

Research



Cite this article: Cai C *et al.* 2022 Integrated phylogenomics and fossil data illuminate the evolution of beetles. *R. Soc. Open Sci.* **9**: 211771.

<https://doi.org/10.1098/rsos.211771>

Received: 10 November 2021

Accepted: 15 February 2022

Subject Category:

Organismal and evolutionary biology

Subject Areas:

evolution/taxonomy and systematics

Keywords:

Coleoptera, classification, diversification, phylogenomics, substitution modelling, CAT-GTR

Authors for correspondence:

Chenyang Cai

e-mail: cycal@nigpas.ac.cn

Erik Tihelka

e-mail: wn20250@bristol.ac.uk

Philip C. J. Donoghue

e-mail: phil.donoghue@bristol.ac.uk

[†]These authors contributed equally to this study.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5894006>.

Integrated phylogenomics and fossil data illuminate the evolution of beetles

Chenyang Cai^{1,2,†}, Erik Tihelka^{1,2,†}, Mattia Giacomelli³, John F. Lawrence⁴, Adam Ślipiński⁴, Robin Kundrata⁵, Shūhei Yamamoto⁶, Margaret K. Thayer⁷, Alfred F. Newton⁷, Richard A. B. Leschen⁸, Matthew L. Gimmel⁹, Liang Lü¹⁰, Michael S. Engel^{11,12}, Patrice Bouchard¹³, Diying Huang¹, Davide Pisani^{2,3} and Philip C. J. Donoghue²

¹State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China

²School of Earth Sciences, and ³School of Biological Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK

⁴Australian National Insect Collection, CSIRO, GPO Box 1700, Canberra, ACT 2601, Australia

⁵Department of Zoology, Faculty of Science, Palacký University, 17. listopadu 50, 771 46 Olomouc, Czech Republic

⁶Hokkaido University Museum, Hokkaido University, Kita 8, Nishi 5, Kita-ku, Sapporo 060-0808, Japan

⁷Negaunee Integrative Research Center, Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, USA

⁸Manaaki Whenua Landcare Research, New Zealand Arthropod Collection, Private Bag 92170, Auckland, New Zealand

⁹Invertebrate Zoology Department, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, USA

¹⁰College of Life Science, Hebei Normal University, Shijiazhuang 050024, People's Republic of China

¹¹Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, University of Kansas, 1501 Crestline Drive – Suite 140, Lawrence, KS 66045, USA

¹²Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

¹³Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario, K1A 0C6, Canada

ET, 0000-0002-5048-5355; SY, 0000-0002-4162-8457; LL, 0000-0001-7533-6244; PCJD, 0000-0003-3116-7463

Beetles constitute the most biodiverse animal order with over 380 000 described species and possibly several million more yet unnamed. Recent phylogenomic studies have arrived at

considerably incongruent topologies and widely varying estimates of divergence dates for major beetle clades. Here, we use a dataset of 68 single-copy nuclear protein-coding (NPC) genes sampling 129 out of the 193 recognized extant families as well as the first comprehensive set of fully justified fossil calibrations to recover a refined timescale of beetle evolution. Using phylogenetic methods that counter the effects of compositional and rate heterogeneity, we recover a topology congruent with morphological studies, which we use, combined with other recent phylogenomic studies, to propose several formal changes in the classification of Coleoptera: Scirtiformia and Scirtoidea *sensu nov.*, Clambiformia *ser. nov.* and Clamboidea *sensu nov.*, Rhinorhipiformia *ser. nov.*, Byrrhoidea *sensu nov.*, Dryopoidea *stat. res.*, Nosodendriiformia *ser. nov.* and Staphyliniformia *sensu nov.*, and Erotyloidea *stat. nov.*, Nitiduloidea *stat. nov.* and Cucujoidea *sensu nov.*, alongside changes below the superfamily level. Our divergence time analyses recovered a late Carboniferous origin of Coleoptera, a late Palaeozoic origin of all modern beetle suborders and a Triassic–Jurassic origin of most extant families, while fundamental divergences within beetle phylogeny did not coincide with the hypothesis of a Cretaceous Terrestrial Revolution.

1. Introduction

Beetles (Coleoptera) are a textbook example of a hyperdiverse clade, known from more than 380 000 living species and upwards of 1.5 million awaiting description [1,2], that display extraordinary morphological, taxonomic and ecological diversity [3]. Constituting nearly a quarter of extant animal diversity on our shared planet, beetles play indispensable roles in nearly all terrestrial and freshwater ecosystems. The ecological dominance of beetles is reflected by their fossil record. The earliest unequivocal stem beetles are early Permian [4,5], while crown beetles belonging to extant suborders (Adephaga, Archostemata, Myxophaga and Polyphaga) first occur in the late Permian [6,7], and most extant families are first encountered in the fossil record in the Jurassic to Cretaceous [8–10]. A multitude of hypotheses have been proposed to explain beetle megadiversity, focusing principally on the importance of key anatomical innovations, co-diversification with other clades such as angiosperms during the Cretaceous Terrestrial Revolution [11] and mass extinction events [9,12–15]. Tests of these hypotheses of the causes and consequences of beetle diversification require a robust time-calibrated phylogeny. However, considering the long evolutionary history, exceptional species richness and unparalleled morphological disparity as well as apparent morphological convergence of beetles, resolving the phylogeny and timescale of Coleoptera evolution has proven challenging.

The lack of a consensus on higher level relationships within Coleoptera has compromised attempts to derive an evolutionary timescale. To date, the majority of molecular phylogenetic studies of beetles with the most comprehensive taxon sampling [9,16–18] have sampled eight or fewer genes, with a matrix length of less than 10 000 nucleotides [19]. While this limited gene sampling has helped shed light on the relationships of some subfamilies and families, it is insufficient to accurately resolve the deep evolutionary relationships within Coleoptera. As exemplified in the most comprehensive studies based on morphology [20], eight-gene markers [16], mitochondrial genomes [21,22], phylogenomic datasets [10,23] and transcriptomes [23], the interrelationships of the suborders and most series and superfamilies of the most diverse beetle suborder, Polyphaga, still lack consistency and sufficient statistical support. As such, relationships among many families remain effectively unresolved [19]. Compositional and rate heterogeneity are among the most common sources of phylogenetic incongruence [24–26]. While models such as WAG and LG account for replacement rate heterogeneity and can account for across-site rate heterogeneity when combined with a Gamma distribution (e.g. the WAG+G and LG+G models), these models cannot account for across-site compositional heterogeneity. Reducing site compositional heterogeneity in datasets combined with the utilization of evolutionary models accounting also for compositional heterogeneity (such as the CAT-based models [27]) has been shown to improve the fit of the model to the data and reduce attraction artefacts that are frequent source of error in phylogenetics [27,28]. Consequently, site and rate heterogeneous models have been widely used to resolve difficult phylogenomic problems, such as deep and rapid radiations that are otherwise hard to resolve [29–32]. In different groups of beetles, compositionally site-heterogeneous models have recovered topologies that are highly congruent, sometimes identical, to traditional morphology-based classification schemes [21,25,33], thus contributing to resolving the often perceived ‘conflict’ between morphological and molecular phylogenies [34]. However, the

compositionally site-heterogeneous CAT model has not been used widely for the analysis of protein-coding sequences of beetles.

Reconstructing the timescale of beetle evolution also has to explicitly account for sources of error in molecular clock estimates and the biases of the fossil record. Despite the rich fossil record of beetles, molecular clock analyses have generally incorporated few fossil calibrations, ranging from 7 to 34 [9,10,16,23,35], a practice that may lead to inaccurate divergence time estimates [36,37] as the congruence between molecular clock estimates and the fossil record tends to increase logarithmically with an increasing number of calibrations used [38]. The selection and phylogenetic placement of fossil calibrations is another significant factor influencing divergence dates [39,40], and past studies have either not followed best practice in justifying the phylogenetic position and stratigraphic age of the fossils [41], or used fossils to calibrate more derived nodes than they truly represent [9,10,16], skewing divergence time estimates. Finally, the commonplace use of arbitrary statistical distributions to establish a prior on clade age unduly biases clade age estimates [42]. Fossils can only directly inform minimum constraints on clade ages [43], which is particularly important for taxa such as beetles that are restricted to a small number of fossil deposits with exceptional preservation [44], making the criteria used to define maximum age constraints on when nodes are imposed an important consideration for molecular clock studies. These variables have contributed to uncertainties in dating key events in beetle evolution, such as the timing of origin of the beetle clade or the timing of Polyphaga radiation relative to the diversification of angiosperms—a key tenet of the Cretaceous Terrestrial Revolution hypothesis [11].

Here, we infer a timescale for beetle evolution that integrates the fossil record and refined sampling of 68 nuclear protein-coding (NPC) genes (16 206 amino acid sites) generated from Zhang *et al.* [10,45] with the addition of *Rhinorhipus* [46]. We established 57 new calibrations established in accordance with best practice recommendations [41], fully justified with respect to their stratigraphic age and systematic position, more than have been used in any previous analysis of the timing of beetle evolution. We provide a well-resolved phylogeny of beetles with a comprehensive taxon sampling based on the site-heterogeneous CAT-GTR+G4 model. This phylogeny is more consistent with morphological data [20,25] and whole-genome analyses [23] and we use it to propose formal changes to the classificatory scheme of beetles.

2. Methods

2.1. Dataset collation

We used the published NPC gene sequences from Zhang *et al.* [10] supplemented with the *Rhinorhipus* sequences from Kusy *et al.* [46], a morphologically peculiar genus suspected to represent an isolated early diverging polyphagan lineage. Zhang *et al.* [10] presented and analysed both nucleotide and amino acid alignments of their data; their decisive alignment was based upon a concatenated amino acid dataset of 95 NPC genes. We excluded 27 genes that contain up to 21 copies in some beetle genomes and could not be homologized confidently, following [46], keeping only single-copy orthologues. All NPC genes were individually aligned using the ‘Translation Align’ option with the FFT-NS-i- \times 2 algorithm of MAFFT 7.2 [47]. Ambiguously aligned regions were trimmed with BMGE 1.1 (-m BLOSUM30) [48]. The sequences were then concatenated into a supermatrix (376 taxa, 16 206 sites) using FASconCAT [49]. The concatenated supermatrix (68 NPC genes, 376 taxa, data occupancy: 54.2%) consisted of 16 206 amino acids. The dataset and output files are available from Mendeley Data (<http://dx.doi.org/10.17632/7v27xcyv99.2>).

2.2. Compositional heterogeneity and model-specific artefacts

General statistics for the dataset, compositional homogeneity tests (χ^2 test of heterogeneity) and compositional heterogeneity (relative composition frequency variability (RCFV)) were computed using BaCoCa v. 1.105 [50]. To assess the prevalence of model-specific incongruences in beetle phylogeny, we generated a reduced dataset with 136 taxa, sampling only a single representative for each family, and applied the site-homogeneous models LG, JTT and WAG alongside the site-heterogeneous models C10 and C30. Analyses were conducted in IQ-TREE 1.6.3 [51] with 1000 bootstraps. The fit of these models to the dataset was assessed using ModelFinder [52] implemented in IQ-TREE 1.6.3.

2.3. Model selection and phylogenetic analysis

We tested the impact of accounting for compositional heterogeneity on phylogenetic inferences of Coleoptera. We tested the replacement rate heterogeneously and compositionally and rate site-heterogeneous infinite mixture model CAT-GTR + G4, which has been shown both theoretically and empirically to be frequently effective at suppressing attraction artefacts [24,28], and the site-homogeneous model GTR. In addition, we tested the use of LG + C20, a pre-computed replacement rate heterogeneously and compositionally and rate site-heterogeneous model, which has been used in recent phylogenomic studies of Coleoptera [10,16,23]. The C20 component in the LG-C20 model accounts for site-specific compositional heterogeneity (it is a CAT model), but differs from CAT (as used in CAT-GTR + G4) as it offers only 20 substitutional categories, while the CAT model estimates the optimal number of categories from the data. Similarly, the LG component is a pre-computed GTR matrix where replacement rates are not estimated from the data. To test whether the CAT-GTR + G4 model fits the decisive amino acid alignment better than the GTR model, a variant of which was used by Zhang *et al.* [10], a Bayesian cross-validation analysis was run with 10 replicates in PhyloBayes. CAT-GTR + G4 was run in PhyloBayes MPI 1.7 [53]; two independent Markov chain Monte Carlo (MCMC) chains were run until convergence maxdiff less than 0.3 for up to 14 months of real time. The bpcomp program was used to generate output of the largest (maxdiff) and mean (meandiff) discrepancies observed across all bipartitions. The models GTR and LG + C20 were implemented in IQ-TREE 1.6.3 [51] with 1000 bootstraps.

