *Raphirus*. Based on information given by Coiffait (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, including identifiers, accession numbers, preservation type and target enrichment success.

File S2. Genomic resources used for development of StaphBaits target enrichment probe set.

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

Acknowledgements

We thank all colleagues who provided specimens sequenced or otherwise examined in this study: A. Schomann (Copenhagen, Denmark); V. Grebennikov (Canadian Food Inspection Agency, Canada); R. Anderson (Canadian Museum of Nature, Canada); H. Douglas (AAFC, Canada); M. Fikáček (National Museum

Prague, Czech Republic), Y. Hayashi (Kawanishi, Japan); S. Paiero (University of Guelph, Canada); C. Maier, M. Thayer (Field Museum of Natural History, U.S.A.); V. Gusarov (Natural History Museum of Oslo, Norway); M. Hartmann (Naturkundemuseum Erfurt, Germany); H. Schillhammer (Natural History Museum of Vienna, Austria); Z. Falin (Snow Entomological Museum, U.S.A.); Z.-W. Yin, L. Tang (Shanghai Normal University Insect Collection, China). HE thanks R. Waterhouse (Univ. of Lausanne), K. Meusemann (Univ. Freiburg), B. Misof (Koenig Museum) and O. Niehuis (Univ. Freiburg) for training and advice on bioinformatics and O. Hlinka (CSIRO) for assistance with cluster computing. D. Hartley and V. Caron (CSIRO) helped to process TransANIC samples. T.H. Pham (Mientrung Institute for Scientific Research, Vietnam Academy of Science and Technology, Hue, Vietnam) is thanked for coordinating fieldwork in Vietnam. We thank the CIPRES Scientific Gateway for access to computational resources. Thanks to M. E. Smirnov (www.zin.ru/animalia/coleoptera), L. Tang, H. Schillhammer and the Centre for Biodiversity Genomics (Guelph, Canada) for the use of their habitus photographs. This research received financial support from Agriculture and Agri-Food Canada Projects 'J-002276, Systematics of Beneficial Insects' and 'J-001564, Biological Collections Data Mobilization Initiative (BioMob, Work Package 2), as well as the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement no. 642241 and fieldwork grants from Carlsberg Foundation. AKH thanks the Danish Ministry for Culture's Research Fund (KFU grant FORM.2018-0006) for financial support giving him the opportunity to visit the CNC. RL was supported in part by the Core funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science and Innovation Group. JH was supported by the Ministry of Culture of the Czech Republic (DKRVO 2019-2023/5.I.b, National Museum, 00023272). The authors declare that there are no conflicts of interest.

Data availability statement

The data that support the findings of this study are openly available in at the github repositories at: https://github.com/AAFC-BICoE/staphylinidae-ortholog-baitset, https://github.com/AAFC-BICoE/snakemake-partial-genome-pipeline

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Accepted 7 January 2021