2.4. Fossil calibrations

We selected 57 calibrations spread throughout the tree of beetles based on a combination of fossil, phylogenetic, stratigraphic, geochronological and biogeographic evidence (electronic supplementary material, table S2). Fossil calibration choice was conducted conservatively following the criteria set out by Parham *et al.* [41]. Care was taken to select fossils that are the earliest members of their respective clades and are distributed equitably throughout the tree. The fossils were selected to calibrate nodes based on the presence of unambiguous synapomorphies. Soft maximum node age constraints were based on the absence of fossils in well-studied Lagerstätten to circumvent the use of arbitrary statistical distributions with uniformed maxima. Soft maxima are often established arbitrarily but objectively on key fossil Lagerstätten that demonstrate evidence of the absence of clade members based on the presence of taphonomic, ecologic and/or biogeographic counterparts. Note, however, that this conclusion is not based only on the named deposit. Rather, the soft maximum is based on the cumulative evidence of the absence of clade members (and presence of taphonomic, ecologic and/or biogeographic counterparts) in deposits intermediate in age between the minimum and soft maximum constraints. The deposit on which the soft maximum is defined is simply an arbitrary but objective reference datum reflecting our view that there is very little (but non-zero—hence it is a soft maximum) prior probability that the clade originated before this time.

2.5. Markov chain Monte Carlo tree analysis

Divergence time estimation was performed using the approximate likelihood calculation in MCMCtree implemented in PAML 4.7 [54], incorporating softbound fossil calibrations on nodes on the tree [55]. We used MCMCtree in place of competing Bayesian relaxed molecular clock software because of its computational efficiency, facilitating exploration of the impact of methodological variables. We obtained 200 000 trees with a sampling frequency of 50 and discarded 10 000 as burn-in. Default parameters were set as follows: 'cleandata = 0', 'BDparas = 1 1 0', 'kappa_gamma = 6 2', 'alpha_gamma = 1 1', 'gene_gamma = 2 20', 'sigma2_gamma = 1 10' and 'finetune = 1: 0.1 0.1 0.1 0.01 0.5'. Convergence was tested in Tracer [56] by comparing estimates from the two independent chains. Analyses were run using both autocorrelated rate (AC) and independent rate (IR) clock models using uniform prior distributions to reflect ignorance of the true clade between the minimum and soft maximum constraints. In all analyses, the soft minimum and maximum bounds were augmented by a 2.5% tail probability. To ensure our priors were appropriate, we ran the MCMCtree analysis without sequence data to establish whether the effective priors are compatible with the specified priors.

2.6. Taxonomic acts

The present paper has been registered under ZooBank publication LSID: urn:lsid:zoobank.org:pub:3B5E77C8-FA20-4622-9362-2F1C97F92D4E.

3. Results

3.1. Systematic bias in beetle phylogenomics

Prior to phylogenetic reconstruction, we subjected our 68-gene dataset to tests to determine possible sources of systematic error. Of the 376 analysed taxa, 115 failed the compositional homogeneity test ($p < 0.05$) (electronic supplementary material, table S1 available on Mendeley Data). Moreover, the dataset displayed a relatively high RCFV value (0.0229) [57]. High RCFV values are indicative of pronounced amino acid compositional heterogeneity, which is characteristic of fast-evolving taxa [58] (long branches) and may lead to misleading phylogenetic inference [24–26]. This was confirmed in preliminary analyses with reduced taxon sampling, which showed that the recovery of relationships at deep nodes was heavily influenced by the model used in phylogenetic reconstruction. The site-homogeneous models LG, WAG, GTR and JTT recovered topologies with high statistical support, but differed profoundly from the better fitting site-heterogeneous model C10 (electronic supplementary material, table S1), with respect to the placement of numerous polyphagan groups, namely within Cucujiformia (electronic supplementary material, figures S1–S5). The recovered model-dependent phylogenetic signal is strongly suggestive of systemic incongruence of phylogenetic signal, attributable in part to long-branch attraction (LBA) artefacts and other sources of systematic error such as the heterogeneity of the substitution process. Hence, we expect systematic bias to be an important source of incongruence in beetle phylogenomics, corroborating previous phylogenomic studies of beetle mitochondrial genomes [25,33,59].

3.2. Phylogenomic reconstruction

To overcome bias associated with compositional heterogeneity, we tested site-homogeneous and site-heterogeneous models for their fit to the whole analysed dataset with 376 taxa by running a cross-validation analysis in PhyloBayes. The site-heterogeneous model CAT-GTR + G4 fitted the dataset better than the site-homogeneous GTR model, variations of which have been used in some previous analyses of beetle phylogeny (CAT-GTR + G4 > GTR; CV score = 8094.35 ± 341.776). This is in line with previous studies that show that site-heterogeneous models consistently outperform site-homogeneous ones, albeit at the expense of a greater computational burden [30,32,60]. As such, we present the topology reconstructed by the site-heterogeneous model CAT-GTR + G4 implemented in PhyloBayes as our main tree. Topologies recovered with the site-homogeneous model (GTR, electronic supplementary material, figure S7) and a variant of the site-heterogeneous CAT model (LG + C20, electronic supplementary material, figure S8) varied with respect to the support of key deep clades and recovered relationships. For example, the GTR and LG + C20 models recovered the suborders Archostemata and Myxophaga as sister to Adephaga, an alternative branching order of superfamilies within Cucujiformia inconsistent with recent analyses [10,16,23], and differed with respect to the relationships among some polyphagan families such as Boganiidae. Nonetheless, the monophyly of major series and superfamilies has been supported by the site-homogeneous models as well as CAT-GTR + G4, which is further discussed below.

Our PhyloBayes analyses with the CAT-GTR + G4 model (figures 1 and 2) recovered deep relationships among suborders with Adephaga as the earliest diverging lineage, Adephaga (Polyphaga (Myxophaga, Archostemata)), a novel hypothesis [10,16], albeit with low support (figure 3). As noted in Zhang *et al.* [10], the two smallest coleopteran suborders, Archostemata and Myxophaga, were insufficiently sampled (each represented by a single taxon) and this may, in part, account for such a result. Despite extensive morphology-based phylogenetic studies [61–63], the intersubordinal relationships should be considered tentative, awaiting future phylogenomic studies [19]. Consistent with Zhang *et al.* [10], McKenna *et al.* [23] and an analysis of ultraconserved elements [64] within Adephaga, we recovered a paraphyletic ‘Hydradephaga’ with the aquatic Haliplidae and Gyrinidae forming a clade sister to other aquatic and terrestrial adephagans. A paraphyletic ‘Hydradephaga’ with Gyrinidae as the earliest diverging adephagan branch was also recovered by a number of morphological analyses of adults and larvae [65].

Among Polyphaga, five families formed three branching clades sister to the remaining polyphagan families (figure 2), in congruence with all recent studies [9,10,16]. As in previous analyses [9,10,16,23], Derodontidae was recovered as sister to Clambidae + Eucinetidae. In contrast with Zhang *et al.* [10], our analysis also included the enigmatic Australian endemic family Rhinorhipidae (superfamily Rhinorhipoidea), sequenced by Kusy *et al.* [46], which was strongly supported as sister to the remaining polyphagans. Thus, we can reject the recent hypothesis that it may be sister to

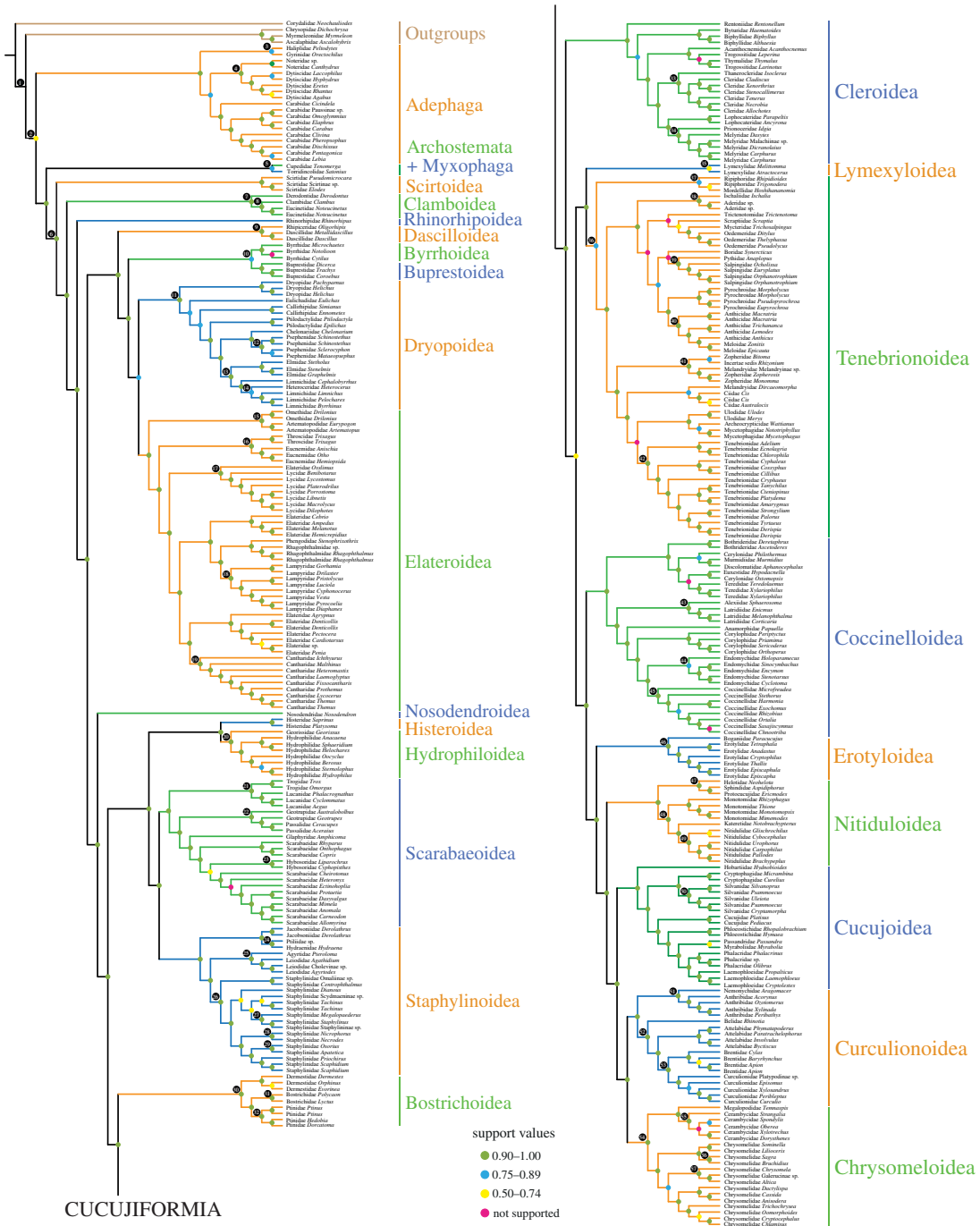


Figure 1. A full phylogeny of beetles displaying the systematic position of all sampled taxa analysed under the site-heterogeneous CAT-GTR + G4 model. Branch lengths have been omitted for clarity. Newly proposed taxonomic changes are followed. Support values are shown as BPP. Black numbered nodes indicate calibrations, see electronic supplementary material for full list of calibrations.

Nosodendridae or to Elateriformia based on mitogenomes and Sanger sequence data analysed under site-homogeneous models [46]. This finding is congruent with the genome-scale analysis of McKenna *et al.* [23] and selected analyses of Kusy *et al.* [46].

Next to Rhinorhipidae, the monophyletic series Elateriformia was recovered as the fourth polyphagan branch with strong support, a result consistent with genomic analyses [21,22,46], rejecting a more derived position based on an eight-gene phylogeny [16,19]. Within Elateriformia, Dascilloidea were corroborated as the sister group to the remaining elateriform superfamilies, as in Zhang *et al.* [10], Kusy *et al.* [66] and McKenna *et al.* [23], rejecting a weakly supported and ambiguous Dascilloidea–Byrrhidae relationship in Timmermans *et al.* [21]. The poorly supported monophyletic Byrrhoidea in Zhang *et al.* [10] and McKenna *et al.* [16] was not supported here, with Byrrhidae forming a sister group to Buprestidae.

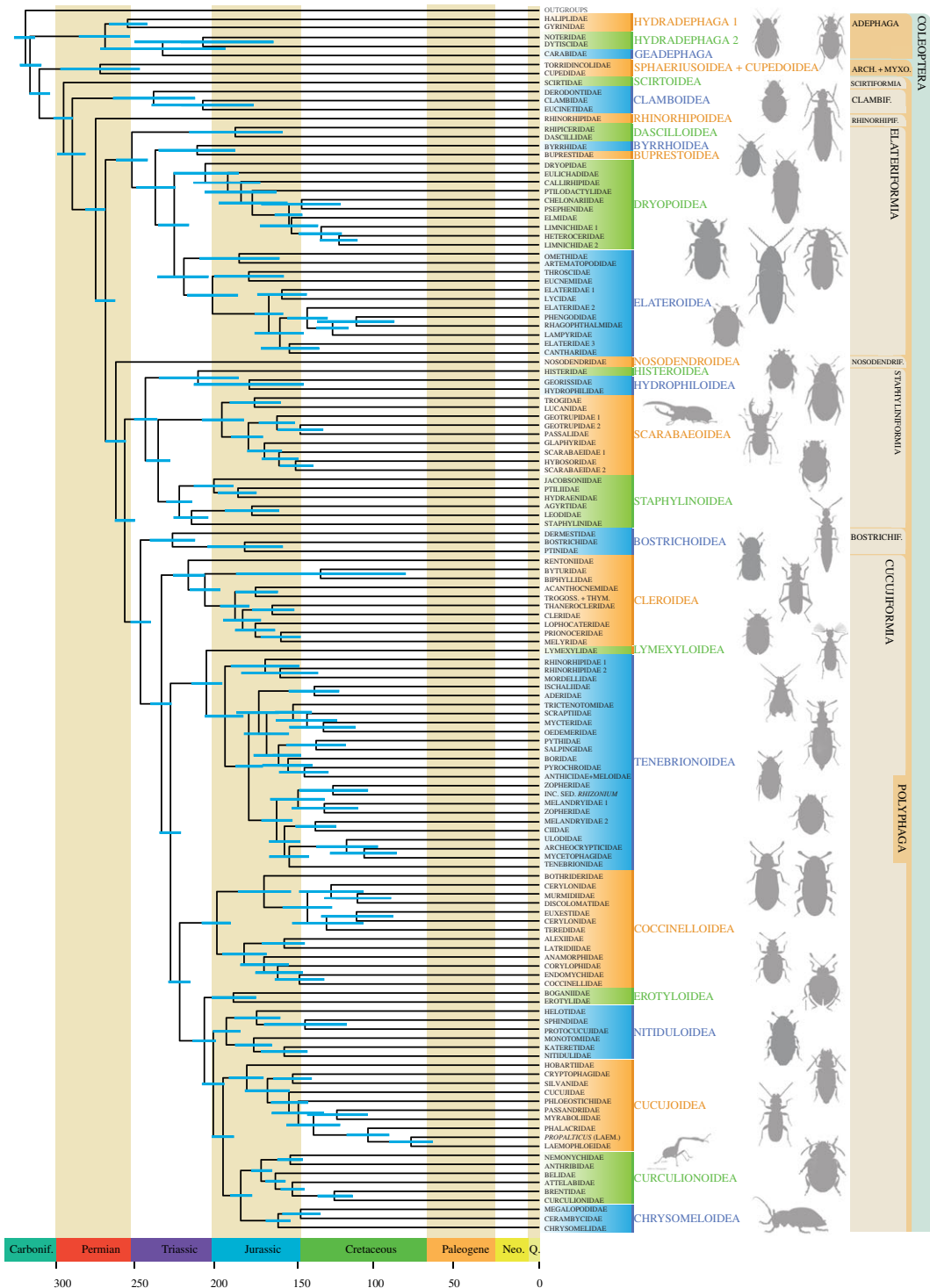


Figure 2. Timescale of beetle evolution displayed as a family-level tree adapted from figure 1. Ages were estimated based on 57 calibrated nodes, integrating the results of analyses using IR and AC molecular clock models in MCMCtree. Newly proposed taxonomic changes are followed. Abbreviations: Arch., Archostemata; Bostrichif., Bostrichiformia; Carbonif., Carboniferous; Clambif., Clambiformia *ser. nov.*; Laem., Laemophloeidae; Myxo., Myxophaga; Neo., Neogene; Nosodendriformia *ser. nov.*; Rhinorhipif., Rhinorhipiformia *ser. nov.*; Trogoss. + Thym., Trogossitidae + Thymalidae; Q., Quaternary.

A polyphyletic Byrrhoidea was also recovered based on mitogenomes [21], whole genomes [23] and a small number of genes [9], in which the name Dryopoidea was used for defining Byrrhoidea minus Byrrhidae, and Byrrhoidea *s. str.* for the moss-feeding Byrrhidae. As supported by numerous plesiomorphic characters (especially larval traits), Byrrhoidea *s. str.* and Buprestoidea have been long

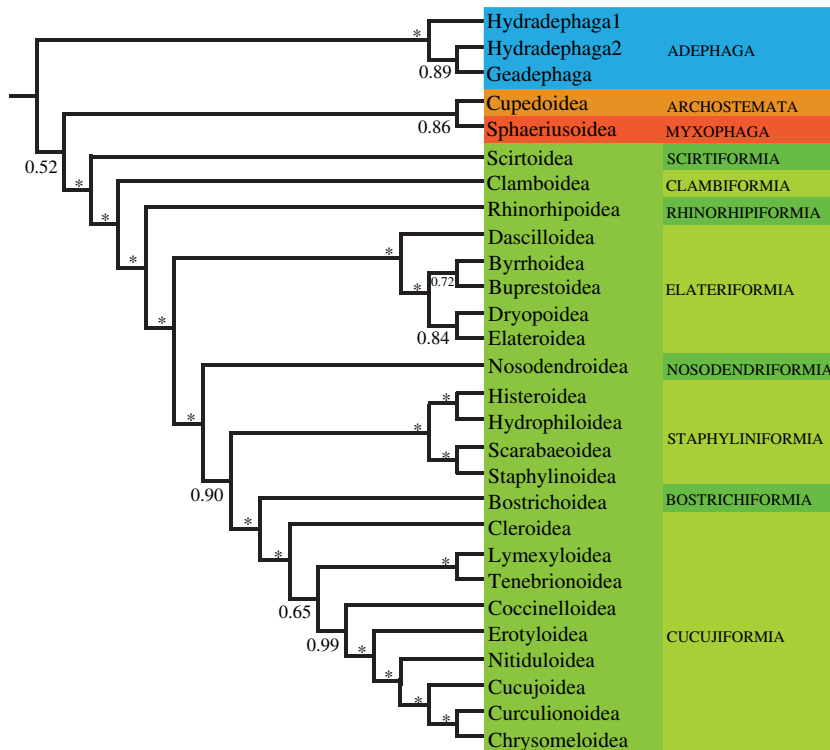


Figure 3. Proposed classification of Coleoptera showing the relationships of the suborders, series and superfamilies of beetles. Asterisks denote well-supported nodes with BPP ≥ 0.95 .

regarded to be isolated from other elateriforms [67–69], in concert with our new topology. Additionally, Dryopoidea have been well defined by a unique rearrangement of tRNA gene order [70]. The interfamilial relationships among Dryopoidea are exactly the same as those based on a site-homogeneous model [10], providing the best-supported relationships and clarifying uncertainties in the phylogeny of Dryopoidea based on a few genes [16,71]. Within Elateroidea, the clade of ‘higher elateroids’ *sensu* Kundera *et al.* [72] was strongly supported, which is consistent with previous studies [9,10,16]. The clade Lycidae + Elateridae (Lissomini) was strongly supported to occupy a more basal position compared with Cantharidae, which is inconsistent with Zhang *et al.* [10], but consistent with McKenna *et al.* [16]. Elateridae were recovered non-monophyletic as in other recent studies [10,16,23,73].

Next to Elateriformia, Nosodendridae was strongly supported as sister to the remaining polyphagans (Staphyliniformia, Bostrichiformia and Cucujiformia), in congruence with McKenna *et al.* [23] and rejecting its placement within Elateriformia [9,16,23,72].

Monophyly of the clade encompassing Histeroidea, Hydrophiloidea, Staphylinoidea (including Jacobsoniidae [10,16]) and Scarabaeoidea, collectively known as Haplogastra, was strongly supported (Bayesian posterior probabilities (BPP) = 1), consistent with various previous studies [10,16,21,74,75]. These results are congruent with the recent molecular clock analysis focused on Staphylinoidea that used 50 calibrations [76]. Histeroidea + Hydrophiloidea was recovered as sister to Staphylinoidea + Scarabaeoidea (BPP = 1), resolving challenging relationships difficult to reconstruct based on morphology [74], mitogenomes [21], or few genes [16,77]. Bostrichiformia were recovered as a sister group to Cucujiformia, corroborating previous results [16,21].

Within Cucujiformia, the superfamily Cleroidea (including Biphylidae and Byturidae), instead of Coccinelloidea [10,16], was recovered as the earliest diverging clade (BPP = 1). Lymexyloidea + Tenebrionoidea was moderately supported as sister to the rest of Cucujiformia (BPP = 0.66). Coccinelloidea formed a sister group to Cucujoidea *sensu* Robertson *et al.* [78] + Phytophaga (Curculionoidea and Chrysomeloidea) (BPP = 1), representing a relationship never recovered before [9,10,16,21,78]. Intriguingly, the monophyly of the superfamily Cucujoidea *sensu* Robertson *et al.* [78] was not supported, consistent with other phylogenomic studies [21,23], but not recent studies based on site-homogeneous models (e.g. [10,16,78]). The clade Boganiidae + Erotylidae was strongly supported as a sister group to other cucujoid families plus Phytophaga (BPP = 1). Helotidae, Sphindidae, Protocucujidae, Monotomidae and the Nitidulidae group (Kateretidae, Nitidulidae and Smicripidae) formed the next branch (BPP = 1). Within this clade, Cybocephalinae *stat. nov.* were recovered as

members of Nitidulidae, as defined by morphology [79], rejecting their previously proposed status as a separate family [10,80]. The remaining cucujoid families formed a monophyletic group, with Hobartiidae being the first branching lineage (BPP=1). Monophyly of Phytophaga was strongly supported (BPP=1), congruent with recent phylogenies [10,16,21], but see [9,18]. Belidae were recovered as the second branch within Curculionoidea (BPP=1), rejecting previous hypotheses that recovered them as a sister group to Nemonychidae + Anthribidae [81] or to all other curculionoids [16].

3.3. Fossil calibrations

We derived 57 calibrations spread throughout the tree of beetles based on a combination of fossil, phylogenetic, stratigraphic, geochronological and biogeographic evidence. Fossil calibration choice was conducted conservatively following best practice [41]. Care was taken to calibrate nodes distributed equitably throughout the tree, informed by fossils that are the earliest phylogenetically secure members of their respective clades based on the presence of unambiguous synapomorphies.

For example, we selected *Ponomarenkium belmonthense* from the late Permian Newcastle Coal Measures at Belmont, Australia, to calibrate the node representing crown Coleoptera [82]. The type series is deposited in a public institutional collection, the Australian Museum in Sydney (holotype, 40278; paratype, 41618) [82]. The fossils possess open procoxal cavities, a narrow prosternal process and lack a broad prothoracic postcoxal bridge; these characteristics place them into crown Coleoptera. However, the combination of characters present in *Ponomarenkium* excludes it from the crown group of all four extant beetle suborders: internalized metatrochantin, metanepisternum only marginally part of the closure of the mesocoxal cavity, elytra without window punctures, antennae moniliform (Archostemata); transverse ridge of the mesoventrite, short metacoxae not reaching the hind margin of abdominal sternite III, absence of coxal plates (Adephaga); absence of a broad contact between the meso- and meta-ventrites (Myxophaga); and exposed propleuron (Polyphaga) [82]. The age of the Tatarian insect beds in the Newcastle Coal Measures at Belmont, from which the fossils originate, is derived from stratigraphic correlation and high-precision CA-TIMS U-Pb zircon dating and hence a conservative minimum age for the fossil can be taken from the top of the Changhsingian, dated at 251.902 Ma \pm 0.024 Myr [82,83], thus, 251.878 Ma. The maximum constraint on the root of Coleoptera was 307.1 Ma, based on the age of the Mazon Creek Lagerstätte [84]. Despite its highly diverse fossil insect assemblage that has been intensively studied for decades [84], no unequivocal crown beetles are known from Mazon Creek or other younger Carboniferous insect Lagerstätte such as Commeny in France, Wettin Formation in Germany, Obora in Czechia, Chekarda, the Kuznetsk Basin, Soyana, Tikhie Gory and Isady in Russia. As such, the choice of soft maximum constraint was based on the absence of a clade from several well-explored deposits older than that on which the minimum is defined, which were typically studied for decades and/or comprehensively monographed. Crucially, these deposits are biogeographically diverse and preserve insects, demonstrating that were representatives of crown Coleoptera present, they would have been preserved. While *Adiphlebia* from Mazon Creek has been interpreted as the earliest beetle [85], this has since been shown to be erroneous, based on clay artefacts attached to the wing membrane [86]. Full details of all 57 calibrations used are provided in the electronic supplementary material. This comprehensive set of fully justified calibrations serves as a basis for future divergence time analyses in Coleoptera, as well as our own. The suitability of our specified priors was evaluated by running an analysis without molecular data, yielding the effective priors for comparison [87].

3.4. Divergence time estimates

To derive an integrative timescale of beetles, we combined the results of alternative molecular clock models: IR and AC. Both models yielded comparable results, with the IR clocks proposing earlier dates on average (table 1; electronic supplementary material, figures S9 and S10). In the following discussion, results from both AC and IR analyses are combined to provide a single date range, since we cannot discriminate between the efficacies of these clock models.

We recovered a late Carboniferous origin of crown Coleoptera (322–306 Ma). This inferred divergence time is somewhat older than the age of the earliest unequivocal stem-group coleopteran, *Coleopsis archaica* from the Sakmarian Meisenheim Formation in Germany (approx. 290 Ma) [5], which has not been used as a calibration point. Despite a controversial Carboniferous record of putative stem Coleoptera and Coleopterida (i.e. Coleoptera + Strepsiptera) [85,88] that have been recommended for calibration in some studies [89], the affinities of these fossils have been questioned as they do not preserve unambiguous coleopteran apomorphies [4,86].

Table 1. Divergence dates (95% CI of the posterior distribution of age estimates, in Ma) of the crown groups of beetle suborders and series from IR and AC molecular clock analyses with uniform prior distributions.

clade	IR	AC
Coleoptera	321–306	322–318
Adephaga	287–259	288–266
Archostemata – Myxophaga	286–236	314–285
Polyphaga	301–288	307–286
Scirtiformia	177–77	227–90
Clambiformia	254–202	286–239
Rhinorhipiformia	287–271	283–264
Elateriformia	269–246	268–249
Nosodendriformia	276–258	271–253
Staphyliniformia	258–241	257–238
Bostrichiformia	237–203	250–228
Cucujiformia	249–231	233–220

Crown Adephaga are estimated to have originated in the latter half of the Permian (282–257 Ma). The earliest diverging adephagan family, Gyrinidae, originated in the Permian–Triassic. Adephagans colonized land once, between the Triassic and the Late Jurassic (248–162 Ma), when the clade including ground beetles and tiger beetles (Geadephaga) diverged from their aquatic ancestors.

The suborders Adephaga and Myxophaga diverged between the Pennsylvanian and mid-Triassic (314–236 Ma), in congruence with most other recent views of the group's evolution (figure 4).

Polyphaga was estimated to have originated in a relatively narrow interval between the latest Carboniferous and Early Permian (307–286 Ma). These dates are significantly older than those estimated by previous studies [9,10,16], which inferred a Permian to Triassic origin of the clade, but fall within the range estimated by Toussaint *et al.* [35] and McKenna *et al.* [23]. The two earliest diverging coleopteran clades including Scirtidae and Clambidae diverged in the Late Triassic–Late Cretaceous (227–77 Ma) and Permian–latest Triassic (286–202 Ma), respectively. Despite their position on the polyphagan tree, these clades are scarcely represented in the pre-Palaeogene fossil record [90], which may contribute to their broad credibility intervals (CIs). The lineage comprising the isolated family Rhinorhipidae was inferred to be Permian in age (287–264 Ma).

The species-rich series Elateriformia diverged in the Late Permian to Middle Triassic (269–246 Ma). The last common ancestor of the Histeroidea, Hydrophiloidea and Staphyloidea clade diverged in the Early to Late Triassic (258–238 Ma). Staphylinidae, the most diverse beetle family [91], originated between the Late Triassic and Early Jurassic (209–184 Ma), and subsequently diversified in the Early Jurassic to Late Cretaceous. The origin of Cleroidea was estimated as Late Triassic (236–209 Ma). The Lymexyloidea + Tenebrionoidea clade diverged between the Late Triassic and earliest Jurassic (227–201 Ma), with most families subsequently diverging in the Jurassic and Early Cretaceous. Coccinelloidea diverged in the Late Triassic to Early Jurassic (217–182 Ma). Major derived cucujiform branches originated roughly contemporaneously; the early diverging Boganiidae + Erotylidae clade is Late Triassic to Middle Jurassic (210–167 Ma) in age, Helotidae and kin are Late Triassic to Early Jurassic (210–180 Ma), and the most derived clade including Hobartiidae and relatives is Early to Middle Jurassic (198–164 Ma), with the lineages of most extant families originating in the Jurassic to Early Cretaceous. Phytophaga dates back to the Early to Middle Jurassic.

4. Discussion

4.1. Taxonomic implications

Molecular phylogenetic studies conducted over the last decade have lent support to several deep relationships among coleopteran groups suspected by earlier workers on the basis of morphological data alone. Considering that some of these relationships are strongly supported in different molecular

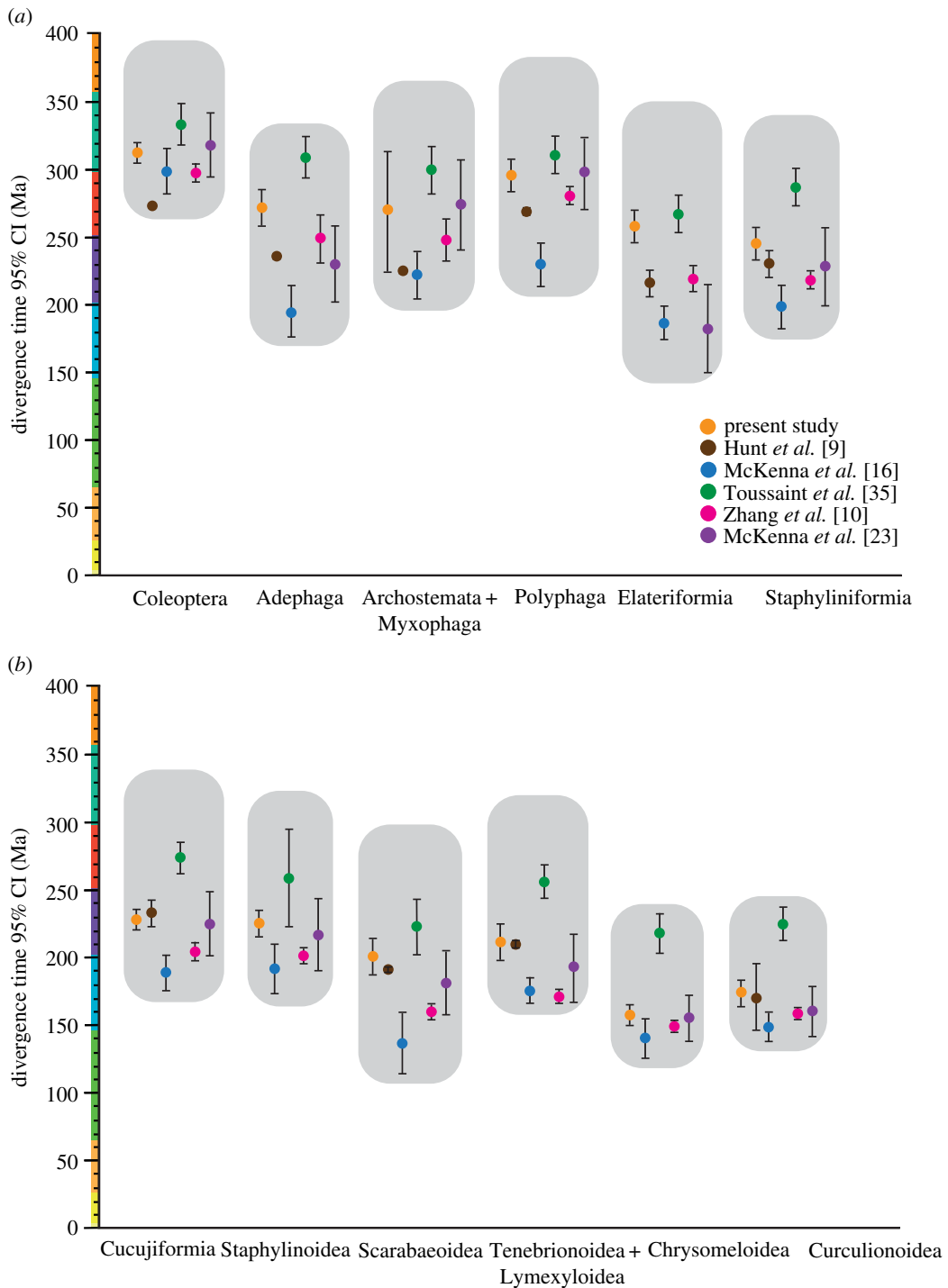


Figure 4. 95% CIs for the divergence of selected major beetle clades in the present and previous studies.

studies [10,19,21,23,77] and are thereby robust to taxon and gene sampling as well as to LBA artefacts, we herein propose several changes to the taxonomy of Coleoptera. All taxonomic changes, including morphological diagnoses, lists of included taxa and detailed commentaries, are provided in the electronic supplementary material and are briefly summarized below. In total, 234 families are recognized of which 194 are extant. A hypothesis of the relationships among the higher taxonomic units within Coleoptera is outlined in figure 3.

The traditional series Derodontiformia, classically defined as containing the three problematic families Derodontidae, Nosodendridae and Jacobsoniidae, does not form a natural group in our analyses and other previous phylogenomic studies [10,23]. The monophyly of the group has been doubted based on morphological characters as well [20,68,92]. We consider Jacobsoniidae a member

of Staphylinioidea, and Nosodendridae as belonging to a series of its own. Consequently, Scirtiformia and Scirtoidea *sensu nov.*, and Clambiformia Cai and Tihelka *ser. nov.* and Clamboidea *sensu nov.* (with Clamboidea Fischer, 1821 taking priority over Derodontoidea LeConte, 1861) are redefined, the former comprising the extant families Decliniidae and Scirtidae, and the latter Clambidae, Derodontidae and Eucinetidae.

The enigmatic Rhinorhipidae, represented in the recent fauna by only a single species endemic to northeastern Australia, are resolved with strong support as an isolated branch falling outside of Elateriformia (where it was placed by Lawrence and Newton [93]). We propose to include the family in a series of its own, Rhinorhipiformia Cai, Engel and Tihelka *ser. nov.*

Byrrhoidea in the current sense was recovered as paraphyletic, with Byrrhidae forming the sister group to Buprestidae and the remainder of the superfamily forming a sister group to Elateroidea. This split roughly corresponds to Crowson's concept [67] of Byrrhoidea as containing only a single family, Byrrhidae, and is not unexpected as the monophyly of Byrrhoidea has been doubted [23,71]. Thus, we regard Byrrhidae as constituting Byrrhoidea *sensu nov.* and treat the remaining former byrrhoid families within Dryopoidea *stat. res.* Relationships among clades within Elateroidea are not resolved with sufficient support to justify taxonomic revision, which is consistent with the results based on the anchored hybrid enrichment method using 2260 single-copy orthologous genes by Douglas *et al.* [73].

In congruence with other phylogenomic analyses [10,23], Nosodendridae were recovered as an isolated lineage sister to Staphyliniformia, Bostrichiformia and Cucujiformia, outside of Clambiformia *ser. nov.*, where the family was provisionally placed by previous workers [68]. To maintain the monophyly of the remaining well-defined series, and considering the long-established morphological distinctiveness of the family, a new series is instituted for Nosodendridae, Nosodendriformia Cai and Tihelka *ser. nov.*

We recovered Scarabaeiformia (Scarabaeoidea) nested within Staphyliniformia, as a sister group to Staphylinioidea, in line with other genomic analyses [10,23]. As this would render the well-defined Staphyliniformia polyphyletic, we integrate Scarabaeiformia within Staphyliniformia *sensu nov.* This newly defined Staphyliniformia essentially corresponds to the Haplogastra concept proposed more than a century ago by Kolbe [94] which was subsequently supported by a range of morphological studies of adult and larval characters (see electronic supplementary material for full discussion).

The superfamily Cucujoidea is a diverse (approx. 10 000 described species) and heterogeneous group of beetles, frequently considered the most problematic taxon in Coleoptera [95]. Its monophyly has been questioned and various authors in the past have suggested splitting it (see electronic supplementary material for full review). In genomic analyses [10,23,96], the group is consistently recovered as a grade consisting of three clades: (i) Boganiidae + Erotylidae; (ii) Helotidae, Sphindidae, Protocucujidae, Monotomidae, Kateretidae, Nitidulidae and Smicripidae; and (iii) Hobartiidae, Cryptophagidae, Silvanidae, Cucujidae, Phloeostichidae, Passandridae, Myraboliidae, Phalacridae, Propalticidae (=Laemophloeidae) and Laemophloeidae. We consequently split the old Cucujoidea *sensu* Robertson *et al.* [78] into three superfamilies: Erotyloidea *stat. nov.*, Nitiduloidea *stat. nov.* and Cucujoidea *sensu nov.* to provide a phylogenetically sound, more balanced and practical classification of this diverse group that reflects its evolutionary history.

Our results support the downgrading of the carrion beetles from a family to a subfamily of Staphylinidae *sensu nov.*, as Silphinae *stat. nov.*, and reconsideration of other recent phylogenetic studies supports the restoration of Colonidae *stat. nov.* as a separate family, not subfamily of Leiodidae *sensu nov.* Moreover, click beetles (Elateridae), minute marsh-loving beetles (Limnichidae), earth-boring dung beetles (Geotrupidae), scarabs (Scarabaeidae), bark-gnawing beetles (Trogossitidae), ant-like beetles (Anthicidae), ironclad beetles (Zopheridae) and false darkling beetles (Melandryidae) were not recovered as natural groups, in congruence with some previous analyses [66,97]. These latter issues remain to be formally treated and will require a more extensive taxon sampling within and outside these groups to help redefine their boundaries.

4.2. Carboniferous origin of Coleoptera

Despite a history of problematic purportedly coleopteran fossils from the Carboniferous [85,88], the earliest unequivocal stem-group beetles appear in the fossil record in the early Permian [5], providing few clues into the initial history of the order. Molecular clock studies have broadly converged on two principal models of beetle origins: the explosive model, suggesting that total-group Coleoptera originated and diversified in the Permian [9,10], while the long-fuse model argues for a much earlier Carboniferous origin [35], implying a long cryptic evolutionary history of the group undocumented in

the fossil record. Our molecular clock studies lend support to the latter model, recovering a fully Carboniferous origin of Coleoptera and suggesting a 55–134 Myr gap in the known fossil record between the origin of Coleoptera and the earliest fossil record of the order. The paucity of early beetle fossils may be because of the rarity of early beetles, their narrow ecological niche, lower fossilization potential, insufficient sampling of fossiliferous formations of this age, as well as secular biases in the rock record. The former two appear especially likely, since stem-beetles were rare in the Permian and coleopterans only came to dominate fossil insect assemblages in the Mesozoic [98]. Moreover, stem-beetles were apparently not considerably more morphologically diverse than modern beetles [99,100]. The early Carboniferous is part of the ‘Hexapod gap’, a stratigraphic interval known for its lack of insect fossils [101], which may further contribute to the lack a pre-Permian fossil record of beetles.

Adaptative radiations of successful clades in the fossil record are often associated with new morphological innovations that enable the colonization of new niches [102]. The heavily sclerotized bodies of beetles with forewings modified into hardened protective elytra are often cited to explain the diversification of beetles [8,9,14]. However, the long-fuse model, with a long cryptic history of Carboniferous–Permian beetles that apparently were neither abundant [98] nor morphologically disparate [100], argues for a more complex scenario of beetle diversification.

4.3. Early diversification of beetles

The recovery of Adephaga as the earliest diverging clade of Coleoptera, and the aquatic families Gyrinidae and Haliplidae as the earliest diverging families within Adephaga, implies that the ancestral coleopteran may have been aquatic. This seems reasonable based on the fossil record because the Permian stem-coleopteran families †Tshekardocoleidae and †Phoroschizidae may have been fully or partly aquatic [103] even though the life history of †Alphacoleoptera Engel, Cai and Tihelka *subord. nov.* (refer to electronic supplementary material) remains mysterious [104]. Different phylogenetic reconstructions among the four suborders and the internal relationships of Polyphaga may refute the hypothesis for an aquatic ancestor [16]. Consistent with Zhang *et al.* [10] and McKenna *et al.* [23], Scirtiformia are resolved as the basal-most polyphagans and are a group with mainly aquatic and semi-aquatic larvae [105], though some forms are fully terrestrial [106]. Their placement supports the reconstruction of an aquatic ancestor for Archostemata + Myxophaga and the Polyphaga. An understanding of the phylogenetic relationships within scirtiforms [107] is critical for testing the aquatic-ancestor hypothesis.

Under the aquatic-ancestor hypothesis, beetles subsequently invaded terrestrial ecosystems independently four times, once each in the ancestor of Geadephaga, Archostemata, some Myxophaga and Polyphaga, although many beetles have subsequently returned to fresh water again. The radiation of basal Coleoptera was rapid and occurred over a period of 17–78 Ma; the split between Archostemata and Myxophaga was estimated as Permian (269–246 Ma), while Polyphaga diverged at the Carboniferous–Permian boundary (314–236 Ma). The basal diversification of crown Coleoptera and their invasion of land occurred in the Permian, a time of drastic environmental change that saw the replacement of Carboniferous hygrophytic and permanently wetted terrestrial ecosystems inhabited by (semi)aquatic alphacoleopterans with seasonally dry ecosystems [108]. Palaeozoic plant families were replaced by more modern Mesozoic groups and ecological communities became more complex, with a higher number of trophic levels [108,109]. It is therefore possible that the Permian ecosystem change played a pivotal role in shaping the early diversification of beetles [5,103]. Early diverging beetle lineages survived the End-Permian mass extinction event to diversify in the Mesozoic, most beetle superfamilies having diverged by the Jurassic.

4.4. Cretaceous co-diversification with angiosperms

Angiosperms replaced the previously dominant gymnosperms during the Cretaceous, in a period known as the Cretaceous Terrestrial Revolution (KTR) [110,111]. Co-diversification with flowering plants has been proposed as a mechanism explaining the species richness of herbivorous clades such as the weevils [9,15] and beetles have been regarded as the earliest pollinators of angiosperms [15,112,113]. Our molecular clock analyses suggest that major beetle clades were present before the KTR. This is corroborated by the beetle fossil record [12]; elateroids, staphylinoids and weevils in particular have a diverse fossil record since the Jurassic [8]. Nonetheless, some scarabaeoid and cucujiform clades underwent diversification during the Late Jurassic to Early Cretaceous, partly overlapping with the diversification of major angiosperms clades in the Early to mid-Cretaceous [114,115].

Besides directly affecting herbivorous lineages, the diversification of the angiosperms in the Cretaceous precipitated a diversification of vertebrate herbivores and predators [11]. Our molecular clock estimates corroborate the controversial idea, famously portrayed in numerous palaeontological reconstructions, that coprophagous beetles, namely geotrupids (dung beetles) and scarabaeoids (scarabs), may have been associated with Cretaceous herbivorous dinosaurs [23,116,117]. Our analyses also corroborate a Cretaceous origin of the bioluminescent lampyroid clade [118], temporally overlapping with the diversification of visually hunting predators such as anurans and stem-group birds during the KTR [119]. At the same time, some Mesozoic beetle families have their last appearance in the fossil record during the KTR, highlighting complex dynamics of transitioning from a gymnosperm- to angiosperm-dominated world [120].

Overall, our results provide support for a more nuanced view [15] of the KTR as an event that did not increase the superfamilial diversity of beetles, since most major beetle clades had already diverged by this time. Instead, the diversification of angiosperms was followed by clade-specific radiations in some beetle groups, such as scarabs [112] or weevils [13], in response to newly formed niches.

4.5. Cretaceous–Palaeogene mass extinction

The impacts of the Cretaceous–Palaeogene (K–Pg) mass extinction on beetles remain controversial, as herbivorous insects would be expected to have experienced elevated extinction levels given their close association with their host plants [121]. Our results suggest no diversification of beetles, at the level of families, in the aftermath of the K–Pg crisis, corroborating previous palaeontological macroevolutionary studies suggesting that the mass extinction was hardly devastating for beetles [12,98,122]. It is, however, possible that the K–Pg extinction may have had different impacts on lower taxonomic ranks [121] that have to be assessed by future studies focusing on specific herbivorous clades.

5. Summary

Our new beetle phylogeny corroborates many relationships inferred by phylomitogenomic analyses using models accounting for compositional and rate heterogeneity [21], but the resolution is significantly improved by a careful selection of single-copy NPC genes analysed with methods accounting for compositional and rate heterogeneity. We recovered with credibility the phylogenetic positions of the enigmatic Rhinorhipidae and recently recognized Coccinelloidea, as well as the paraphyly of Cucujoidea *sensu* Robertson *et al.* [78]. We also unravelled the isolated position of the peculiar Byrrhidae, consistent with the traditional classification of elateriform beetles [67,68,123]. Our molecular clock analyses suggest a Carboniferous origin of Coleoptera and a Palaeozoic origin of all four beetle suborders. A Carboniferous origin of Coleoptera implies a 55–134 Ma long ‘beetle gap’ in the fossil record. Early diverging beetle lineages survived the End-Permian mass extinction event to diversify in the Mesozoic, with major clades having originated by the Jurassic. Most major beetle clades were present by the Late Jurassic, although some groups diversified during the Cretaceous, in concert with the radiation of angiosperms.

We provide a revised treatment of the higher classification of Coleoptera that reflects the findings of phylogenomic studies conducted over the past decade. Scirtiformia and Scirtoidea *sensu nov.* are restricted to Decliniidae and Scirtidae, while Clambiformia Cai and Tihelka *ser. nov.* and its single constituent superfamily Clamboidea *sensu nov.* is considered to contain the extant families Clambidae, Derodontidae and Eucinetidae. The other members of the former Derodontoidea, Nosodendridae and Jacobsoniidae are placed into Nosodendriformia Cai and Tihelka *ser. nov.* and Staphylinoidea, respectively. To maintain the monophyly of the well-defined Elateriformia, we erect the new series Rhinorhipiformia Cai, Engel and Tihelka *ser. nov.* for the family Rhinorhipidae. Scarabaeoidea is formally incorporated into Staphyliniformia *sensu nov.* The former Cucujoidea is divided into three superfamilies: Erotyloidea *stat. nov.*, Nitiduloidea *stat. nov.* and Cucujoidea *sensu nov.* Silphinae *stat. nov.* are treated as a subfamily of Staphylinidae *sensu nov.*, and Colonidae *stat. nov.* is restored as an independent family and not a subfamily of Leiodidae. In addition, we recognize that the extinct suborder †Protocoleoptera (established for †Protocoleidae) comprises a group of polyneopterans allied to earwigs (Dermaptera) rather than beetles, and that the younger †Archecoleoptera were defined on the basis of a temporal fauna rather than any characters, tax, or phylogenetic details. Accordingly, the earliest fossil beetles are here included in the new extinct suborder †Alphacoleoptera *subord. nov.* (refer to electronic supplementary material).

Data accessibility. All analysed datasets and outputs are available from Mendeley Data (<http://dx.doi.org/10.17632/7v27xcyv99.2>). All sequences are deposited in GenBank under the accession numbers provided by Zhang *et al.* [10] and Kusy *et al.* [46].

The data are provided in the electronic supplementary material [124].

Authors' contributions. C.C.: conceptualization, data curation, formal analysis, funding acquisition, supervision, writing—original draft and writing—review and editing; E.T.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft and writing—review and editing; M.G.: formal analysis, methodology and writing—review and editing; J.F.L.: investigation, supervision and writing—review and editing; A.Š.: investigation and writing—review and editing; R.K.: investigation and writing—review and editing; S.Y.: investigation and writing—review and editing; M.K.T.: investigation and writing—review and editing; A.F.N.: investigation and writing—review and editing; R.A.B.L.: investigation and writing—review and editing; M.L.G.: investigation and writing—review and editing; L.L.: investigation and writing—review and editing; M.S.E.: investigation and writing—review and editing; P.B.: investigation and writing—review and editing; D.H.: funding acquisition, investigation and writing—review and editing; D.P.: conceptualization, investigation, project administration, supervision and writing—review and editing; P.C.J.D.: conceptualization, funding acquisition, methodology, project administration, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein. Competing interests. We declare we have no competing interests.

Funding. Support for the present study was provided by the Strategic Priority Research Program of the Chinese Academy of Sciences (grant nos. XDB26000000 and XDB18000000), the National Natural Science Foundation of China (grant nos. 41672011 and 41688103), the Second Tibetan Plateau Scientific Expedition and Research (grant no. 2019QZKK0706), the Biotechnology and Biological Sciences Research Council (BBSRC) (grant no. BB/T012773/1), and a Newton International Fellowship from the Royal Society awarded to C.C. and P.C.J.D. This study was partly supported by a Grant-in-Aid for JSPS Fellows (grant no. 20J00159) given to S.Y. from the Japan Society for the Promotion of Science (JSPS) and the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement (764840 to D.P. and M.L.G.). R.A.B.L. 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.

Acknowledgements. We are grateful to Ladislav Bocak (Palacký University, Czech Republic) and Jiří Háva (Forestry and Game Management Research Institute, Czech Republic) for comments on an earlier version of the manuscript.

Appendix A. Overview of the updated higher classification of Coleoptera

Order Coleoptera Linnaeus, 1758

†Suborder Alphacoleoptera Engel, Cai, and Tihelka, *nov.*

†Superfamily Coleopsoidea Kirejtshuk and Nel, 2016

†Superfamily Permocupedoidea Martynov, 1932

†Superfamily Permosynoidea Tillyard, 1924

Capaxorder Zacoletoptera Engel, Cai, and Tihelka, *nov.*

†Suborder Metaxycoleoptera Engel, Cai, and Tihelka, *nov.*

Hyporder Eucoleoptera Engel, Cai, and Tihelka, *nov.*

Suborder Adephaga Claireville, 1806

Suborder Archostemata Kolbe, 1908

Superfamily Cupedoidea Laporte, 1838

†Superfamily Asiocoleoidea Rohdendorf, 1961

†Superfamily Rhombocoleoidea Rohdendorf, 1961

†Superfamily Schizocoleoidea Rohdendorf, 1961

Suborder Myxophaga Crowson, 1955

Superfamily Lepiceroidea Hinton, 1936 (1882)

Superfamily Sphaeriusoidea Erichson, 1845

Suborder Polyphaga Emery, 1886

Series Scirtiformia Lawrence, Ślipiński, Seago, Thayer, Newton, and Marvaldi, 2011 *sensu nov.*

Superfamily Scirtoidea Fleming, 1821 *sensu nov.*

Series Clambiformia Cai and Tihelka *ser. nov.*

Superfamily Clamboidea Fischer, 1821 *sensu nov.*

Series Rhinorhipiformia Cai, Engel and Tihelka *ser. nov.*

Superfamily Rhinorhipoidea Lawrence, 1988

Series Elateriformia Crowson, 1960

Superfamily Dascilloidea Guérin-Méneville, 1843 (1834)

Superfamily Buprestoidea Crowson, 1955

- Superfamily Byrrhoidea Latreille, 1804 *sensu nov.*
 Superfamily Dryopoidea Billberg, 1820 (1817) *stat. res.*
 Superfamily Elateroidea Leach, 1815
 Series Nosodendriformia Cai and Tihelka *ser. nov.*
 Superfamily Nosodendroidea Erichson, 1846
 Series Staphyliniformia Lameere, 1900 *sensu nov.*
 Superfamily Histeroidea Gyllenhaal, 1808
 Superfamily Hydrophiloidea Latreille, 1802
 Superfamily Scarabaeoidea Latreille, 1802
 Superfamily Staphyloidea Latreille, 1802
 Series Bostrichiformia Forbes, 1926
 Superfamily Bostrichoidea Latreille, 1802
 Series Cucujiformia Lameere, 1938
 Superfamily Cleroidea Latreille, 1802
 Superfamily Lymexyloidea Fleming, 1821
 Superfamily Tenebrionoidea Latreille, 1802
 Superfamily Coccinelloidea Latreille, 1807
 Superfamily Erotyloidea Latreille, 1802 *stat. nov.*
 Superfamily Nitiduloidea Latreille, 1802 *stat. nov.*
 Superfamily Cucujoidea Latreille, 1802 *sensu nov.*
 Superfamily Curculionoidea Latreille, 1802
 Superfamily Chrysomeloidea Latreille, 1802

References

- Stork NE. 2018 How many species of insects and other terrestrial arthropods are there on Earth? *Annu. Rev. Entomol.* **63**, 31–45. (doi:10.1146/annurev-ento-020117-043348)
- Erwin TL. 1982 Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* **36**, 74–75.
- Ślipiński A, Leschen RAB, Lawrence JF. 2011 Order Coleoptera Linnaeus, 1758. in Zhang, Z. (ed.) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness.* *Zootaxa* **3148**, 203–208. (doi:10.11646/zootaxa.3148.1.39)
- Beutel RG, Yan EV, Kukalová-Peck J. 2019 Is †Skleroptera (†Stephanastus) an order in the stemgroup of Coleopterida (Insecta)? *Insect Syst. Evol.* **50**, 670–678. (doi:10.1163/1876312X-00002187)
- Kirejtshuk AG, Poschmann M, Prokop J, Garrouste R, Nel A. 2014 Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tshekardocoleidae). *J. Syst. Palaeontol.* **12**, 575–600. (doi:10.1080/14772019.2013.821530)
- Yan EV, Beutel RG, Lawrence JF. 2018 Whirling in the late Permian: ancestral Gyrinidae show early radiation of beetles before Permian-Triassic mass extinction. *BMC Evol. Biol.* **18**, 33. (doi:10.1186/s12862-018-1139-8)
- Beutel RG, Yan EV, Lawrence JF. 2019 Phylogenetic methods applied to extinct beetles — the case of †*Tunguskagyris* (Gyrinidae or †Triaplidae). *Palaeoentomology* **2**, 372–380. (doi:10.11646/palaeoentomology.2.4.11)
- Grimaldi D, Engel MS. 2005 *Evolution of the insects*, 1st edn. Cambridge, UK: Cambridge University Press.
- Hunt T *et al.* 2007 A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**, 1913–1916. (doi:10.1126/science.1146954)
- Zhang SQ, Che LH, Li Y, Liang D, Pang H, Ślipiński A, Zhang P. 2018 Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nat. Commun.* **9**, 205. (doi:10.1038/s41467-017-02644-4)
- Lloyd GT, Davis KE, Pisani D, Tarver JE, Ruta M, Sakamoto M, Hone DWE, Jennings R, Benton MJ. 2008 Dinosaurs and the Cretaceous Terrestrial Revolution. *Proc. R. Soc. B* **275**, 2483–2490. (doi:10.1098/rspb.2008.0715)
- Smith DM, Marcot JD. 2015 The fossil record and macroevolutionary history of the beetles. *Proc. R. Soc. B* **282**, 20150060. (doi:10.1098/rspb.2015.0060)
- McKenna DD, Sequeira AS, Marvaldi AE, Farrell BD. 2009 Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl Acad. Sci. USA* **106**, 7083–7088. (doi:10.1073/pnas.0810618106)
- Crowson RA. 1981 *The biology of the Coleoptera*. London, UK: Academic Press.
- Farrell BD. 1998 ‘Inordinate fondness’ explained: why are there so many beetles? *Science* **281**, 555–559. (doi:10.1126/science.281.5376.555)
- McKenna DD *et al.* 2015 The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Syst. Entomol.* **40**, 835–880. (doi:10.1111/syen.12132)
- Vogler AP. 2005 Molecular systematics of Coleoptera: what has been achieved so far? In *Handbook of zoology. Arthropoda: insecta. Coleoptera, beetles. Vol. 1: morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)* (eds RG Beutel, RAB Leschen), pp. 17–22. Berlin, Germany: Walter De Gruyter.
- Bocak L, Barton C, Crampton-Platt A, Chesters D, Ahrens D, Vogler AP. 2014 Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Syst. Entomol.* **39**, 97–110. (doi:10.1111/syen.12037)
- McKenna DD. 2016 Molecular systematics of Coleoptera. In *Handbook of zoology. Arthropoda: insecta. Coleoptera, beetles. Vol. 1: morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)* (eds RG Beutel, RAB Leschen), pp. 23–34. Berlin, Germany: Walter De Gruyter.
- Lawrence JF, Ślipiński A, Seago AE, Thayer MK, Newton AF, Marvaldi AE. 2011 Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Ann. Zool.* **61**, 1–217. (doi:10.3161/000345411X576725)
- Timmermans MJTN *et al.* 2016 Family-level sampling of mitochondrial genomes in Coleoptera: compositional heterogeneity and phylogenetics. *Genome. Biol. Evol.* **8**, 161–175. (doi:10.1093/gbe/evw241)
- Yuan ML, Zhang QL, Zhang L, Guo ZL, Liu YJ, Shen YY, Shao R. 2016 High-level phylogeny of the Coleoptera inferred with mitochondrial genome sequences. *Mol. Phylogenet. Evol.* **104**, 99–111. (doi:10.1016/j.ympev.2016.08.002)
- McKenna DD *et al.* 2019 The evolution and genomic basis of beetle diversity. *Proc. Natl Acad. Sci. USA* **116**, 24 729–24 737. (doi:10.1073/pnas.1909655116)

24. Philippe H, Brinkmann H, Lavrov DV, Littlewood DTJ, Manuel M, Wörheide G, Baurain D. 2011 Resolving difficult phylogenetic questions: why more sequences are not enough. *PLoS Biol.* **9**, e1000602. (doi:10.1371/journal.pbio.1000602)
25. Cai C, Tihelka E, Pisani D, Donoghue PCJ. 2020 Data curation and modeling of compositional heterogeneity in insect phylogenomics: a case study of the phylogeny of Dytiscoidea (Coleoptera: Adephaga). *Mol. Phylogenet. Evol.* **147**, 106782. (doi:10.1016/j.ympev.2020.106782)
26. Kapli P, Flouri T, Telford MJ. 2021 Systematic errors in phylogenetic trees. *Curr. Biol.* **31**, R59–R64. (doi:10.1016/j.cub.2020.11.043)
27. Lartillot N, Philippe H. 2004 A Bayesian mixture model for across-site heterogeneities in the amino-acid replacement process. *Mol. Biol. Evol.* **21**, 1095–1109. (doi:10.1093/molbev/msh112)
28. Lartillot N, Brinkmann H, Philippe H. 2007 Suppression of long-branch attraction artefacts in the animal phylogeny using a site-heterogeneous model. *BMC Evol. Biol.* **7**, S4. (doi:10.1186/1471-2148-7-S1-S4)
29. Pisani D, Pett W, Dohmann M, Feuda R, Rota-Stabelli O, Philippe H, Lartillot N, Wörheide G. 2015 Genomic data do not support comb jellies as the sister group to all other animals. *Proc. Natl Acad. Sci. USA* **112**, 15 402–15 407. (doi:10.1073/pnas.1518127112)
30. Feuda R, Dohmann M, Pett W, Philippe H, Rota-Stabelli O, Lartillot N, Wörheide G, Pisani D. 2017 Improved modeling of compositional heterogeneity supports sponges as sister to all other animals. *Curr. Biol.* **27**, 3864–3870.e4. (doi:10.1016/j.cub.2017.11.008)
31. Puttick MN *et al.* 2018 The interrelationships of land plants and the nature of the ancestral embryophyte. *Curr. Biol.* **28**, 733–745.e2. (doi:10.1016/j.cub.2018.01.063)
32. Williams TA, Cox CJ, Foster PG, Szöllösi GJ, Embley TM. 2020 Phylogenomics provides robust support for a two-domains tree of life. *Nat. Ecol. Evol.* **4**, 138–147. (doi:10.1038/s41559-019-1040-x)
33. Song H, Sheffield NC, Cameron SL, Miller KB, Whiting MF. 2010 When phylogenetic assumptions are violated: base compositional heterogeneity and among-site rate variation in beetle mitochondrial phylogenomics. *Syst. Entomol.* **35**, 429–448. (doi:10.1111/j.1365-3113.2009.00517.x)
34. Cai CY, Wang YL, Liang L, Yin ZW, Thayer MK, Newton AF, Zhou YL. 2019 Congruence of morphological and molecular phylogenies of the rove beetle subfamily Staphylininae (Coleoptera: Staphylinidae). *Sci. Rep.* **9**, 1–11. (doi:10.1038/s41598-019-51408-1)
35. Toussaint EFA, Seidel M, Arriaga-Varela E, Hájek J, Král D, Sckerka L, Short AEZ, Fikáček M. 2017 The peril of dating beetles. *Syst. Entomol.* **42**, 1–10. (doi:10.1111/syen.12198)
36. Linder HP, Hardy CR, Rutschmann F. 2005 Taxon sampling effects in molecular clock dating: an example from the African Restionaceae. *Mol. Phylogenet. Evol.* **35**, 569–582. (doi:10.1016/j.ympev.2004.12.006)
37. Duchêne S, Lanfear R, Ho SYW. 2014 The impact of calibration and clock-model choice on molecular estimates of divergence times. *Mol. Phylogenet. Evol.* **78**, 277–289. (doi:10.1016/j.ympev.2014.05.032)
38. Clarke JT, Warnock RCM, Donoghue PCJ. 2011 Establishing a time-scale for plant evolution. *New Phytol.* **192**, 266–301. (doi:10.1111/j.1469-8137.2011.03794.x)
39. Inoue J, Donoghue PCJ, Yang Z. 2010 The impact of the representation of fossil calibrations on Bayesian estimation of species divergence times. *Syst. Biol.* **59**, 74–89. (doi:10.1093/sysbio/syp078)
40. Sauquet H *et al.* 2012 Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Syst. Biol.* **61**, 289–313. (doi:10.1093/sysbio/syr116)
41. Parham JF *et al.* 2011 Best practices for justifying fossil calibrations. *Syst. Biol.* **61**, 346–359. (doi:10.1093/sysbio/syr107)
42. Hipsley CA, Müller J. 2014 Beyond fossil calibrations: realities of molecular clock practices in evolutionary biology. *Front. Genet.* **5**, 138. (doi:10.3389/fgene.2014.00138)
43. Donoghue PCJ, Yang Z. 2016 The evolution of methods for establishing evolutionary timescales. *Phil. Trans. R. Soc. B* **371**, 20160020. (doi:10.1098/rstb.2016.0020)
44. Schacht SR, Labandeira CC. 2020 Are insects heading toward their first mass extinction? Distinguishing turnover from crises in their fossil record. *Ann. Entomol. Soc. Am.* **114**, 99–118. (doi:10.1093/aesa/saaa042)
45. Che LH, Zhang SQ, Li Y, Liang D, Pang H, Šlipiříski A, Zhang P. 2017 Genome-wide survey of nuclear protein-coding markers for beetle phylogenetics and their application in resolving both deep and shallow-level divergences. *Mol. Ecol. Res.* **17**, 1342–1358. (doi:10.1111/1755-0998.12664)
46. Kusy D *et al.* 2018 Genome sequencing of *Rhinorhipis* Lawrence exposes an early branch of the Coleoptera. *Front. Zool.* **15**, 21. (doi:10.1186/s12983-018-0262-0)
47. Katoh K, Standley DM. 2013 MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780. (doi:10.1093/molbev/mst010)
48. Criscuolo A, Gribaldo S. 2010 BMGE (block mapping and gathering with entropy): a new software for selection of phylogenetic informative regions from multiple sequence alignments. *BMC Evol. Biol.* **10**, 210. (doi:10.1186/1471-2148-10-210)
49. Kück P, Meusemann K. 2010 FASconCAT: convenient handling of data matrices. *Mol. Phylogenet. Evol.* **56**, 1115–1118. (doi:10.1016/j.ympev.2010.04.024)
50. Kück P, Struck TH. 2014 BaCoCa – a heuristic software tool for the parallel assessment of sequence biases in hundreds of gene and taxon partitions. *Mol. Phylogenet. Evol.* **70**, 94–98. (doi:10.1016/j.ympev.2013.09.011)
51. Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2015 IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **32**, 268–274. (doi:10.1093/molbev/msu300)
52. Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermini LS. 2017 ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods* **14**, 587–589. (doi:10.1038/nmeth.4285)
53. Lartillot N, Lepage T, Blanquart S. 2009 PhyloBayes 3: a Bayesian software package for phylogenetic reconstruction and molecular dating. *Bioinformatics* **25**, 2286–2288. (doi:10.1093/bioinformatics/btp368)
54. Yang Z. 2007 PAML 4: phylogenetic analysis by maximum likelihood. *Mol. Biol. Evol.* **24**, 1586–1591. (doi:10.1093/molbev/msm088)
55. Yang Z, Rannala B. 2006 Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Mol. Biol. Evol.* **23**, 212–226. (doi:10.1093/molbev/msj024)
56. Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018 Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**, 901–904. (doi:10.1093/sysbio/syy032)
57. Fernández R, Edgecombe GD, Giribet G. 2016 Exploring phylogenetic relationships within Myriapoda and the effects of matrix composition and occupancy on phylogenomic reconstruction. *Syst. Biol.* **65**, 871–889. (doi:10.1093/sysbio/syw041)
58. Kocot KM *et al.* 2017 Phylogenomics of Lophotrochozoa with consideration of systematic error. *Syst. Biol.* **66**, 256–282. (doi:10.1093/sysbio/syw079)
59. Sheffield NC, Song H, Cameron SL, Whiting MF. 2009 Nonstationary evolution and compositional heterogeneity in beetle mitochondrial phylogenomics. *Syst. Biol.* **58**, 381–394. (doi:10.1093/sysbio/syp037)
60. Tihelka E, Cai C, Giacomelli M, Lozano-Fernandez J, Rota-Stabelli O, Huang D, Engel MS, Donoghue PCJ, Pisani D. 2021 The evolution of insect biodiversity. *Curr. Biol.* **31**, R1299–R1311. (doi:10.1016/j.cub.2021.08.057)
61. Beutel RG, Haas F. 2000 Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* **16**, 103–141. (doi:10.1006/clad.1999.0124)
62. Kukulová-Peck J, Lawrence JF. 2004 Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *Eur. J. Entomol.* **101**, 95–144. (doi:10.14411/eje.2004.018)
63. Beutel RG, Pohl H, Yan EV, Anton E, Liu SP, Šlipiříski A, McKenna D, Friedrich F. 2019 The phylogeny of Coleoptera (Hexapoda) – morphological characters and molecular phylogenies. *Syst. Entomol.* **44**, 75–102. (doi:10.1111/syen.12316)
64. Baca SM, Alexander A, Gustafson GT, Short AEZ. 2017 Ultraconserved elements show utility in phylogenetic inference of Adephaga (Coleoptera) and suggest paraphyly of ‘Hydradephaga’. *Syst. Entomol.* **42**, 786–795. (doi:10.1111/syen.12244)
65. Beutel RG, Ribera I, Fikáček M, Vasilikopoulos A, Misof B, Balke M. 2020 The morphological evolution of the Adephaga (Coleoptera). *Syst. Entomol.* **45**, 378–395. (doi:10.1111/syen.12403)

66. Kusy D, Motyka M, Bocek M, Vogler AP, Bocak L. 2018 Genome sequences identify three families of Coleoptera as morphologically derived click beetles (Elateridae). *Sci. Rep.* **8**, 17084. (doi:10.1038/s41598-018-35328-0)
67. Crowson RA. 1955 *The natural classification of the families of Coleoptera*, 1st edn. London, UK: Nathaniel Lloyd & Co., Ltd.
68. Lawrence JF, Newton AF. 1982 Evolution and classification of beetles. *Annu. Rev. Ecol. Syst.* **13**, 261–290. (doi:10.1146/annurev.es.13.110182.001401)
69. Lawrence JF. 1991 Byrrhidae (Byrrhoidea). In *Immature insects*, vol. 2 (ed. FW Stehr), pp. 384–386. Dubuque, IA: Kendall/Hunt Publishing.
70. Timmermans MJTN, Vogler AP. 2012 Phylogenetically informative rearrangements in mitochondrial genomes of Coleoptera, and monophyly of aquatic elateriform beetles (Dryopoidea). *Mol. Phylogenet. Evol.* **63**, 299–304. (doi:10.1016/j.ympev.2011.12.021)
71. Kundrata R, Jäch MA, Bocak L. 2017 Molecular phylogeny of the Byrrhoidea–Buprestoidea complex (Coleoptera, Elateriformia). *Zool. Scr.* **46**, 150–164. (doi:10.1111/zsc.12196)
72. Kundrata R, Bocakova M, Bocak L. 2014 The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Mol. Phylogenet. Evol.* **76**, 162–171. (doi:10.1016/j.ympev.2014.03.012)
73. Douglas HB *et al.* 2021 Anchored phylogenomics, evolution and systematics of Elateridae: are all bioluminescent Elateroidea derived click beetles? *Biology* **10**, 451. (doi:10.3390/biology10060451)
74. Hansen M. 1997 Phylogeny and classification of the staphyliniform beetle families (Coleoptera). *Biol. Skr.* **48**, 1–339.
75. Caterino MS, Hunt T, Vogler AP. 2005 On the constitution and phylogeny of Staphyliniformia (Insecta: Coleoptera). *Mol. Phylogenet. Evol.* **34**, 655–672. (doi:10.1016/j.ympev.2004.11.012)
76. Lü L, Cai CY, Zhang X, Newton AF, Thayer MK, Zhou HZ. 2020 Linking evolutionary mode to palaeoclimate change reveals rapid radiations of staphylinoid beetles in low-energy conditions. *Curr. Zool.* **66**, 435–444. (doi:10.1093/cz/zoz053)
77. McKenna DD *et al.* 2015 Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. *Syst. Entomol.* **40**, 35–60. (doi:10.1111/syen.12093)
78. Robertson JA *et al.* 2015 Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Syst. Entomol.* **40**, 745–778. (doi:10.1111/syen.12138)
79. Kirejtshuk AG, Mantic M. 2015 On systematics of the subfamily Cybocephalinae (Coleoptera: Nitidulidae) with description of new species and generic taxa. *Proc. Zool. Inst. Rus. Acad. Sci.* **319**, 196–214.
80. Cline AR, Smith TR, Miller K, Moulton M, Whiting M, Audisio P. 2014 Molecular phylogeny of Nitidulidae: assessment of subfamilial and tribal classification and formalization of the family Cybocephalidae (Coleoptera: Cucujoidea). *Syst. Entomol.* **39**, 758–772. (doi:10.1111/syen.12084)
81. Shin S *et al.* 2018 Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. *Mol. Biol. Evol.* **35**, 823–836. (doi:10.1093/molbev/msx324)
82. Yan EV, Lawrence JF, Beattie R, Beutel RG. 2018 At the dawn of the great rise: †*Ponomarenkia belmonthensis* (Insecta: Coleoptera), a remarkable new Late Permian beetle from the Southern Hemisphere. *J. Syst. Palaeontol.* **16**, 611–619. (doi:10.1080/14772019.2017.1343259)
83. Metcalfe I, Crowley JL, Nicoll RS, Schmitz M. 2015 High-precision U-Pb CA-TIMS calibration of Middle Permian to Lower Triassic sequences, mass extinction and extreme climate-change in eastern Australian Gondwana. *Gondwana Res.* **28**, 61–81. (doi:10.1016/j.gr.2014.09.002)
84. Clements T, Purnell M, Gabbott S, Purnell M, Gabbott S. 2019 The Mazon Creek Lagerstätte: a diverse late Paleozoic ecosystem entombed within siderite concretions. *J. Geol. Soc.* **176**, 1–11. (doi:10.1144/jgs2018-088)
85. Béthoux O. 2009 The earliest beetle identified. *J. Paleontol.* **83**, 931–937. (doi:10.1666/08-158.1)
86. Kukulova-Peck J, Beutel RG. 2012 Is the Carboniferous *Adiphebia lacoana* really the “oldest beetle”? Critical reassessment and description of a new Permian beetle family. *Eur. J. Entomol.* **109**, 633–645. (doi:10.14411/eje.2013.027)
87. Warnock RCM, Parham JF, Joyce WG, Lyson TR, Donoghue PCJ. 2015 Calibration uncertainty in molecular dating analyses: there is no substitute for the prior evaluation of time priors. *Proc. R. Soc. B* **282**, 20141013. (doi:10.1098/rspb.2014.1013)
88. Nel A *et al.* 2013 The earliest known holometabolous insects. *Nature* **503**, 257–261. (doi:10.1038/nature12629)
89. Wolfe JM, Daley AC, Legg DA, Edgecombe GD. 2016 Fossil calibrations for the arthropod Tree of Life. *Earth Sci. Rev.* **160**, 43–110. (doi:10.1016/j.earscirev.2016.06.008)
90. Cai C, Lawrence JF, Yamamoto S, Leschen RAB, Newton AF, Ślipiński A, Yin Z, Huang D, Engel MS. 2019 Basal polyphagan beetles in mid-Cretaceous amber from Myanmar: biogeographic implications and long-term morphological stasis. *Proc. R. Soc. B* **286**, 20182175. (doi:10.1098/rspb.2018.2175)
91. Parker J. 2017 Staphylinids. *Curr. Biol.* **27**, R49–R51. (doi:10.1016/j.cub.2016.07.050)
92. Lawrence JF, Ślipiński A. 2013 *Australian beetles, volume 1: morphology, classification and keys*. Clayton, Australia: CSIRO.
93. Lawrence JF, Newton AF. 1995 Families and subfamilies of Coleoptera. In *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson* (eds J Pakaluk, AS Ślipiński), pp. 779–1006. Warsaw, Poland: Muzeum i Instytut Zoologii PAN.
94. Kolbe H. 1908 Mein system der coleopteren. *Zeitschr. wiss. Insectbil.* **4**, 116–123, 153–162, 219–226, 246–251, 286–294, 389–400.
95. Leschen RAB, Lawrence JF, Ślipiński SA. 2005 Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. *Invert. Syst.* **19**, 17–73. (doi:10.1071/IS04007)
96. Liu J, Wang Y, Zhang R, Shi C, Lu W, Li J, Bai M. 2021 Three complete mitochondrial genomes of Erotylidae (Coleoptera: Cucujoidea) with higher phylogenetic analysis. *Insects* **12**, 524. (doi:10.3390/insects12060524)
97. Gunter NL, Levkaničová Z, Weir TH, Ślipiński A, Cameron SL, Bocak L. 2014 Towards a phylogeny of the Tenebrionoidea (Coleoptera). *Mol. Phylogenet. Evol.* **79**, 305–312. (doi:10.1016/j.ympev.2014.05.028)
98. Labandeira CC, Sepkoski JJ. 1993 Insect diversity in the fossil record. *Science* **261**, 310–315. (doi:10.1126/science.11536548)
99. Kukulová J. 1969 On the systematic position of the supposed Permian beetles, Tšhecardocoleidae, with a description of a new collection from Moravia. *Sb. geol. věd řada P. Paleontol.* **11**, 139–161.
100. Ponomarenko AG. 1969 Historical development of the Coleoptera-Archostemata. *Trud. Paleontol. Inst. Akad. Nauk SSSR* **125**, 1–240.
101. Schachat SR, Labandeira CC, Saltzman MR, Cramer BD, Payne JL, Boyce CK. 2018 Phanerozoic pO₂ and the early evolution of terrestrial animals. *Proc. R. Soc. B* **285**, 20172631. (doi:10.1098/rspb.2017.2631)
102. Gavriltes S, Losos JB. 2009 Adaptive radiation: contrasting theory with data. *Science* **323**, 732–737. (doi:10.1126/science.1157966)
103. Ponomarenko AG, Prokin AA. 2015 Review of paleontological data on the evolution of aquatic beetles (Coleoptera). *Paleontol. J.* **49**, 1383–1412. (doi:10.1134/s0031030115130080)
104. Ponomarenko AG. 1995 The geological history of beetles. In *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson*, pp. 155–172. Warsaw, Poland: Muzeum i Instytut Zoologii PAN.
105. Bocak L. 2016 Scirtiformia Fleming, 1821. In *Handbook of zoology; Arthropoda: insecta, Coleoptera, beetles. Vol. 1: morphology and systematics (Polyphaga partim)* (eds RG Beutel, RAB Leschen), pp. 201–202. Berlin, Germany: Walter de Gruyter.
106. Ruta R, Klausnitzer B, Prokin A. 2018 South American terrestrial larva of Scirtidae (Coleoptera: Scirtoidea): the adaptation of Scirtidae larvae to saproxylic habitat is more common than expected. *Austral. Entomol.* **57**, 50–61. (doi:10.1111/aen.12270)
107. Lawrence JF, Yoshitomi H. 2007 *Nipponocyphon*, a new genus of Japanese Scirtidae (Coleoptera) and its phylogenetic significance. *Elytra* **35**, 507–527.
108. Looy C, Kerp H, Duijnsteer I, DiMichele B. 2014 The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. *Sedimentary Rec.* **12**, 4–18. (doi:10.2110/sedred.2014.4.4)
109. Benton MJ. 2013 No gap in the Middle Permian record of terrestrial vertebrates: REPLY. *Geology* **41**, e294. (doi:10.1130/G34595Y.1)
110. Barba-Montoya J, Reis MD, Schneider H, Donoghue PCJ, Yang Z. 2018 Constraining uncertainty in the timescale of angiosperm

- evolution and the veracity of a Cretaceous Terrestrial Revolution. *New Phytol.* **218**, 819–834. (doi:10.1111/nph.15011)
111. Condamine FL, Silvestro D, Koppelhus EB, Antonelli A. 2020 The rise of angiosperms pushed conifers to decline during global cooling. *Proc. Natl Acad. Sci. USA* **117**, 28 867–28 875. (doi:10.1073/pnas.2005571117)
112. Ahrens D, Schwarzer J, Vogler AP. 2014 The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. *Proc. R. Soc. B* **281**, 20141470. (doi:10.1098/rspb.2014.1470)
113. Faegri K, van der Pijl L. 1979 *The principles of pollination ecology*, 3rd edn. Oxford, UK: Pergamon Press.
114. Li HT *et al.* 2019 Origin of angiosperms and the puzzle of the Jurassic gap. *Nat. Plants* **5**, 461–470. (doi:10.1038/s41477-019-0421-0)
115. Silvestro D *et al.* 2021 Fossil data support a pre-Cretaceous origin of flowering plants. *Nat. Ecol. Evol.* **5**, 449–457. (doi:10.1038/s41559-020-01387-8)
116. Arillo A, Ortuño VM. 2008 Did dinosaurs have any relation with dung-beetles? (The origin of coprophagy). *J. Nat. Hist.* **42**, 1405–1408. (doi:10.1080/00222930802105130)
117. Chin K, Gill BD. 1996 Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *Palaeos* **11**, 280–285. (doi:10.2307/3515235)
118. Kusý D, He JW, Bybee SM, Motyka M, Bi WX, Podsiadlowski L, Li XY, Bocak L. 2020 Phylogenomic relationships of bioluminescent elateroids define the ‘lampyroid’ clade with clicking Sinopyrophoridae as its earliest member. *Syst. Entomol.* **46**, 111–123. (doi:10.1111/syen.12451)
119. Li YD, Kundrata R, Tihelka E, Liu Z, Huang D, Cai C. 2021 Cretophengodidae, a new Cretaceous beetle family, sheds light on the evolution of bioluminescence. *Proc. R. Soc. B* **288**, 20202730. (doi:10.1098/rspb.2020.2730)
120. Peris D *et al.* 2020 Unlocking the mystery of the mid-Cretaceous Mysteriomorphidae (Coleoptera: Elateroidea) and modalities in transitioning from gymnosperms to angiosperms. *Sci. Rep.* **10**, 16854. (doi:10.1038/s41598-020-73724-7)
121. Labandeira CC, Johnson KR, Wilf P. 2002 Impact of the terminal Cretaceous event on plant–insect associations. *Proc. Natl Acad. Sci. USA* **99**, 2061–2066. (doi:10.1073/pnas.042492999)
122. Whalley P. 1987 Insects and Cretaceous mass extinction. *Nature* **327**, 562. (doi:10.1038/327562b0)
123. Crowson RA. 1960 The phylogeny of Coleoptera. *Annu. Rev. Entomol.* **5**, 111–134. (doi:10.1146/annurev.en.05.010160.000551)
124. Cai C *et al.* 2022 Integrated phylogenomics and fossil data illuminate the evolution of beetles. Figshare. (doi:10.6084/m9.figshare.c.5894006)